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# Early-diverging bumblebees from across the roof of the world: the high-mountain subgenus *Mendacibombus* revised from species' gene coalescents and morphology (Hymenoptera, Apidae)

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## Abstract

The bumblebees of the subgenus *Mendacibombus* of the genus *Bombus* are the sister group to all other extant bumblebees and are unusual among bees for specialising in some of the highest elevation habitats with entomophilous plants on Earth. Most named taxa in this group (24 available names, from a total of 49 published names) were described originally from small differences in the colour pattern of the hair, many as parts (e.g. subspecies) of just one species. Subsequent taxonomic treatments recognised multiple species, but have described very few morphological characters, most of which are in the male genitalia. We examined 4413 specimens representing all of the named taxa from throughout the group's global range to describe variation in DNA, in skeletal morphology, and in the colour patterns of the hair. Using Bayesian inference of the phylogeny from an evolutionary model for the fast-evolving COI gene, and fitting either general mixed Yule/coalescent models or Poisson tree process models, we identify COI gene coalescents, which are expected to characterise species as evolutionarily independent lineages. None of the conditions most likely to compromise this interpretation (biased sampling, paralogy, introgression, heteroplasmy, incomplete lineage sorting) appears to be a substantial problem in this case. In an integrative analysis, we show that colour patterns are often variable within these groups and do not diagnose the same groups as we recognise from genes; in contrast, the groups recognised from gene coalescents can also be diagnosed from differences we identify in morphology. We infer that the 12 groups with coalescents in the COI gene that are corroborated by morphology constitute species, whereas many of these species are polymorphic in colour pattern. Lectotypes are designated for 15 taxa in order to reduce uncertainty in the identity and application of the names. We provide new morphological keys and distribution maps for the species. Then we use four genes (fast-evolving mitochondrial COI and 16S; and slower nuclear PEPCK and opsin) to obtain an absolute chronogram of phylogenetic relationships among the species. From published estimates that the most recent common ancestor of the subgenus *Mendacibombus* diverged from the other bumblebees at the beginning of the Oligocene, our results support the crown group of *Mendacibombus* as having diversified in the late Miocene, events that both appear to have been associated with periods of climate cooling. Relative conservatism in the alpine/subalpine climate niche of *Mendacibombus,* as compared with the much more diversified climate niches in the sister group of all other bumblebees, may have contributed to constraining the number of *Mendacibombus* species to just one twentieth of the total number of extant bumblebee species.

**Key words**: alpine, biogeography, COI, distribution, elevation, phylogeny, taxonomy

**Introduction**

The subgenus *Mendacibombus* is unique as a group of particularly ancient divergence among bumblebees and the sister group to all of the other extant bumblebees (P.H. Williams 1985; Kawakita *et al.* 2004; Cameron *et al.* 2007). *Mendacibombus* species are found at high elevations in the mountains of the Old World (Skorikov 1923, 1931; Pittioni 1937a), often occurring as high on mountains as there are flowers, typically in flower-rich subalpine and alpine grassland and on glacial moraines (P.H. Williams 1991; Rasmont & Flagothier 1996; P.H. Williams *et al.* 2009; Rasmont *et al.* 2015). There are other alpine bumblebees in other subgenera, and although some of them also occur above 5000 m elevation (Richards 1930; P.H. Williams *et al.* 2010), few of these other groups as a whole specialise in the alpine zone or have species that reach into the central Tibetan plateau to the same extent (P.H. Williams, Bystriakova, *et al.* 2015). We present evidence that while *Mendacibombus* species may be high elevation specialists, they are still relatively uncommon even among high mountain bumblebees. *Mendacibombus* species' geographical distributions are relatively narrow compared to other bumblebee species and they appear to show strong patterns arising from their history that are likely to be of broader interest for biogeography. Understanding *Mendacibombus* species will help in understanding Old World high alpine ecosystems, although people at high elevations may be less dependent on bumblebee-pollinated crop plants than they are in the lowlands. There are growing concerns about recent pronounced climate warming of the alpine zone (Qiu 2008; Xu *et al.* 2009; Kääb *et al.* 2012; Gardner *et al.* 2013), warming that is likely to affect the distributions of bumblebees (P.H. Williams *et al.* 2007; Pyke *et al.* 2012; Ploquin *et al.* 2013; Rasmont *et al.* 2015; P.H. Williams, Bystriakova, *et al.* 2015).

**Behaviour and ecology.** Species of the subgenus *Mendacibombus* have distinctive ecology and behaviour. Compared with other bumblebees, these species tend to have small body sizes (body lengths 9–19 mm). Despite their small size, they are among the longer-tongued bumblebees and visit a range of correspondingly deep (long corolla) flowers for both nectar and pollen (Pittioni 1937a; Aichhorn 1976; Haas 1976; Rasmont 1988; P.H. Williams 1991; Özbek 1997; Hagen & Aichhorn 2003; P.H. Williams *et al.* 2009; An *et al.* 2010; P.H. Williams 2011). Bumblebees in general are unusual among pollinating insects in being (facultatively) especially effective thermoregulators (Heinrich 1979). This gives *Mendacibombus* an advantage over many insects in the cool habitats of the alpine zone, because these bumblebees can be active for foraging at a broad range of temperatures.

Nests of species of the subgenus *Mendacibombus* have been described in detail only for *Bombus mendax* and *B. handlirschianus* (Aichhorn 1976; Haas 1976; De Meulemeester *et al.* 2010), but these nests show an architecture unique to this subgenus (reviewed in P.H. Williams *et al.* 2008: their table III). Unusually for bumblebees, larvae are reared separately, one in each wax cell. In contrast to all other bumblebees, cocoons are almost completely torn down soon after the emergence of the adults, which may be an adaptation to nesting in small hard-walled cavities in rock scree. Consequently, pollen and honey must be stored elsewhere. Food reserves are held in wax cells peripherally, outside the wax envelope of the brood nest for *B. mendax* (no envelope was found for *B. handlirschianus*), and the honey cells may sometimes be arranged hexagonally. Cocoon destruction and this manner of food storage show similarities to the nest architecture of some stingless bees (P.H. Williams 1991), a group that genetic evidence supports as likely to be the closest relatives of *Mendacibombus* outside of the bumblebees (Cameron & Mardulyn 2001; Woodard *et al.* 2011; Romiguier *et al.* 2015).

All species of the subgenus *Mendacibombus* belong to a minority of bumblebee species in which the males have the eyes much enlarged (Streinzer & Spaethe 2014; species placed in the 'section' *Boopobombus* by Frison 1927). This assemblage of species is polyphyletic (Franklin 1954; P.H. Williams 1985; Cameron *et al.* 2007), perhaps because in some cases even sister species may have diverged in male mate-searching behaviour and the associated specialised male morphology when they occupy different habitats with different distributions of receptive mates (P.H. Williams 1991). The large-eyed males of *B. mendax* often perch on prominent objects from which any similar-sized passing insects are pursued at high speed and with a characteristic high-pitched buzz (Aichhorn 1976; Haas 1976). The same behaviour is reported for *B. handlirschianus* (De Meulemeester *et al.* 2010). These large-eyed *Mendacibombus* males also have short antennae, a combination of morphological characteristics associated in *B. avinoviellus* and *B. himalayanus* where studied in the Himalaya with a particular, territorial form of male mate-searching behaviour (P.H. Williams 1991; other bumblebees with this morphology and behaviour include species of the subgenus *Bombias* and some *Melanobombus*). In this (true) territorial behaviour (pure dominance or lek polygyny, Thornhill & Alcock 1983), the males chase and displace other males, sometimes resulting in turnover in the occupancy of perches (something not seen for males of some other perching

species that do not permanently displace one another – these males also have large eyes but in contrast have very long antennae, including some species of the subgenera *Sibiricobombus* and *Cullumanobombus*; P.H. Williams 1991). The male perches are marked with secretions from the labial glands when mate-searching activity begins in the morning (P.H. Williams 1991). The perches are often prominent inflorescences, sometimes of grasses, but may also be leaves above or near ground level, stones, or even cow pats (Figs 1–6). Presumably, receptive females are more likely to visit the vicinity of these territories than anywhere else, perhaps because of local 'hilltopping' and perhaps because perches are marked by the males with sex-attractant pheromones. While perching, males with territorial behaviour (as well as the non-territorial 'racing' behaviour of *Sibiricobombus* and *Cullumanobombus*) adopt a characteristic pose in which the wings are articulated together at the hamuli and semi-extended, while the antennae are extended anteriorly (Figs 1–6). *Mendacibombus* males, in the Himalaya and Qinghai-Tibetan plateau at least, also show some tendency towards local 'hilltopping' behaviour, in which they search for mates only in open areas at the higher end of the species' elevational ranges on local hills or near mountain tops (P.H. Williams 1991).

**Sampling problems.** By far the best known species of the subgenus *Mendacibombus* is the subgeneric type-species, *B. mendax,* which occurs in the mountains of western and central Europe, where it is easily accessible and where it has been the focus of several studies (e.g. Pittioni 1937a; Aichhorn 1976; Haas 1976; Rasmont 1988; Hagen & Aichhorn 2003). In contrast, the majority of *Mendacibombus* species lives in parts of Asia that have long been difficult to access for logistical and political reasons, especially in the higher mountains of Central Asia and on and around the Qinghai-Tibetan plateau, so that they have received relatively little study (but see e.g. Skorikov 1910b, 1914, 1923; Reinig 1930; Skorikov 1931). After a slow start, recently there has been an increase in collecting activity in Asia (Fig. 7, the larger collections in this figure include: from the 1900s O. Neshivov; 1920s W. Reinig; 1950s F. Schmid; 1980s PW; 2000 onwards JA/JH/PW). Despite this increase, the Asian species remain rare in collections. Recent reviews of Asian bumblebee faunas show that even within samples from just the higher mountains where these species occur, *Mendacibombus* specimens make up only about 4% of all bumblebees collected (30/757 for Central Asia, P.H. Williams 2011; 289/6312 for Kashmir, P.H. Williams 1991; and 263/6705 for Sichuan, P.H. Williams *et al.* 2009).

In addition, there are problems with some of the associated data. First, some specimens have labels ostensibly from expeditions to parts of Asia from which that particular species is otherwise unknown. These labels appear to have been added later in error (see the comments on *B. superbus, B. waltoni*). Second, there are high levels of uncertainty as to the location of some of the older sample sites, partly because of changes in place names through time (with changes in administration) and partly because of confusion of the many homonyms for some place names (see the comments on *B. margreiteri*).

**Taxonomic problems**. The subgenus *Mendacibombus* is widely accepted because it is strongly supported as a monophyletic group by evidence from five genes (Cameron *et al.* 2007) and is easily recognised as a group from morphological characters (Richards 1968; Ito 1985). Because of its distinctive ecology and morphology, a recent simplification of the subgeneric classification of bumblebees (P.H. Williams *et al.* 2008) maintained *Mendacibombus* as one of the subgenera that was unchanged in its concept.

In contrast, and despite the relatively great age of the subgenus *Mendacibombus* among bumblebees, most of the extant species are weakly differentiated in morphology. Significantly, many of the species were first described (by Skorikov, 1910b) as subspecies or varieties of just one species, *B. mendax* (these taxa are recognised here as eight species). These initial descriptions were of females, distinguished at that stage only by slight differences in the colour pattern of the hair and with no differences in skeletal morphology reported. Many of the taxa were recognised as separate species subsequently only when the relatively pronounced differences in the male genitalia were discovered (Skorikov 1931). However, the difficulties in identifying females were such that, because several species co-occur broadly in Central Asia, there were doubts about the associations of the sexes among species (Skorikov 1931). This is a problem that has otherwise been rare in bumblebee taxonomy when compared to some other groups of bees. Further attempts to describe morphological differences among the females confirmed that morphological differences are at best subtle (Skorikov 1914; Richards 1930; P.H. Williams 1991). Now that more specimens have become available, showing other apparently intermediate colour patterns, it has become increasingly unclear in which cases the minor differences in colour pattern are truly diagnostic of separate species (P. H. Williams, 1991). Unsurprisingly, there are many misidentifications in collections.

**FIGURES 1–6.** Views of perching males of species of the subgenus *Mendacibombus*, showing the anteriorly extended antennae and laterally extended wings that are characteristic of their form of male mate-searching behaviour: 1, *B. waltoni* at Diebu *ca* 3910 m, Minshan mountains, Gansu, China, 29.viii.2009; 2, *B. convexus* at Diebu *ca* 3340 m, Minshan mountains, Gansu, China, 29.viii.2009; 3, *B. avinoviellus* at Gulmarg *ca* 2700 m, Pir Panjal mountains, Kashmir, India, 16.viii.1985; 4, *B. himalayanus* at Apharwat *ca* 4100 m, Pir Panjal mountains, Kashmir, India, 30.viii.1986; 5–6, *B. margreiteri* near Dulan *ca* 3520 m, Burhan Budai mountains, Qinghai, China, 31.viii.2010. Photos by PW (Figs 3–4 are the best available for these species).

Evidence from genes should help to clarify the taxonomy. These poorly known bumblebees are especially important for our understanding of the evolution of the earliest bumblebees and for understanding the relationships among bumblebee faunas of the highest mountains of the Old World.

**This study**. The aim of this study is a taxonomic revision of the species of the subgenus *Mendacibombus* world-wide, based on explicit and consistent criteria, in order to provide identification keys and distribution maps. We emphasise phylogeny because taxonomy is expected to be most usefully predictive of morphology, behaviour, and ecology when it is based on phylogenetic relationships, as a consequence of the underlying evolutionary model of descent with modification (Kitching *et al.* 1998; but see Kelly *et al.* 2014). First, we survey what is already known of the range of variation across the group as represented by the previously named taxa. Second, we seek to recognise species among this variation. Third, we seek to improve estimates of phylogenetic relationship among the species.

## Material and methods

**Sampling.** The subgenus *Mendacibombus* is strongly supported as monophyletic (Cameron *et al.* 2007), making it a complete group appropriate for revision. We bring together samples of taxa of *Mendacibombus* from throughout their global distributions. Taxonomic and geographical breadth is essential for achieving a representative sample for a revision so that we can assess the full range of patterns of variation (Bolton 2007; P.H. Williams, Byvaltsev, *et al.* 2015). It is especially important to reduce the bias that might otherwise result if sampling were restricted to just one or two isolated parts of the group's global distribution or were to exclude major lineages. The most realistic fit for evolutionary models is expected when an entire monophyletic group is included and when the breadth of sampling of differing individuals from within the species' populations is maximized (Maddison & Knowles 2006). The best estimates of phylogenetic relationships available at present (at least when there are not profound shifts in evolutionary rates within lineages) are likely to depend on fitting evolutionary models to DNA data within a Bayesian framework (Baum & Smith 2012).

Within the subgenus *Mendacibombus,* we have found 24 available names for nominal taxa in the species group that represent the known variation to be treated in this revision (Table 1). We examine many new samples together with older specimens from museum collections (Table 2) for all of these named taxa. Where possible we include individuals from across the breadths of each constituent taxon's global distribution. Specimens are given unique database identifiers (referred to by MD#) and data are recorded in an Access database (version 2003 SP3). New samples have GPS data, but for older specimens without GPS data, site coordinates are estimated from GoogleEarth (accessed 2015) and coded in the database with lower spatial precision.

**Recognising species.** We accept the unified *theoretical* concept of species as evolutionarily independent lineages (de Queiroz 2007). There are then a variety of properties that can be used operationally for the *practice* of species discovery, recognition, or 'delimitation' (de Queiroz 2007). Any one of these properties could in principle provide evidence to support the existence of separate species, if interpreted appropriately (de Queiroz 2007). However, these properties are expected to diverge at different stages in the process of speciation, so that among species of different ages, some of these properties may be present more or less generally. This has two consequences. First, evidence of divergence in more of these properties could increase the strength of support for speciation through corroboration (de Queiroz 2007). The practice of examining multiple properties in search of this form of corroboration has become known as 'integrative' taxonomy (Schlick-Steiner *et al.* 2010). Second, some properties, such as gene coalescents, are expected to diverge earlier in the speciation process and it has been suggested that using these properties represents significant progress in studies for discovering species (de Queiroz 2007).

Integrative approaches have already been applied to revising some groups of bumblebees (P.H. Williams *et al.* 2011; De Meulemeester 2012; Lecocq *et al.* 2015). From Skorikov's (1931) account of *Mendacibombus*, we might expect to encounter cryptic species with weak or absent morphological characters, at least for the females. This might be expected to yield morphological groups discordant with groups based on analysis of genes within an integrative assessment.

The anticipated lack of agreement among the groups recognised from different criteria prompts us to consider whether there might be preferred criteria for species recognition (P.H. Williams, Byvaltsev, *et al.* 2015).

Coalescents in rapidly evolving genes have been suggested to be especially useful compared to other properties (including indirect criteria related to reproductive isolation) because they should be evidence of the early stages in the species' lineage separation that is emphasized in the unified species concept (de Queiroz 2007; Fujita *et al.* 2012; Leliaert *et al.* 2014). We seek to assess the prospective species we identify from gene coalescents within an integrative review of morphology and colour patterns. We do not recognise subspecies here (P.H. Williams, Byvaltsev, *et al.* 2015).

**TABLE 1.** List of available names in the species group for named taxa of the subgenus *Mendacibombus* (for details of references, see the text), together with informally associated barcoded proxy type specimens. Sex and caste are shown as: q queen, w worker, and m male; project ID refers to the specimen number of the proxy type in the project database.

| Taxon name | Species' name (here) | Original type locality mountain region | Barcode proxy type mountain region | Sex / caste | Project ID |
|---|---|---|---|---|---|
| *afghanus* | *marussinus* | Hindu Kush | Hindu Kush | w | MD#410 |
| *altaicus* | *margreiteri* | Altai | Altai | q | MD#329 |
| *anonymus* | *mendax* | Alps | Alps | w | MD#303 |
| *asellus* | *waltoni* | Tibetan plateau (?Qinghai) | Tibetan plateau (Qinghai) | m | MD#300 |
| *avinoviellus* | *avinoviellus* | Himalaya | Himalaya | w | MD#3863 |
| *callophenax* | *avinoviellus* | ?Pir Panjal | Pir Panjal | m | MD#853 |
| *chinensis* | *waltoni* | Tibetan plateau (Xining) | Tibetan plateau (Qionglai) | w | MD#193 |
| *convexus* | *convexus* | Tibetan plateau (Hengduan) | Tibetan plateau (Hengduan) | w | MD#1470 |
| *defector* | *defector* | Alai | Tian Shan | q | MD#1251 |
| *handlirschianus* | *handlirschianus* | Caucasus | Lesser Caucasus | q | MD#427 |
| *himalayanus* | *himalayanus* | Ladakh | Ladakh | q | MD#316 |
| *latofasciatus* | *mendax* | Pyrenees | Pyrenees | w | MD#3857 |
| *lugubris* | *convexus* | Tibetan plateau (?Gansu) | Tibetan plateau (Gansu) | m | MD#283 |
| *makarjini* | *makarjini* | Pamir | Tian Shan (Chatkal) | q | MD#330 |
| *margreiteri* | *margreiteri* | Tian Shan | Altai | q | MD#319 |
| *marussinus* | *marussinus* | Pamir | – | – | – |
| *mendax* | *mendax* | Alps | Alps | w | MD#301 |
| *rufitarsis* | *waltoni* | ?Tibetan plateau (Qinghai) | Tibetan plateau (Qinghai) | w | MD#3868 |
| *shaposhnikovi* | *handlirschianus* | Caucasus | Pontic (Anadolu Daglari) | w | MD#3859 |
| *superbus* | *superbus* | ?Tibetan plateau (Qinghai) | Tibetan plateau (Xizang) | w | MD#4112 |
| *turkestanicus* | *turkestanicus* | Alai | Alai | q | MD#324 |
| *varius* | *himalayanus* | Himalaya | Himalaya | w | MD#675 |
| *waltoni* | *waltoni* | Himalaya | Himalaya | w | MD#1482 |

The unnecessary replacement name *pyrenes* is excluded.

**Gene coalescents.** In practice, we recognise species coalescents in a fast-evolving gene using statistical procedures to identify the transition expected in tree-branching patterns between low branching rates between species (Yule model) and high branching rates within species (coalescent model). We use maximum likelihood to fit the single-threshold form of general mixed Yule/coalescent (GMYC) models to single-locus data (Monaghan *et al.* 2005; Pons *et al.* 2006; Papadopoulou *et al.* 2008; Reid & Carstens 2012; P.H. Williams, Brown, *et al.* 2012; Fujisawa & Barraclough 2013; Talavera *et al.* 2013).

For insects, sequences of the mitochondrial gene COI (cytochrome *c* oxidase subunit 1, or *cox-1*) have been shown to be especially useful for investigating species, because they have a high substitution rate (Hebert, Cywinska, *et al.* 2003; Baker *et al.* 2009) and show rapid coalescence (Zink & Barrowclough 2008). COI sequences are sufficiently variable among closely related taxa that they can often be used to diagnose species identical to those recognised by morphological methods (Monaghan *et al.* 2009). Even COI sequences as short as 100 nucleotides have been diagnostic for 90% of the species in other animal groups (Meusnier *et al.* 2008). There

are also more copies per cell for mitochondrial genes, so that they are easier to extract, even from some older dried specimens in museum collections. A problem with older museum specimens is that the sequences obtained are often not of full length (Strange *et al.* 2009). Consequently, despite potential pitfalls and the need for external supporting evidence, the single-locus COI approach can be a useful starting point for recognising morphologically cryptic species (Brower 2006).

**TABLE 2.** Abbreviations for depositories from which material of the subgenus *Mendacibombus* has been examined. Collections of the former Zoölogisch Museum der Universiteit van Amsterdam are now held at the RMNH, Leiden.

| Abbreviation | Address |
| --- | --- |
| AA | Ambros Aichhorn, Salzburg, Austria |
| AM | Alireza Monfared, Yasouj, Iran |
| AMNH | American Museum of Natural History, New York, New York, USA |
| AS | Adolf Scholl, Bern, Switzerland |
| NHM | Natural History Museum, London, UK |
| ENAM | Ecole Nationale d'Agronomie à Montpellier, Montpellier, France |
| HH | Heather Hines, Champaign, Illinois, USA |
| HO | Hikmet Özbek, Erzurum, Turkey |
| HUS | Hokkaido University Museum, Sapporo, Hokkaido, Japan |
| IAR | CAAS Institute of Apicultural Research, Beijing, China |
| IBSSV | RAS Institute of Biology and Soil Science, Vladivostok, Russia |
| INHS | Illinois Natural History Survey, Champaign, USA |
| ISEAN | Institute of Systematics and Ecology of Animals, Novosibirsk, Russia |
| IZB | CAS Institute of Zoology, Beijing, China |
| KUK | Kyushu University, Kyushu, Japan |
| LC | Leopoldo Castro, Teruel, Spain |
| MS | Maximilian Schwarz, Ansfelden, Austria |
| MSI | Malkiat Saini, Patiala, Punjab, India |
| MNHN | Muséum National d'Histoire Naturelle, Paris, France |
| MNHU | Museum für Naturkunde an der Humboldt-Universität, Berlin, Germany |
| NME | Naturkundemuseum Erfurt, Erfurt, Germany |
| OLL | Oberösterreichisches Landesmuseum, Linz, Austria |
| PW | Paul Williams, London, UK |
| RBIN | Royal Belgian Institute of Natural Sciences, Brussels, Belgium |
| RMNH | National Museum of Natural History, Leiden, The Netherlands |
| RR | Rifat Raina, Srinagar, Jammu & Kashmir, India |
| SC | Sydney Cameron, Champaign, Illinois, USA |
| SMNS | Staatliches Museum für Naturkunde, Stuttgart, Germany |
| UMONS | Laboratoire de Zoologie, Université de Mons, Mons, Belgium |
| USNM | US National Museum of Natural History, Washington DC, USA |
| YT | Tang Ya, Chengdu, Sichuan, China |
| ZISP | Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia |
| ZIUB | Zoologisches Institut, Universität Bern, Bern, Switzerland |
| ZMMU | Zoological Museum of the Moscow State University, Moscow, Russia |
| ZSM | Zoologisches Staatssammlung, München, Germany |
| ZX | Zhenghua Xie, Kunming, Yunnan, China |

For selected specimens, we had DNA extracted from a foreleg. The standard barcode region of the COI gene was amplified and sequenced (length 657 base pairs (bp)). Much of this work was done at the Biodiversity Institute of Ontario, University of Guelph, using the standard protocols described by Hebert *et al.* (2003) and using the universal primers for the COI-barcode sequence for insects (Table 3). In some cases the work was done by HJ in the IAR laboratory in Beijing. Gene sequences (without primer regions) were aligned using the MUSCLE function within MEGA (version 6.06, accessed 2014: megasoftware.net). Nucleotide composition was checked with MEGA and alignment of codons and amino-acid translation was tested with MEGA and with the online software EMBOSS Transeq (accessed 2014: ebi.ac.uk/Tools/st/emboss_transeq/). COI sequence data for the specimens processed at Guelph have been uploaded to the BOLD online database in the publicly accessible folder BBMD (www.boldsystems.org; Ratnasingham & Hebert 2007) and to GenBank.

**TABLE 3**. Primer sequences for the sequenced regions of the four genes.

| Gene | Primer name | Primer sequence | Reference |
|------|-------------|-----------------|-----------|
| COI | LepF | 5'- ATTCAACCAATCATAAAGATATTGG -3' | Hebert *et al.* 2004 |
| | LepR | 5'- TAAACTTCTGGATGTCCAAAAAATCA -3' | Hebert *et al.* 2004 |
| 16S | 16SWb | 5'- CACCTGTTTATCACCTGTTTATCAAAAACAT -3' | Dowton & Austin 1994 |
| | 874–16SlR | 5'- TATAGATAGAAACCAAYCTG -3' | Cameron *et al.* 1992 |
| Opsin | LWRhF | 5'- AATTGCTATTAYGARACNTGGGT -3' | Mardulyn & Cameron 1999 |
| | LWRhR | 5'- ATATGGAGTCCANGCCATRAACCA -3' | Mardulyn & Cameron 1999 |
| PEPCK | FHv4 | 5'- TGTATRATAATTCGCAAYTTCAC -3' | Cameron *et al.* 2007 |
| | RHv4 | 5'- CTGCTGGRGTYCTAGATCC -3' | Cameron *et al.* 2007 |

GMYC analysis requires an ultrametric estimate of the phylogenetic tree for the unique COI haplotypes. We use only unique haplotypes (Monaghan *et al.* 2009; Reid & Carstens 2012) to avoid biasing the terminal branching-rate estimates. For each of these haplotypes we use the longest sequences available. These are identified using Collapse (version 1.2, accessed 2011: darwin.uvigo.es/software/collapse.html), after ranking sequences by their length in order to avoid matching longer to shorter sequences and thereby rejecting longer sequences, which might otherwise obscure real differences. As outgroups, we include close relatives of *Mendacibombus,* plus a selection of species from those other bumblebee subgenera (P.H. Williams *et al.* 2008) for which relationships have low uncertainty (Cameron *et al.* 2007): *B. (Bombias) confusus* Schenck, *B. (Kallobombus) soroeensis* (Fabricius), *B. (Subterraneobombus) difficillimus* Skorikov, *B. (Megabombus) gerstaeckeri* Morawitz, *B. (Alpinobombus) balteatus* Dahlbom, *B. (Pyrobombus) bimaculatus* Cresson, and *B. (Alpigenobombus) nobilis* Friese. Other more distantly related groups of bees (see Cameron *et al.* 2007) were not included because for the fast-changing gene COI they have too many nucleotide changes. BEAUti was used to prepare XML files for submission to BEAST (both of version 1.8.2, accessed 2015: beast.bio.ed.ac.uk) for Bayesian analysis of multiple trees using the chosen nucleotide-substitution model (Drummond & Rambaut 2007). The best available model for our COI data according to the Bayesian information criterion (BIC) obtained from MEGA is the general time-reversible model with a gamma-frequency distribution of changes among sites (GTR+$\Gamma$). The number of gamma categories was set to six, the clock model was set to the uncorrelated lognormal (relaxed clock), the tree speciation prior was set to a constant-size coalescent process (consistent with the null hypothesis that there is a single species in the data), and the chain length for the Markov-chain Monte Carlo (MCMC) algorithm was set to two billion generations, with sampling of the resulting trees every 200,000 generations. The sample of resulting trees was examined for convergence and effective sample size using Tracer (version 1.6.0, accessed 2013: beast.bio.ed.ac.uk/Tracer; Drummond & Rambaut 2007). The large number of MCMC generations was needed for these data in order to increase effective sample sizes. Tracer also showed that stationarity had been achieved by 1% of the total MCMC generations. A maximum clade-credibility tree was obtained from the post burn-in tree sample after rejecting the first 1% of sampled trees using TreeAnnotator, keeping target heights (version 1.8.2, as for BEAST). The outgroups were trimmed from the tree before the GMYC analysis.

We expect the GMYC analysis to perform best with representative data in the form of complete COI-barcode sequences. Ambiguous data are known to affect tree results (Lemmon *et al.* 2009) and an effect of short sequences

on terminal branch length has been suggested (S.T. Williams & Ozawa 2006). A preliminary test of all unique COI haplotypes showed that the longest terminal branches in the resulting BEAST tree are associated with the shortest of these sequences (Fig. 8; significant Spearman rank correlation $\rho = -0.45$, $p < 0.005$). Short sequences that increase terminal branch lengths as an artefact could bias the GMYC results, causing samples isolated on long terminal branches to be interpreted falsely as separate species. To reduce this bias and the possible consequent inflation with a number of false 'species', sequences shorter than 650 bp were removed from the GMYC analysis in cases where other longer sequences were available for a taxon. This approach could be unduly conservative if true species were present but represented only by short sequences, perhaps because they are rare and represented only by old specimens. Therefore exceptions were made for described taxa for which all available sequences were short.

After removal of the outgroups from the maximum clade-credibility tree, the GMYC models were applied using the SPLITS software tools (T. Ezard: accessed 2011, r-forge.r-project.org/projects/splits/) running on the R platform (version 2.12.2, accessed 2015: cran.r-project.org/bin/windows/base/old/2.12.2/).

As a way of checking the number of species recognised, we use a second approach for recognising species from gene coalescents in single-locus data, based on Poisson tree processes (PTP: Zhang *et al.* 2013). This procedure looks for changes in the numbers of nucleotide substitutions along branches, from many substitutions in branches between species to few substitutions in branches within species. PTP requires less tree information than the GMYC approach and is claimed to perform better (Zhang *et al.* 2013). We use the Bayesian implementation on the bPTP server (accessed 2015: species.h-its.org) with a metric tree from COI data obtained with MrBayes (version 3.1.2, accessed 2011: Huelsenbeck & Ronquist 2001), using the same outgroups, nucleotide-substitution model, four chains (temperature 0.2), and 100 million generations of the MCMC algorithm with a 1% burn-in. We used the default bPTP options after removing the outgroups from the rooted tree.

Multiple runs of all analyses were made to check the stability of the results.

**Integrating morphology and colour patterns**. The morphology and colour patterns of named taxa are examined for an integrative assessment of species by scoring characters using a light microscope (morphological terms follow Williams *et al.*, 2011). Group structure in the character data is assessed using the TNT procedure within WINCLADA (ASADO version 1.7, accessed 2009: cladistics.com).

Morphological terms follow Michener (2000) and Williams *et al.* (2009). Pile or pubescence is referred to as hair for simplicity, following Michener (2000). Several terms are used as shorthand when describing components of the colour pattern that do not correspond precisely with particular segments or sclerites. On the head, the 'face' is used for the patch of hair around the antennal bases between the eyes, dorsal to the clypeus and ventral to the ocelli (frons + supraclypeal area + paraocular area). The 'side' of the thorax refers to the hair covering the lateral parts of the thorax ventral to the wing bases (on the lateral pronotum + mesepisternum + metepisternum + lateral propodeum). On the abdomen, the term 'tail' is used more flexibly, referring to the contrasting palest long hair covering all or parts of metasomal terga 4–6 (e.g. 'red-tail' or 'white-tail' colour patterns). Metasomal terga 1–7 and sterna 1–6 are abbreviated to T1–7 and S1–6 respectively.

**Naming species**. We seek to represent all of the formally-named taxa of the subgenus *Mendacibombus* in our analysis with COI sequences in order to identify the oldest available (valid) names of species (ICZN 1999) from among them. We follow a pragmatic procedure (described in the appendix in P.H. Williams, Brown, *et al.* 2012) of associating the original name-bearing type specimens (which we cannot sequence) with COI sequences via the identification of informal proxy type specimens for which we have COI sequences (Table 1). Although still subjective, this procedure at least provides explicit accountability in applying names. This is especially important when revising the subgenus *Mendacibombus* because species are often closely similar in morphology and in colour pattern. Informal proxies for the types were chosen by: (1) matching morphology and colour pattern of the hair; (2) proximity of the proxy locality to the type locality; (3) long COI sequences; and (4), for some of the Central Asian taxa in particular, it is desirable where possible to match the sex and caste of the proxies with the original type specimens, because of difficulties in associating sexes and castes among species from morphology alone. The proxies are intended only for use in this analysis, to make the process of associating names explicit, accountable, and open to easy revision when necessary. They are not intended to have any formal nomenclatural status, or to have any persistent significance beyond this analysis.

Geographical distributions of species were mapped from the project database using ArcMap (version 10.2.2 from ESRI, accessed 2015).

**Phylogeny and dating divergences**. To seek a better estimate of phylogeny among species within the

subgenus *Mendacibombus*, we use multi-locus data. To improve the estimate for especially the older part of the phylogeny for this relatively old group of bumblebees, we use not only fast-evolving mitochondrial genes (COI and 16S), but also the slower nuclear genes (PEPCK, phosphoenolpyruvate carboxykinase; and opsin, long-wavelength rhodopsin copy 1; using sequences from Cameron *et al.* 2007; additional sequences were obtained by HJ using the primers and protocols in Table 3; combined length of sequenced regions 2832 bp). Sequence data for the other genes have been uploaded to GenBank (accession numbers in Table 4).

**TABLE 4.** GenBank accession numbers for gene sequences with the species' names listed according to this study (excluding COI barcodes in BOLD).

| Species | 16S | Opsin | PEPCK |
|---------|-----|-------|-------|
| *confusus* | DQ787992 | DQ788324 | EF051016 |
| *soroeensis* | DQ788107 | AF493008 | EF051013 |
| *difficillimus* | DQ787998 | DQ788327 | EF050990 |
| *gerstaeckeri* | DQ788017 | DQ788335 | EF051003 |
| *balteatus* | DQ787974 | AY739455 | EF050870 |
| *bimaculatus* | DQ787978 | AY739456 | EF050847 |
| *nobilis* | DQ788071 | AY739485 | EF050912 |
| *superbus* | KX452097 | KX452101 | KX452104 |
| *waltoni* | DQ788134 | DQ788385 | EF051022 |
| *convexus* | DQ787993 | DQ788325 | EF051021 |
| *avinoviellus* | AY268416 | AY268394 | EF051020 |
| *turkestanicus* | KX452098 | KX452102 | KX452105 |
| *defector* | KX452099 | KX452103 | KX452106 |
| *margreiteri* | KX452100 | AF493025 | KX452107 |
| *handlirschianus* | DQ788022 | DQ788337 | EF051017 |
| *mendax* | DQ788057 | AF493024 | EF051019 |

For the estimate of phylogeny for species within the subgenus *Mendacibombus*, we use a BEAST analysis with a linked tree for the four genes (Heled & Drummond 2010). We reduce the COI data to a single sequence for each of the species recognised from the GMYC and PTP analyses. For *B. himalayanus* and *B. marussinus*, the COI sequences are composites in order to include data for all of the base positions available for each species (increasing the longest sequence lengths from 623 to 657 bp and from 421 to 622 bp respectively). For *B. makarjini, B. marussinus* and *B. himalayanus* we could not obtain sequences of 16S, opsin, or PEPCK from the older material available.

Most BEAST settings are the same as for the single-gene tree in the GMYC analysis. According to the BIC from MEGA, the best available nucleotide-substitution model for 16S is GTR+Γ, for the PEPCK exon (boundaries and alignment follow Cameron *et al.* 2007) is HKY (Hasegawa-Kishino-Yano), for the opsin exon is HKY+Γ, and for the PEPCK and opsin introns is HKY (with the substitution models unlinked). For each gene, ucld.mean is set to the continuous-time Markov chain rate reference prior (Ferreira & Suchard 2008). The tree-speciation prior is a Yule process appropriate for a multi-species tree that has all of the species sampled (a pure birth process). The uncorrelated lognormal (relaxed) clocks are unlinked. No fossils of *Mendacibombus* species are known that might help with dating parts of the tree, so the phylogeny is calibrated with a date from a molecular study. Hines (2008: her fig. 2) estimated the age of divergence between the subgenus *Mendacibombus* and the remaining extant bumblebees to be 40–25 Ma, but this estimate was then fixed at 34 Ma for most of her analyses. This is consistent with earlier ideas that bumblebees diversified either initially in the early Tertiary with the divergence of *Mendacibombus* (Skorikov 1923) or that this early diversification was associated especially with the Eocene/Oligocene cooling event (P.H. Williams 1985). We use 34 Ma (early Oligocene) for the mean and initial age estimate for the most recent common ancestor prior (tmrca) of all bumblebees, assuming a normal distribution with a standard deviation of 4 Myr, which gives 5% tails of the tmrca distribution of 41–27 Ma (late Eocene to mid

Oligocene). We truncated the distribution at 50 Ma and 20 Ma to prevent extreme values, including 0. To constrain and focus the exploration of trees in the analysis, we also defined monophyletic groups for (1) *Mendacibombus* and (2) for the sister group of all other bumblebees (following the results of Cameron *et al.* 2007). The MCMC algorithm ran for two billion generations. A maximum clade-credibility tree was obtained from the post burn-in tree sample after rejecting the first 1% of sampled trees.
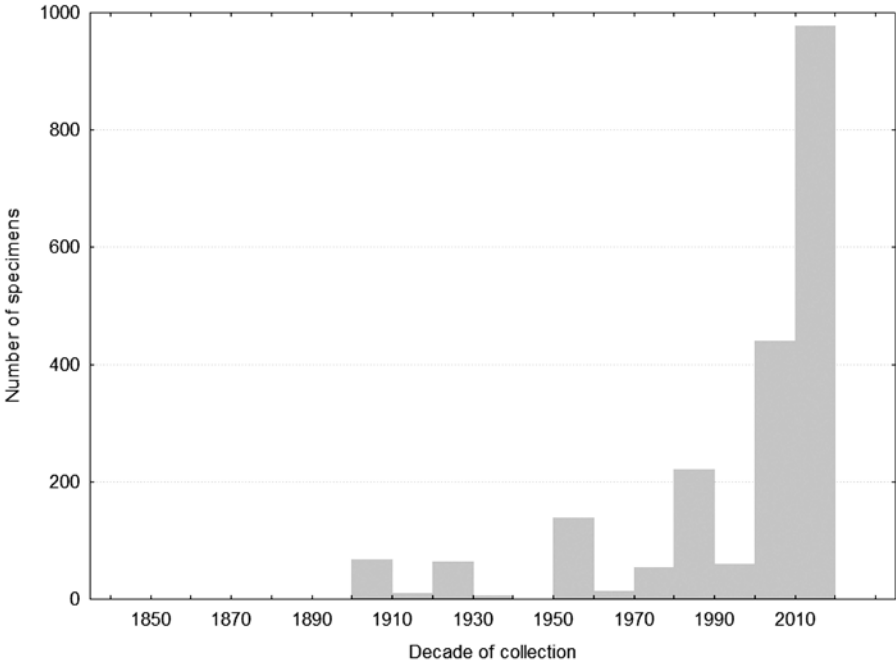


**FIGURE 7.** Frequency of specimen collection by decade among specimens examined for species of the subgenus *Mendacibombus* excluding *B. mendax* and *B. handlirschianus*.
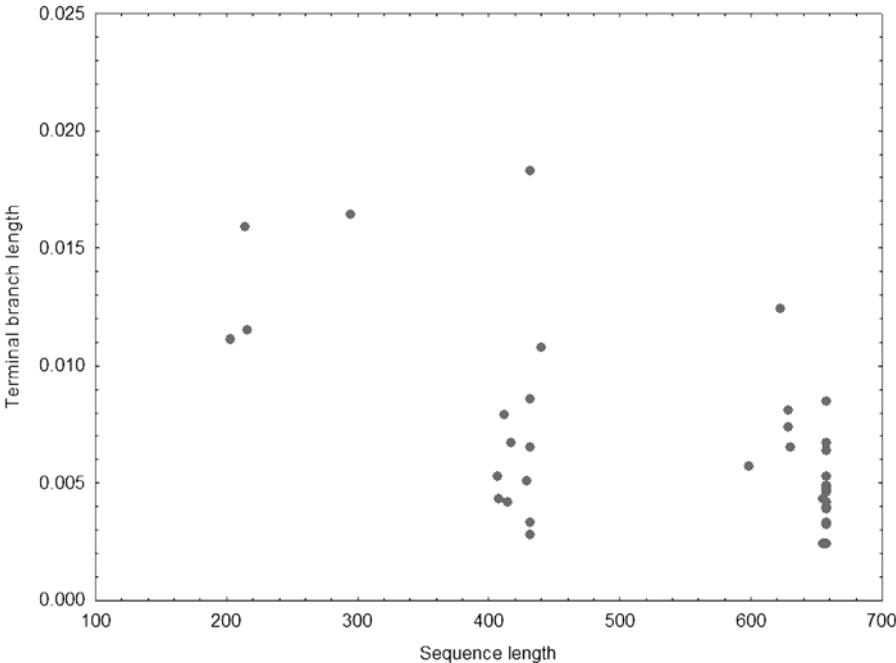


**FIGURE 8.** Plot of (*y axis*) terminal branch lengths from a tree for 43 unique COI haplotypes obtained with BEAST against (*x axis*) lengths of the barcode sequences in numbers of nucleotides.

**Results**

**Sampling.** In total, 4413 specimens of the subgenus *Mendacibombus* were examined for morphological variation, originating from 1045 samples from 802 separate georeferenced localities throughout the known range of the group in 23 countries (Fig. 9).
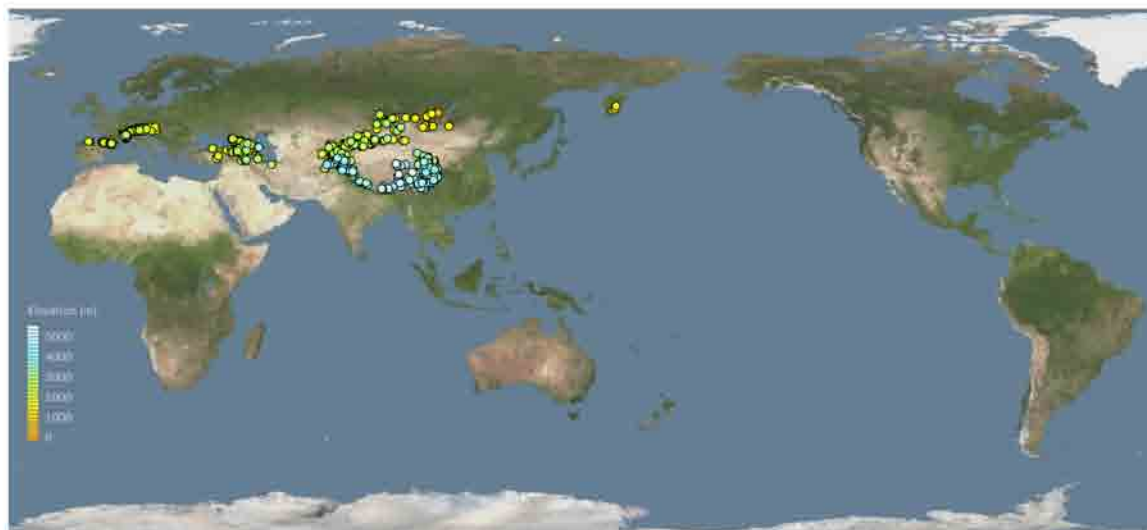


**FIGURE 9.** Map of the global distribution of sites from which samples of the subgenus *Mendacibombus* have been examined (these bees are unknown from any other regions). Spots are coloured to show the site elevation above sea level (scale in metres to the left). Image showing vegetation, Cartesian orthonormal projection, with north at the top of the map.

**Gene coalescents.** Samples from 171 specimens (32% of them collected before 2000 because of lack of recent alternatives or lack of access to sites for new material) were sent for DNA extraction, amplification, and sequencing, yielding 128 useable COI sequences (74% of specimens sent for extraction; 2.9% of the total sample in the database). No amplification of *Wolbachia* (or other obviously non-target) DNA was detected. A few other sequences are very short. Most of these short sequences were discarded from further analysis. The 128 retained sequences lack indels and in-frame stop codons. These sequences also have closely similar GC% (24.5%, SE 0.09) with a strong AT-bias in the third codon position (95.1%, SE 0.19). Consequently they are unlikely to have been amplified from older and more divergent nuclear paralogous copies of the COI gene ('numts'). These 128 sequences include 41 unique haplotypes with 173 variable nucleotide sites that are potentially informative for differentiating groups.

To reduce bias and possible consequent inflation with a number of false 'species' arising as an artefact from including short sequences, sequences shorter than 650 bp were removed from the BEAST analysis in cases for which other longer sequences were available for a taxon. Exceptions were made for described taxa for which all available sequences are short, including the taxa *anonymus* (629 bp), *varius* (623 bp), *makarjini* (622, 603 bp), and *latofasciatus* (635 bp). The taxa *marussinus*, *afghanus,* and *makarjini* are found in areas inaccessible to us at present for collecting fresh material. From older specimens of the taxon *afghanus* we were able to obtain three short sequences (421, 295, 176 bp), all from the same sampling site. For further analysis we combined non-overlapping sequences from this single sampling site for *afghanus* (622 bp). In a few short overlapping sequence segments there are conflicting bases, whereupon we adopted the majority base. The taxon *marussinus s. str.* is closely similar to *afghanus* except that the hair of tergum 2 is yellow for *marussinus s. str.* rather than black as for *afghanus,* so the combined sequence for *afghanus* is used to represent *marussinus s. l.* in some analyses. The final data set consists of 30 of the longer unique haplotypes.

Tracer showed that the BEAST analysis of the 30 longer unique COI haplotypes over two billion MCMC generations after a 1% burn-in had converged on broadly stable traces with effective sample sizes (ESS) for all

trace statistics ≥ 151 (ESS values > 1000 for 91% of reported statistics). When the GMYC model is applied to the BEAST tree after removing the outgroups, it shows a significant change in branching rate through time in the tree (Fig. 10; likelihood ratio 20.44 between the GMYC multiple-species model and the single-species null model, evaluated using a chi-square test with three degrees of freedom, $p < 0.001$). This threshold (at -0.0052 substitutions per nucleotide) supports recognition of 12 lineages as candidates for prospective species (with a 95% confidence interval of 12–13 species) within *Mendacibombus* as shown in Fig. 11. Only the taxa *varius* and *afghanus* (representing the species *B. himalayanus* and *B. marussinus*) are accepted as separate species on the basis of a single sequence that is short. In contrast, the retained short sequences for the taxa *makarjini* and *latofasciatus* are not recognised as the single representatives of separate species. The two sequences for the taxon *makarjini* have only two nucleotide differences between them even though the specimens were collected from sites *ca* 690 km apart, so they are likely to represent a single species' population. All of the species recognised from the GMYC analysis can be diagnosed by fixed base-pair differences between them (Table 5). In every case where we have sufficient samples to recognise multiple haplotypes per species, we also find very strong support (estimated posterior $p = 1$) from the Bayesian analysis for those species as monophyletic groups (Fig. 11). In contrast, some of the older groups are weakly supported, showing that this tree is unreliable as an estimate of the older phylogenetic relationships among the species.

The Bayesian PTP solution with the most support (Fig. 12) recognises the same 12 species as most likely (from a range of 12–17 species, mean 12.68) as are recognised by the GMYC analysis. For all of these species the posterior $p ≥ 0.88$, and the lowest of these probabilities is for the previously broadly accepted concept of *B. mendax*. All of the groups recognised as species have very strong posterior probabilities from MrBayes for supporting those groups (estimated posterior $p = 1$).
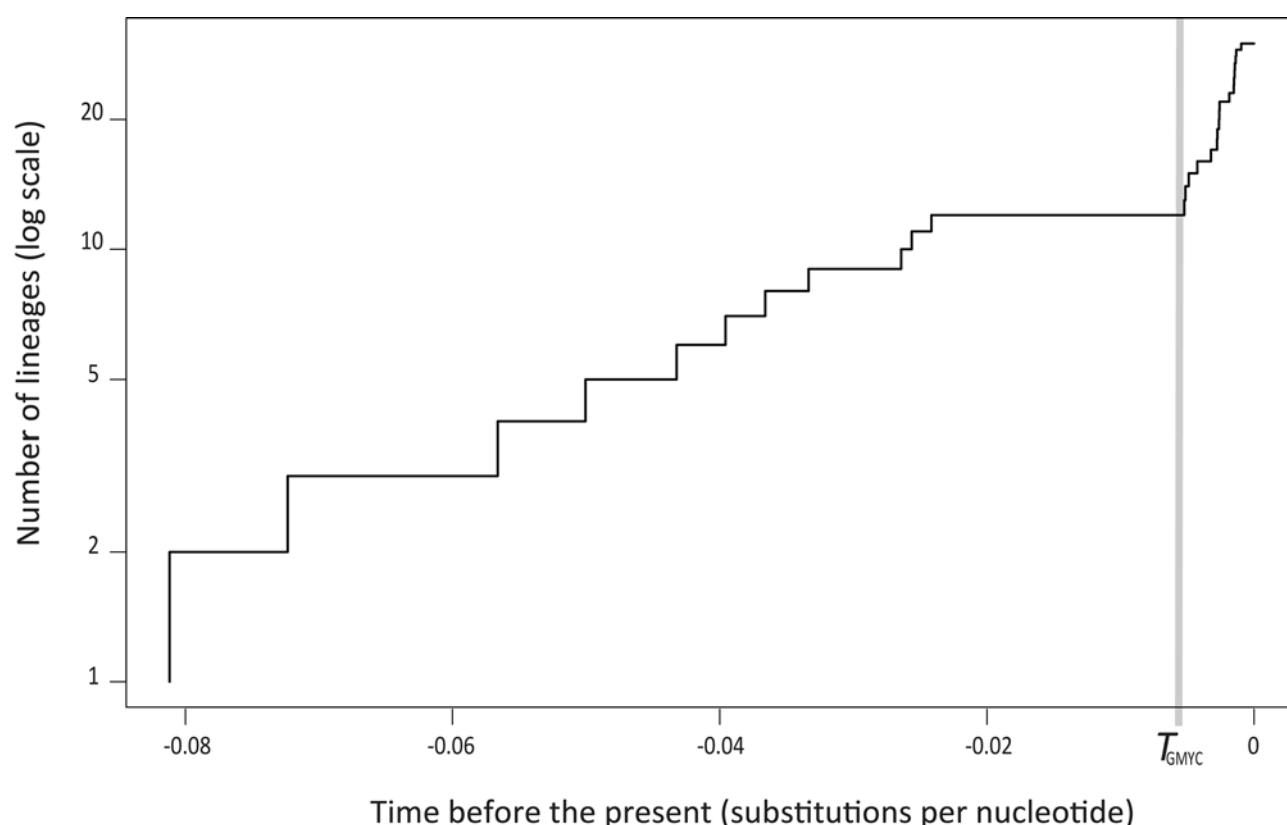


**FIGURE 10.** Plot of (*y axis*) the number of lineages in the BEAST tree (Fig. 11) of unique COI haplotypes excluding outgroups on a log scale against (*x axis*) time as substitutions per nucleotide. *T*, the single threshold at maximum likelihood for the change in branching rate from the GMYC models.
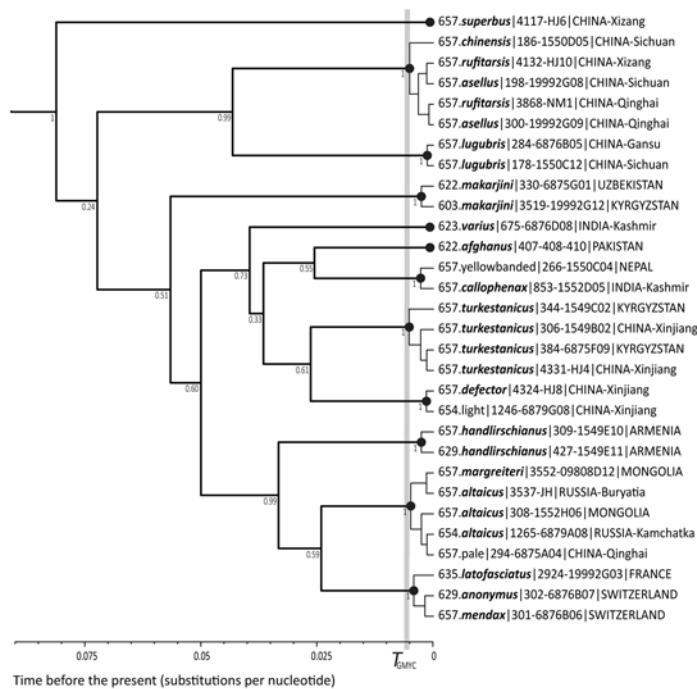
11 GMYC
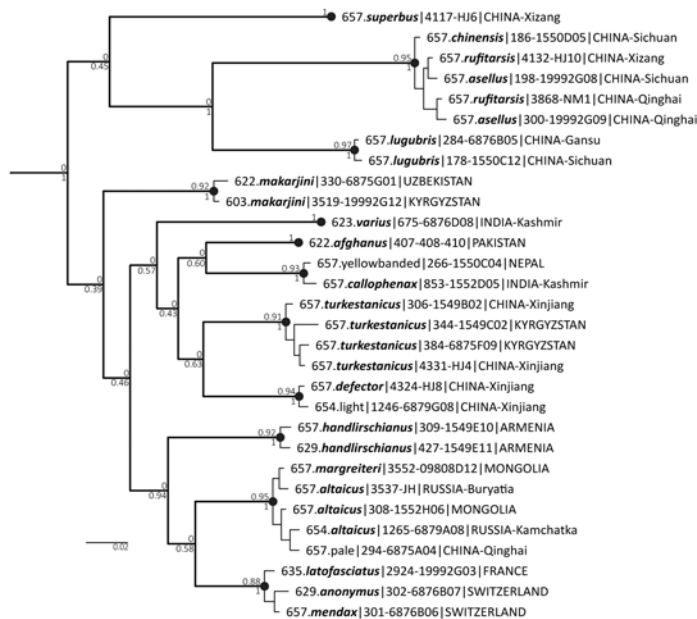


12 PTP

**FIGURES 11–12.** Recognising species from an estimate of phylogeny for 30 unique COI haplotypes of the subgenus *Mendacibombus* by BEAST, using GMYC models and the PTP procedure. From the GMYC models (11), the single threshold *T* is shown by the vertical grey bar so that the intersecting lineages are interpreted as indicating 12 separate species (black spots at coalescent nodes; outgroups not shown). Values below the nodes of the maximum clade-credibility tree are Bayesian posterior probabilities showing branch support (groups with values < 0.8 are considered unreliable) from the BEAST analysis with two billion MCMC generations and a 1% burn-in. The *x*-scale axis is calibrated in substitutions per nucleotide site. From the PTP procedure (12), the Bayesian PTP solution with highest support also indicates 12 species. Values above the nodes are PTP Bayesian support values that all daughter haplotypes are parts of a single species; values below the nodes are Bayesian posterior probabilities showing branch support. The scale bar is calibrated in substitutions per nucleotide site. Each unique haplotype is represented by one of the longest available sample sequences, labelled with: the sequence length in number of base pairs, a taxon name or name for an unpublished colour pattern (light/dark/yellow/white/pale), and then a code that consists of a specimen identifier (MD#) from the project database and (after the hyphen) a sample identifier from BOLD or from GenBank, followed with its geographic origin.
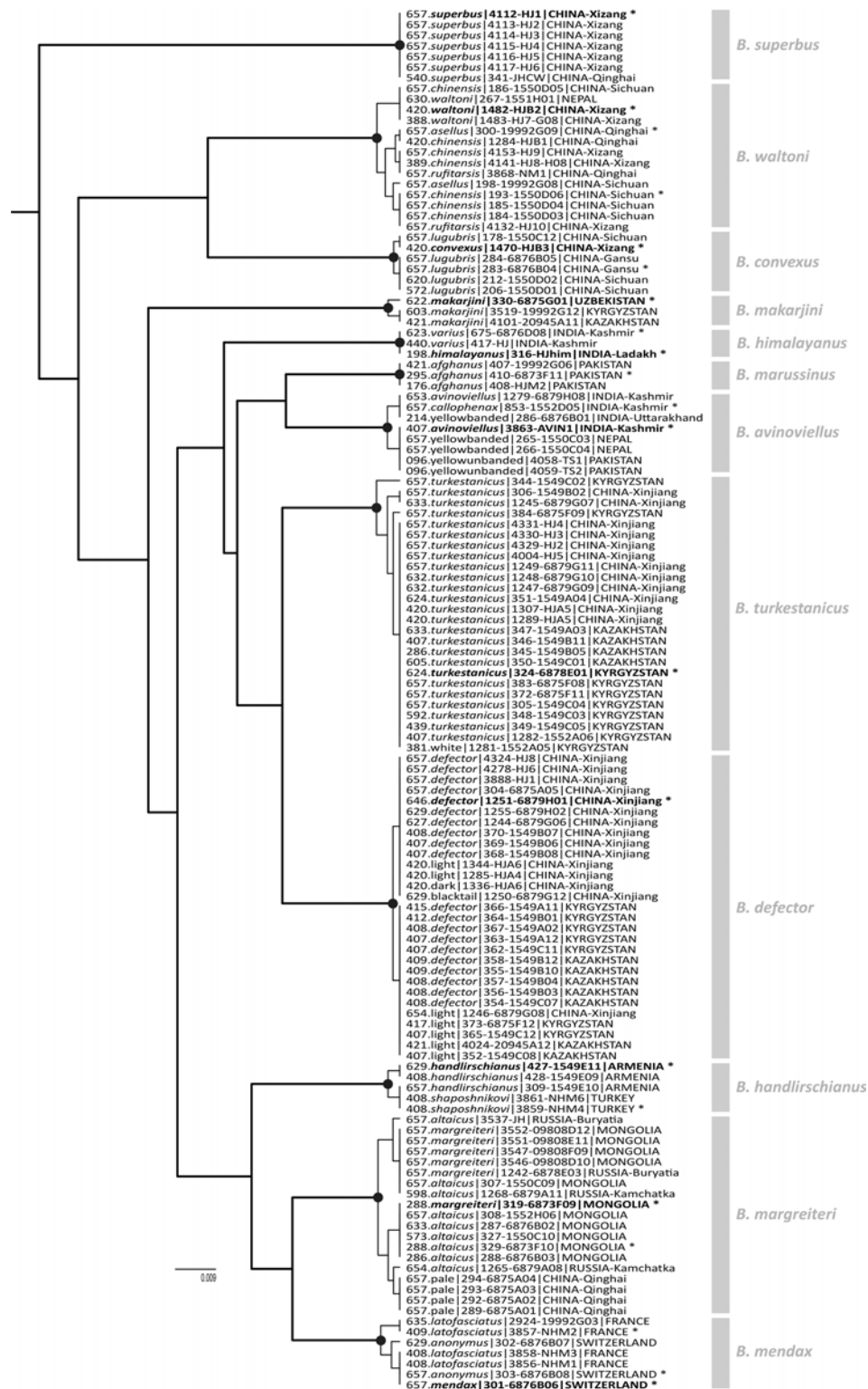
**FIGURE 13.** Assigning names to species from an estimate of phylogeny for 130 COI sequences of the subgenus *Mendacibombus*. Based on a BEAST analysis of the 30 unique haplotypes (Fig. 11), with the remaining sequences interpolated back into the tree with 0 branch lengths from their matching samples (where a sequence matches more than one longer sequence within a species in the Collapse results, it is added after the first matching sequence, with the addition of the two short-sequence yellow unbanded specimens from Pakistan, MD#4058, 4059). The sequence labels follow the format used in Figs 11, 12. Lineages accepted as species from the GMYC models (Fig. 11) are shown as thick branches, the most recent common ancestors of each species are shown with a black spot, and branches within species are shown as thin branches. Asterisks mark samples used as informal proxies for the type specimens of each of the taxon names (Table 1). The proxy sample for the type specimen for the oldest available name (the valid name) for each species (from Fig. 11) is marked in bold. The interpretations of the species with their valid names are shown in grey to the right.

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**TABLE 5.** Fixed nucleotide changes from COI sequences that are diagnostic within the subgenus *Mendacibombus* for each species in Figs 11, 12.

| Species | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *superbus* | 75→C | 78→G | 126→A | 168→T | 216→C | 265→T | 267→A | 283→T | 414→T | 432→C | 495→C | 507→T | 525→T | 609→C |
| *waltoni* | 15→A | 21→A | 189→T | 301→C | 308→T | 375→C | 400→T | 411→T | 432→T | 453→A | 532→C | 541→C | | |
| *convexus* | 42→C | 55→C | 237→C | 327→T | 345→A | 378→C | 387→C | 483→C | 519→C | 522→C | 561→C | 618→C | | |
| *makarjini* | 114→C | 132→T | 183→G | 315→C | | | | | | | | | | |
| *marussinus* | 117→C | 246→C | 394→C | 407→A | | | | | | | | | | |
| *avinoviellus* | 33→A | 78→A | 321→T | 324→C | 369→C | 477→T | | | | | | | | |
| *himalayanus* | 45→G | 60→G | 132→C | 423→C | 460→A | 465→G | 546→C | 567→A | 615→C | | | | | |
| *turkestanicus* | 142→C | 258→C | 357→C | 567→C | | | | | | | | | | |
| *defector* | 54→C | 264→G | 639→C | | | | | | | | | | | |
| *margreiteri* | 42→T | 58→C | 159→G | 354→C | 409→T | 436→C | 555→A | | | | | | | |
| *handlirschianus* | 273→C | 375→G | 654→T | | | | | | | | | | | |
| *mendax* | 87→G | 196→C | 210→G | | | | | | | | | | | |

Numbers show the in-frame nucleotide position. Letters show the nucleotides: A, adenine; C, cytosine; G, guanine; T, thymine.

**TABLE 6.** Hair colour and morphological (male genitalia) character matrix excluding autapomorphies, coded for the outgroup *B. difficillimus* and for all *Mendacibombus* species (see Fig. 15).

| Species | Characters | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
| *difficillimus* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *superbus* | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| *waltoni* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *convexus* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *makarjini* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *marussinus* | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *avinoviellus* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *himalayanus* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *turkestanicus* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *defector* | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| *margreiteri* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *handlirschianus* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *mendax* | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |

| 1 | Hair colour | tail orange | 0 | absent |
|---|---|---|---|---|
| | | | 1 | present |
| 2 | | thorax with yellow | 0 | absent |
| | | | 1 | present |
| 3 | | thorax with white | 0 | absent |
| | | | 1 | present |
| 4 | Gonostylus | broad, thick and robust | 0 | absent |
| | | | 1 | present |
| 5 | | strong interior oblique longitudinal groove | 0 | absent |
| | | | 1 | present |
| 6 | Volsella | toothed ridge | 0 | absent |
| | | | 1 | present |
| 7 | | tip completely recurved towards anterior | 0 | absent |
| | | | 1 | present |
| 8 | Penis valve | outer basal swelling | 0 | absent |
| | | | 1 | present |
| 9 | | broad shoulders at the base | 0 | absent |
| | | | 1 | present |
| 10 | | head more dorso-ventrally than laterally compressed | 0 | absent |
| | | | 1 | present |
| 11 | | strong mismatch in shoulder lengths (ratio of length ratios > 1.3) | 0 | absent |
| | | | 1 | present |
| 12 | | inner shoulder reduced to elbow knuckle and head short | 0 | absent |
| | | | 1 | present |
| 13 | | head lateral flange pronounced at base | 0 | absent |
| | | | 1 | present |
| 14 | | apex narrowing strongly before end of membrane | 0 | absent |
| | | | 1 | present |
| 15 | | membranous channel narrowed on outer shoulder | 0 | absent |
| | | | 1 | present |
| 16 | Spatha | turned outwards strongly laterally to PV | 0 | absent |
| | | | 1 | present |

**Integrating morphology and colour patterns.** The species recognised from the GMYC and PTP analyses of the COI gene are corroborated by morphology, from diagnostic combinations of morphological character states that we identify (see the keys and the diagnoses for each species). Some of these characters are weakly differentiated between species and in some cases they may not be completely discrete between two species. For example, for females the known diagnostic differences are concentrated especially in the form of the labrum and of the clypeus, although the differences are sometimes not clear, especially among small workers.

There is no obvious evidence of genetic introgression between species of the subgenus *Mendacibombus*. Comparison of patterns of COI haplotypes and morphology among species shows no recombination of any one haplotype with more than one divergent morphotype. The only patterns of this form are recombinations between COI haplotypes and yellow/white colour-pattern variation within species (Fig. 13).

Not all previously named taxa of the subgenus *Mendacibombus* are supported as species. Some of the named taxa that were described originally only from differences in colour patterns and that have been interpreted previously as species are not now supported here as species from our analysis of COI data and morphology. These include the taxa *altaicus* and *margreiteri* (as well as an unnamed new 'pale' colour pattern from Qinghai), which are all supported as parts of one species with the valid name *margreiteri*. The changes in nomenclature are summarised in Table 7.

**TABLE 7.** Currently recognised species' names (right) and names applied to the same taxa or to some parts of those taxa by selected authors over the last century.

| Skorikov, 1910 | Skorikov, 1923 | Skorikov, 1931 | Williams, 1998 | This study |
|---|---|---|---|---|
| — | — | — | superbus | superbus |
| *mendax* ssp. *chinensis* | *waltoni* | *chinensis* | *waltoni* | *waltoni* |
| — | *lugubris* | *lugubris* | *convexus* | *convexus* |
| *mendax* ssp. *makarjini* | — | *makarjini* | *makarjini* | *makarjini* |
| *mendax* ssp. *marussinus* | *marussinus* | *marussinus* | *marussinus* | *marussinus* |
| — | *avinoviellus* | — | *avinoviellus* | *avinoviellus* |
| — | *varius* | *varius* | *himalayanus* | *himalayanus* |
| *mendax* ssp. *turkestanicus* | *turkestanicus* | *turkestanicus* | *turkestanicus* | *turkestanicus* |
| *mendax* ssp. *defector* | *defector* | *defector* | *defector* | *defector* |
| *mendax* ssp. *margreiteri* | *margreiteri* | *margreiteri* | *defector* [male not seen] | *margreiteri* |
| *mendax* ssp. *altaicus* | — | *altaicus* | *defector* [male not seen] | *margreiteri* |
| *mendax* ssp. *handlirschianus* | *handlirschianus* | *handlirschianus* | *handlirschianus* | *handlirschianus* |
| *mendax* ssp. *shaposhnikovi* | *shaposhnikovi* | *shaposhnikovi* | *shaposhnikovi* | *handlirschianus* |
| *mendax* ssp. *mendax* | *mendax* | *mendax* | *mendax* | *mendax* |
| *mendax* ssp. *latofasciatus* | — | — | *mendax* | *mendax* |

We also examined inter-specific group structure in data for morphological characters. For males, 13 potentially synapomorphic characters were identified (autapomorphies were not scored), all from the male genitalia (Table 6 and the key). No clear female morphological characters that are synapomorphic for more than one species were found (see the key). Most variation in the colour-pattern of the hair is either autapomorphic or varies substantially within the 12 species, so that only three broad characters were coded among species. TNT analysis of the 17 characters of colour pattern and male morphology yields a single tree (Fig. 14).

**Naming species.** The species recognised in the GMYC and PTP analyses are named by adopting as the valid name for each species from Fig. 11 the oldest available name associated in Fig. 13 with our sequenced proxy types (Table 1). Figure 13 recognises species among the sequences based on the GMYC groups from the COI tree for unique longer sequences in Fig. 11, but with the matching COI-sequence samples interpolated from the Collapse results. In addition, we have interpolated the other short sequences that had been excluded from the GMYC analysis, by adding them to their closest relative according to other BEAST analyses (MD#267 341 352 354–358 362–367 373 428 1268 1285 1470 1482 1483 4024).

Detailed accounts of species of the subgenus *Mendacibombus* follow, with names applied according to matches (Fig. 13) with our sequenced proxy types (Table 1). For *B. mendax* and *B. handlirschianus*, only literature references to the principal names are included because these species are well known and their identities are not in doubt. For the remaining Asian species, more references are included to clarify the breadth of the revised concepts of the species. Square brackets [*Bombus xus*] are used in these lists to indicate unavailable names, as well as for transliterations and for translations of data. Angle braces <*Bombus*> *xus* are used to indicate the parts of names that are interpolated by interpretation from the context of the name within the original publication.

Future identification of species of the subgenus *Mendacibombus* will be most reliable for specimens from which COI data are available for diagnosis by comparison with the nucleotide differences in Table 5. Keys using morphological and hair-colour characters follow below, with the most reliable characters placed at the beginning of each couplet. In some cases (e.g. *B. mendax*) our results imply that we should be able to assign specimens with reliable labels to these species from their collection locality alone, or from this evidence together with morphological evidence (e.g. characters of the female labrum Figs 15–20 and of the female corbicula Figs 21–23; or characters of the male genitalia Figs 24–55). Identifications from the key or from the figures should be checked against the species' diagnoses within the accounts of each species. Geographical distributions of the species have been mapped in Figs 56–67.
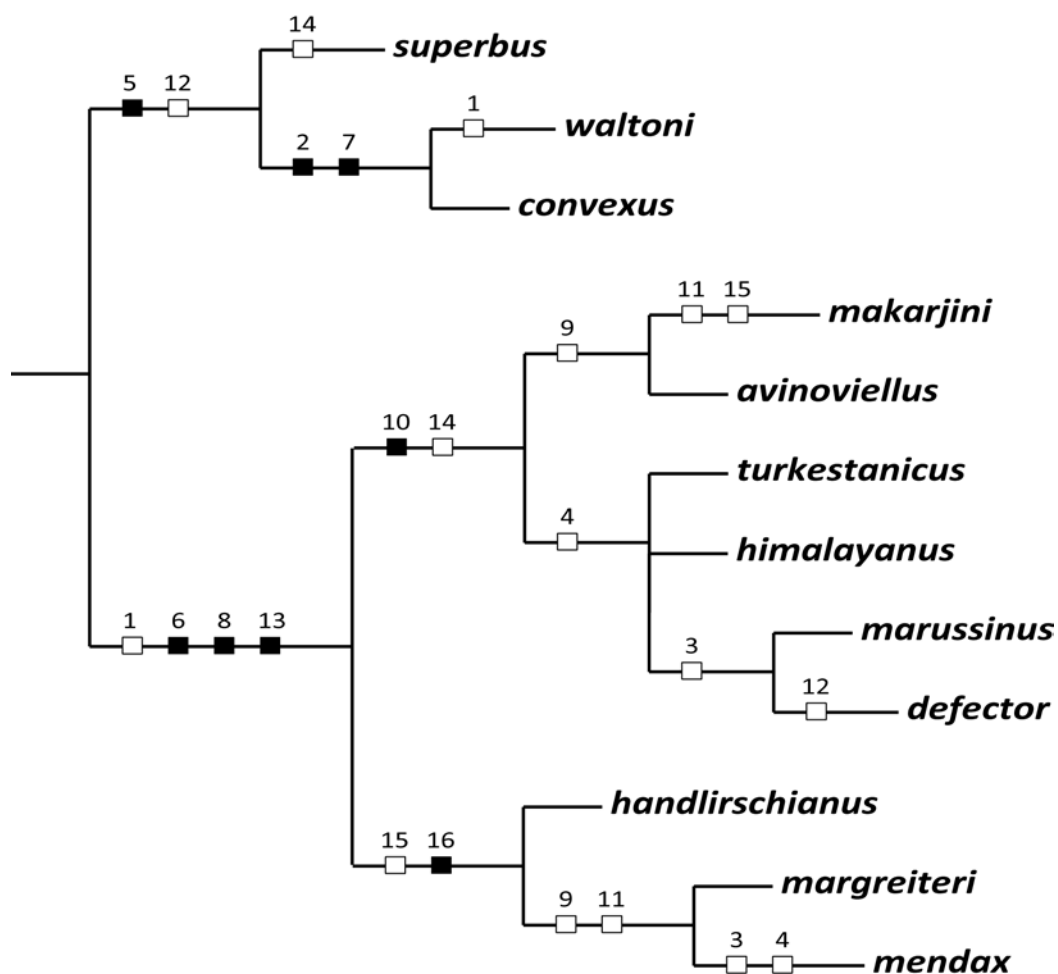


**FIGURE 14.** Assessing morphological characters by assessing groups of species within the subgenus *Mendacibombus* from three characters of hair colour (characters 1–3) and 13 characters of male genital morphology (characters 4–16) by maximum parsimony analysis with TNT. Numbers above the branches of the tree are the character numbers from Table 6; solid squares show unique character-state changes; and open squares show parallel or reverse character-state changes.

**Phylogeny and dating divergences.** The dated phylogeny for the species of the subgenus *Mendacibombus* estimated from the four genes COI, 16S, PEPCK, and opsin is shown in Fig. 68. Two billion MCMC generations with a 1% burn-in showed convergence on broadly stable traces with ESS for all trace statistics ≥ 97 (ESS values > 1000 for 95% of reported statistics).

Support for groups from combining the fast and slow genes is higher (Fig. 68: 5/11 supraspecific groups posterior $p > 0.8$, 8/11 $p > 0.66$) than for the single-gene tree (Fig. 11: 3/11 supraspecific groups posterior support $p > 0.8$, 4/11 $p > 0.66$), reflecting an improved consistency among the sample of four-gene trees. Including evidence from the slower nuclear genes increases support for particular alternative trees, especially for the older groups. The tree for four genes in Fig. 68 moves *B. superbus* into a larger *waltoni*-group (*superbus* + *waltoni* + *convexus*), but supports the same *turkestanicus*-group (*marussinus* + *avinoviellus* + *himalayanus* + *turkestanicus* + *defector*) and the same *mendax*-group (*margreiteri* + *handlirschianus* + *mendax*). But even with the four-genes used for Fig. 68, support for resolution within some of the younger species groups remains low, reflecting the need for more sequence data, especially from *B. marussinus* and *B. himalayanus*. Results from the analysis of morphology (Fig. 14) agrees with the four-gene tree (Fig. 68) in supporting the larger *waltoni*-group as well as the *mendax*-group. It does not support the same monophyletic *turkestanicus*-group, although only because morphology places *B. makarjini* inside an enlarged *turkestanicus*-group. We consider Fig. 68 to be the most reliable estimate of phylogeny for *Mendacibombus* species because it is based on the largest sample of data and has relatively high posterior support.

## Key to *Mendacibombus* species for females

1.      From the region including central and western Europe; hair of the thorax and metasomal T1–2 *either* entirely black, *or* with yellow hairs intermixed extensively with the black in some parts, *or if* with broad pure yellow bands *then both* the posterior half of T2 is broadly black (rarely with a narrow yellow fringe) *and* the thoracic dorsum has a broad black band between the wing bases *and* on the face any yellow hairs are concentrated in a patch at the antennal base whereas the hairs at the side of the clypeus are black . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **B. mendax**

-       From the region including Turkey and the Caucasus east to Kamchatka; hair of the thorax and metasomal T1–2 *either* with white or many white-tipped hairs at least in parts, *or if* with broad pure yellow bands *then either* the posterior half of T2 is predominantly yellow *or* the thoracic dorsum is nearly uniformly yellow *or* the face has pale and black hairs intermixed evenly throughout . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2 (1).  From the region including Turkey and the Caucasus east to Iran; hair of T3 black with very few or no orange hairs posteriorly, T4 orange, T6 orange with very few black hairs. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **B. handlirschianus**

-       From the region including Afghanistan east to Kamchatka; hair of T4 *either* black *and/or* with white hairs, *or if* T4 is extensively orange *then* T3 is black usually with many orange hairs in a narrow posterior fringe *or* T3 with orange hairs with white tips, T6 at least medially with many black hairs. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3 (2).  Hair of the thoracic dorsum *either* entirely black *or* black with white hairs evenly intermixed *or* black with white tips, T1 with black *or* black and orange hairs *or* with black and white hairs intermixed . . . . . . . . . . . . . . . . . . . . . . . . . . . . **B. waltoni**

-       Hair of the thoracic dorsum and T1 *either* with black hairs in part but with separate broad bands of yellow or white hairs *or* with yellow hairs nearly throughout . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4 (3).  Hair of T4–5 without long orange hairs and with at least a few black hairs scattered nearly throughout, *either* sometimes with white tips *or* intermixed with white hairs at least in part . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

-       Hair of T4–5 with long orange hairs at least in part and usually throughout, *and* without white hairs . . . . . . . . . . . . . . . . . 6

5 (4).  Hair of the thoracic dorsum anteriorly and T1 with many white hairs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **B. convexus**

-       Hair of the thoracic dorsum anteriorly and T1 with lemon-yellow hairs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **B. superbus**

6 (4).  Hair of the thoracic dorsum and T1 almost entirely yellow, at most with an obscure small spot of black hairs centrally between the wing bases . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7

-       Hair of the thoracic dorsum and T1 yellow and/or white, but *either* usually with a black band *or* sometimes an obvious large spot of black hairs between the wing bases . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

7 (6).  Wings nearly clear; labrum with a broad convex transverse ridge, broader than the basal depression (adjacent to the clypeus) (Fig. 15), clypeus in its central half with almost as many large as small punctures . . . . . . . . . . . . . . . . . . . . . . **B. marussinus**

-       Wings lightly clouded with brown; labrum with a narrow convex transverse ridge, narrower than the basal depression (adjacent to the clypeus) (Fig. 16), clypeus in its central half with few large punctures relative to the number of small punctures . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **B. avinoviellus** (part)

8 (6).  From the region including northern Asia, Central Asia, south to the Hindu Kush and almost to the Karakorum; hair of the thoracic dorsum always with anterior and posterior pale (yellow or white) bands, the black band between the wing bases usually entirely black, and the pale hair of the side of the thorax and T1–2 of the same colour as the pale dorsal thoracic bands, T6 laterally with orange hair . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

-       From the region including the Himalaya northwest to the Karakorum; hair of the thoracic dorsum *either* usually with the black band between the wing bases intermixed with pale hair *or* with the posterior of the dorsum (scutellum) at least intermixed with black hair, *or if* the pale thoracic bands are white *then* the hair of T1 is yellow, *or if* the pale thoracic bands are yellow *then either* the side of the thorax is a strongly contrasting white *or* T6 is entirely black . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12

9 (8).  Hindleg tibia with the posterior corbicular fringe of predominantly yellow or white hairs, sometimes orange at the base, with few or no dark hairs intermixed (Fig. 23); hair of the thoracic dorsum with the black band between the wing bases narrow, side

of the thorax usually extensively pale, but sometimes only in the upper third; labrum with the transverse ridge broad and low, in the median third subsiding weakly with scattered punctures but not distinctly interrupted (Fig. 17) . . . . . . . . . . . . . . . . . 10

- Hindleg tibia with the posterior corbicular fringe of black or orange hairs, hairs yellow or white at most only at the tips, with many dark hairs intermixed (Figs 21–22); hair of the thoracic dorsum with the black band between the wing bases usually broad, side of the thorax usually extensively black, but sometimes especially in workers pale throughout; labrum with the transverse ridge *either* in the median fifth subsiding and distinctly interrupted by punctures (Fig. 18) *or* consistently high convex and uninterrupted (Fig. 19) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

10 (9). Hindleg tibia with the posterior corbicular fringe predominantly yellow or white, any orange limited to close to the hair bases; side of the thorax in the lower third and the metasoma ventrally (S2–3) entirely pale . . . . . . . . . . . . . . . . . . . . *B. turkestanicus*

- Hindleg tibia with the posterior corbicular fringe extensively yellow or white, the hairs often orange in the basal half; side of the thorax in the lower third and the metasoma ventrally (S2–3) with at least some black hair . . . . . . . . . . . . . . . *B. makarjini*

11 (9). Labrum with the transverse ridge in the median fifth subsiding flattened and interrupted by many dense punctures overflowing from the broad basal depression (adjacent to the clypeus) (Fig. 18); hindleg tibia with all of the corbicular fringes usually black, any orange usually confined to the tips of the hairs, most often extensive on the mid-length hairs on the outer corbicular surface, but rarely with the fringes extensively orange (Fig. 21) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. defector*

- Labrum with the transverse ridge in the median fifth consistently high, convex and not strongly subsiding, shiny and with only a few scattered punctures (Fig. 19); hindleg tibia with the outer corbicular fringes (anteriorly and posteriorly, extending laterally from the outer surface) usually in part black especially anteriorly and proximally, the inner corbicular fringes (the long hairs anteriorly and posteriorly nearest the centre of the outer corbicular surface and often almost perpendicular to it) with many orange hairs especially posteriorly and the mid-length hairs on the outer corbicular surface orange or orange tipped (Fig. 22; the orange is less apparent for individuals from Qinghai and Kamchatka, sometimes more extensive for individuals from Mongolia, all regions in which *B. defector* is not known to occur) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. margreiteri*

12 (8). Wings lightly clouded with brown; labrum with a narrow high transverse ridge, narrower than the basal depression (adjacent to the clypeus), the transverse ridge slightly angled (V-shaped) between the two lateral ends, the ridge in the median third convex and not subsiding and often with few large punctures (Fig. 16) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. avinoviellus* (part)

- Wings nearly clear; labrum with a broad low transverse ridge, broader than the basal depression (adjacent to the clypeus), the transverse ridge nearly straight between the two lateral ends, the ridge in the median third subsiding weakly and with many large punctures (Fig. 20) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. himalayanus*


## Key to *Mendacibombus* species for males

1. Volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point with a raised curved ridge, usually with small teeth, just inside the inner margin, running for 0.3–0.5× the remaining distal length of the volsella (Fig. 36) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

- Volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin (Fig. 37) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

2 (1). Volsella distally terminating in a rounded right angle and barely curled back dorsally and not at all anteriorly (Fig. 38); hair of the anterior thoracic dorsum yellow . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. superbus*

- Volsella distally sharply acute (pointed) and curled back dorsally and anteriorly (Fig. 39); hair of the anterior thoracic dorsum black *or* black with white hairs intermixed . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3 (2). Gonostylus length 1.25× its greatest breadth (Fig. 40); penis-valve head (defined by an outer toothed flange) length 0.33× the penis-valve total length from its distal apex to the broadest point of the spatha (Fig. 40); hair of the anterior thoracic dorsum black and hair of metasomal T4–5 black *or* orange, although often all of these hairs have white tips . . . . . . . . . . . . *B. waltoni*

- Gonostylus length 2× its greatest breadth (Fig. 41); penis-valve head (defined by an outer toothed flange) length 0.25× the penis-valve total length from its distal apex to the broadest point of the spatha (Fig. 41); hair of the anterior thoracic dorsum and hair of metasomal T4–5 with a mixture of entirely white and entirely black hairs . . . . . . . . . . . . . . . . . . . . *B. convexus*

4 (1). Penis-valve inner shoulder located at 0.63× the penis-valve length from the distal end to the broadest point of the spatha (Fig. 42) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. defector*

- Penis-valve inner shoulder located at ≤ 0.5× the penis-valve length from the distal end to the broadest point of the spatha (Fig. 43) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

5 (4). Penis valve proximal to the outer shoulder > 2× as broad as the penis-valve head (defined by an outer toothed flange) (Fig. 44) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

- Penis valve proximal to the outer shoulder < 2× as broad as the penis-valve head (defined by an outer toothed flange) (Fig. 45) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

6 (5). Gonostylus distally strongly dorso-ventrally flattened and plate-like, thickness < 0.25× its own breadth (Fig. 46); wings light brown . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. avinoviellus*

- Gonostylus distally thick, thickness > 0.25× its own breadth (Fig. 47); wings nearly clear . . . . . . . . . . . . . . . . . . . . . . . . 7

7 (6). Gonostylus with the inner distal corner a right angle from both the inner and dorsal aspects (Fig. 48); thoracic dorsum between the wing bases with the hair usually entirely black; hair of T2 yellow with always at least a distinct black band along the posterior margin *or* T2 sometimes predominantly black . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *B. mendax*

- Gonostylus with the inner distal corner distinctly acute from both the inner and the dorsal aspects (Fig. 49); hair of the thoracic dorsum between the wing bases black but sometimes with many yellow or white hairs intermixed; hair of T2 yellow *or* white

with only a few black hairs along the posterior margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

8 (7). Gonostylus thick and nearly black, in dorsal aspect short and broad, 1.5× as long as its greatest breadth, the inner and outer lateral margins strongly diverging in the anterior proximal half, the penis-valve head (defined by an outer toothed flange) in dorsal aspect narrowing towards its distal end often (not always) gradually in its distal two thirds . . . . . . . . . . . . ***B. margreiteri***

- Gonostylus thin and brown, in dorsal aspect long and narrow, 2× as long as its greatest breadth, the inner and outer lateral margins nearly parallel in the anterior proximal half, the penis-valve head (defined by an outer toothed flange) in dorsal aspect narrowing only in its distal third . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***B. makarjini***

9 (5). Penis-valve breadth just proximal to the penis-valve head (defined by an outer toothed flange) 0.06× the penis-valve length from its distal apex to the broadest point of the spatha (Fig. 50) . . . . . . . . . . . . . . . . . . . . . . . . . . ***B. handlirschianus***

- Penis-valve breadth just proximal to the penis-valve head (defined by an outer toothed flange) 0.11× the penis-valve length from its distal apex to the broadest point of the spatha (Fig. 51) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .10

10 (9). Volsella with the apex narrowed, narrower than the adjacent penis-valve head (Fig. 52); hindleg tibia with the anterior and posterior fringes entirely yellow . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***B. turkestanicus***

- Volsella with the apex broad, broader than the adjacent penis-valve head (Fig. 53); hindleg tibia with the anterior and posterior fringes *either* black *or* with many black hairs, only rarely entirely yellow . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

11 (10).Gonostylus from the dorsal aspect rectangular, with a distinct outer distal corner (Fig. 54); hair of the thoracic dorsum between the wing bases *either* usually almost entirely black *or* occasionally yellow with many black hairs intermixed across the breadth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***B. himalayanus***

- Gonostylus from the dorsal aspect almost triangular, without a distinct outer distal corner but broadly rounded (Fig. 55); hair of the thoracic dorsum between the wing bases entirely yellow except in a central spot that sometimes has black hairs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***B. marussinus***


## Revision of the species of the subgenus MENDACIBOMBUS Skorikov

*Mendacibombus* Skorikov 1914:125, type-species *Bombus mendax* Gerstaecker by subsequent designation of Sandhouse 1943:572.
*Bombus (Mendacibombus)* Krüger 1917:62.


### 1. *Bombus superbus* (Tkalců)
(Figs 24, 38, 56, 69)

*Mendacibombus superbus* Tkalců 1968:22, type-locality citation 'Mongolei Monda'. Holotype queen by original designation MNHU examined, 'Mongolei, Monda' believed incorrect (probably Qinghai or Xizang, China). Note 1.
[*Bombus wagneri* Tkalců, 1968:24, published as a junior synonym.]
*Bombus (Mendacibombus) superbus* (Tkalců); P.H. Williams 1991:42; S.-F. Wang & Yao 1996:303; P.H. Williams 1998:99; P.H. Williams 2004:no. 29.

Note 1 (*superbus*). Tkalců's original description of the taxon *superbus* cites 'Mongolei Monda 6. 08 Weiske' as the type locality. The MNHU collection studied by Tkalců contains a queen that agrees with the original description and carries the labels: (1) white, printed 'Mongolei / Monda / 6. 08 / Weiske'; (2) white, handwritten by Friese '*Bombus* / *wagneri* / [female] 1909 Friese *Fr*. Det.' (H. Friese, unpublished); (3) maroon, printed 'Type'; (4) white, printed 'Zool. Mus. / Berlin'; (5) red, printed 'Holo- / typus.'; (6) white, handwritten by Tkalců '*HOLOTYPE* / *Mendacibombus* / *superbus Tk.* / [female] *Tkalců det.*'; (7) green, printed '*Mendacibombus* / MD# 338 det. PHW'; (8) red, printed 'HOLOTYPE [female] / *Mendacibombus* / *superbus* / Tkalců, 1968 / det. PH Williams 2012'; (9) white, printed '[female] *Bombus* / (*Mendacibombus*) / *superbus* / det. PH Williams 2012'. This specimen, which is complete, is regarded as Tkalců's holotype.

The type locality 'Mongolei / Monda' and the style of the printed label appear to refer to collections made by the E. Weiske 1908 expedition (Kerzhner 1972) near the relatively well known town of Mondy, Buryatia, near the Mongolian border (Russia, 51.67281°N 100.98458°E, 1300 m). A. Ebmer (in litt.) also points to the information on G. Potanin's itinerary in 1880 given by Komarov (1928) as evidence that these names both refer to the same place. However, the interpretation that the type locality of *B. superbus* is Mondy was challenged in the original publication by Tkalců (1968), because the spelling Monda was known to him for a locality in the mountains of western Nepal. A likely Nepalese site with this name could not be identified by us. The long hair of the holotype of *B. superbus* resembles the hair of other species from very high elevations (much higher than Mondy). This is consistent with the extreme habitat of the other known specimens of this species (IAR, MD#4110–4131; IZB,

MD#339–342), which are from above 4600 m in Qinghai and Xizang. The holotype specimen is in the H. Friese collection (MNHU, MD#338), a collection that is known to have a number of bumblebee specimens with dubious locality data (see the notes on the nominal taxa *rufitarsus* and *asellus* under *B. waltoni*). Ebmer (2008) has described how for other bees with 'Monda' labels, while in some cases they appear to refer genuinely to Mondy, in other cases these labels appear to be spurious later additions and he discussed how this might have arisen. Ebmer suggests that Friese described some of the material collected by the V. Roborovski and P. Kozlov expeditions of the 1890s and that some specimens from these expeditions ended up erroneously with 'Monda' labels. This seems likely in this case. Roborovski and Kozlov took part in expeditions that visited the eastern Qinghai-Tibetan plateau in the summers of 1879, 1880, 1884, 1894, and 1895 (Bretschneider 1981). Therefore we interpret the origin of the holotype and the type locality as most likely to have been on the Qinghai-Tibetan plateau. Even so, the precise type locality remains very uncertain and consequently no location for the holotype is shown on our map.

**Etymology.** The species is named from the Latin *superbus* for its resplendent ('prangend') or sumptuous ('prächtig') appearance according to the original (German) description.

**Taxonomy and variation.** This species shows a single colour pattern of the hair with little variation. This is the pattern in the original description, which is unique within the subgenus. All known specimens of the species have a yellow-banded and none has a white-banded colour pattern. The males from the Tanggula mountains (MD#339, 4131) have the yellow anterior collar of the thoracic dorsum narrower, barely reaching posteriorly to the tegula, and with many black hairs intermixed, and the metasomal terga 4–7 have many of the hairs white-tipped. The queens and workers are unusually large for species of this subgenus, although the males are similar in size to those of the other species. The form of the male genitalia is diagnostic.

**Diagnostic description.** Wings nearly clear. Hair long, uneven, and slightly sparse. *Female hair colour pattern:* (Fig. 69) generally black, the head sometimes with some yellow hairs dorsally posterior to the ocelli, bright yellow hair in a transverse band in almost the anterior half on the thoracic dorsum and extending laterally and ventrally to just below the wing bases, and on metasomal T1–2, although T2 with a few black hairs intermixed along the posterior margin, T3–6 predominantly black with some white tips or sometimes a few hairs entirely white (*cf.* all other *Mendacibombus* species). Midleg basitarsus with the hair predominantly orange, with long black or orange hairs arising from the outer surface in the proximal third (more apparent in workers than queens); hindleg tibia with the corbicular fringes black, the posterior fringe with some hairs with orange tips or distally some hairs entirely orange (more for queens than for workers); hindleg basitarsus with the hair predominantly orange, with the long posterior fringe orange. *Female morphology:* labrum with the basal depression very narrow, the transverse ridge very broad and low, medially subsiding but not interrupted, with large punctures in the median third, lateral tubercles with few punctures. T2 without a posteriorly-directed convexity of its median posterior edge (even for the queens, *cf. B. convexus*). *Male morphology:* beard of the mandible long, dense and black; genitalia (Fig. 24) with the volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point with a raised curved ridge, just inside the inner margin, running for 0.5× the remaining distal length of the volsella; volsella distally a rounded right angle and barely curled back dorsally and not at all anteriorly.

**Material examined.** 3 queens 22 workers 2 males, from China (Fig. 56: IAR, IZB, MNHU), with 7 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine grassland, at elevations 4800–(5167)–5220 m a.s.l.. A species of the high Qinghai-Tibetan plateau, known so far definitely only from the Hohxilshan (= Kekexili; collected 1990, X.-Z. Zhang) within the eastern Kunlun mountain system and from the Tanggulashan (collected 2014, Z.-Y. Miao, Figs 69, 70) on the Xizang-Qinghai border. This apparent rarity could be explained by the very limited sampling for bumblebees at the highest elevations in the central and northern Qinghai-Tibetan plateau, because access in this region is difficult, with few roads. In this case, the mapped distribution in Fig. 56 could be a small part of the species' true distribution, which could be broader, although patchy, at very high elevations. Alternatively, the map may be a more precise reflection of the species' true distribution, limited by aridity (in the Qiangtang semi-arid area: C.-Z. Wang *et al.* 2013) to a few small patches in the central and northern mountain groups where there are sufficiently large permanent streams to provide water to sustain flower-rich grassland reliably throughout every summer (P.H. Williams, Bystriakova, *et al.* 2015). For example, suitable patches may occur around the large ice caps further west in the Tanggulashan. *Bombus superbus* may be one of the few truly endemic bumblebee species of the extreme habitats of the high Qinghai-Tibetan plateau. This species overlaps with *B. waltoni* in the Hohxil and in the Tanggula mountains.

**FIGURES 15–23.** Morphology of the female (queen) head from the ventral aspect (labrum and mandibles): 15, *B. marussinus* queen, Pakistan MD#482; 16, *B. avinoviellus* queen, India MD#598; 17, *B. turkestanicus* queen, Tajikistan MD#320; 18, *B. defector* queen, Kyrgyzstan MD#1080; 19, *B. margreiteri* queen, Mongolia MD#319; 20, *B. himalayanus* queen, India MD#453. Morphology of the female (queen) left hindleg tibia from the left lateral aspect, dorsal at the top of the image, anterior to the left: 21, *B. defector*, China MD#1251; 22, *B. margreiteri*, Mongolia MD#319; 23, *B. turkestanicus*, Kyrgyzstan MD#324.

**FIGURES 24–35.** Morphology of the male genitalia for species of the subgenus *Mendacibombus* from the dorsal aspect, anterior to the left of the image, posterior to the right: 24, *B. superbus*, China MD#339; 25, *B. waltoni*, China MD#216; 26, *B. convexus*, China MD#215; 27, *B. makarjini*, Kazakhstan MD#1240; 28, *B. marussinus*, Pakistan MD#408; 29, *B. avinoviellus*, India MD#404; 30, *B. himalayanus*, India MD#426; 31, *B. turkestanicus*, China MD#351; 32, *B. defector*, Kyrgyzstan MD#367; 33, *B. margreiteri*, China MD#294; 34, *B. handlirschianus*, Russia MD#835; 35, *B. mendax*, Spain MD#689.

33 *margreiteri*    34 *handlirschianus*    35 *mendax*

**FIGURES 24–35**. (Continued)

**Food plants.** (Asteraceae) *Saussurea tibetica* C. Winkler; (Gentianaceae) *Gentiana algida* Pall.; (Leguminosae) *Hedysarum pseudastragalus* Ulbrich (Z.-Y. Miao: 16.viii.2014, in the Tanggula mountains 5220 m, Xizang, China, Fig. 70).

**Behaviour.** No records.


## 2. *Bombus waltoni* Cockerell
(Figs 1, 25, 36, 40, 57)

[*Bombus mendax* Gerstaecker; Morawitz 1887:199, misidentification.]

<*Bombus mendax*> subsp. *chinensis* Skorikov 1910b(February):330 (not of Morawitz 1890:352, = *B. chinensis* (Morawitz)), type-locality citation (Cyrillic) '[Mountains of Sining and Burkhan Budda]'. **Lectotype** queen by present designation ZISP examined, (Cyrillic) '[Sinin mts]' (Xining range, Qinghai, China). Note 1. Synonymy with *Bombus waltoni* Cockerell implied when *Bombus waltoni* Cockerell was synonymised with *Bombus mendax* ssp. *chinensis* Skorikov by Skorikov in Cockerell (1911).

*Bombus waltoni* Cockerell 1910(September):239, type-locality citation 'Khamba Jong, Sikkim'. Holotype queen by monotypy NHM examined, 'Khamba Jong' (Gamba Dzong, Xizang, China). Note 2.

*Bombus waltoni* Cockerell; Cockerell 1911:176; Wu 1941:281.

[*Bombus waltoni* var. *kozloviellus* Skorikov 1912:608, infrasubspecific.]

*Bombus rufitarsis* Friese 1913:85, type-locality citation 'Zentralasien'. **Lectotype** queen (not a worker) MNHU examined, 'Mongolei, Monda' believed incorrect (probably Qinghai, China). Note 3. Synonymised with *Bombus waltoni* Cockerell by Skorikov (1914).

*Mendacibombus waltoni* (Cockerell); Skorikov 1914:125; Skorikov 1923:149.

*Bombus asellus* Friese 1924:438, type-locality citation 'Mongolei bei Tippeti' believed incorrect (probably Qinghai, China). Syntype workers and male MNHU not found by F. Koch and not seen (but taxon identity not in doubt). Regarded as conspecific with *Bombus waltoni* Cockerell by Bischoff (1936).

*Bombus (Mendacibombus) waltoni* Cockerell; Richards 1930:633; Tkalců 1961:369; S.-F. Wang 1982:430; P.H. Williams 1991:42; S.-F. Wang 1992:1424; S.-F. Wang & Yao 1996:303; P.H. Williams 1998:100; P.H. Williams 2004:no. 30; Burger *et al.* 2009:462; Cameron *et al.* 2007:165; P.H. Williams *et al.* 2009:129; P.H. Williams *et al.* 2010:124; An *et al.* 2011:6; An *et al.* 2014.

*Mendacibombus chinensis* (Skorikov); Skorikov, 1931:fig. 20.

*Bombus (Mendacibombus) waltoni chinensis* Skorikov; Bischoff 1936:17.


Note 1 (*chinensis*). Skorikov's original description of the taxon *chinensis* cites two mountain ranges (Xining and Burhan Budai mountains) distant from one another (and both credible) as the type locality of the taxon

*chinensis*, so that there is likely to have been more than one original syntype. The ZISP collection studied by Skorikov contains a queen that agrees with the original description and carries the labels: (1) gold disc; (2) white, handwritten (Cryrillic) '[[illegible] Sinin mts / [before]] 30.v.90 / [Gr. Grzmailo]'; (3) white, printed (Cyrillic) '[*k. Skorikova*]'; (4) red, handwritten '*Lectotypus Bombus / mendax subsp. / chinensis Skor.* / design. *Podbolotsk.*' (M. Podbolotskaya, unpublished); (5) green, printed '*Mendacibombus* / MD# 3521 det. PHW'; (6) red, printed 'LECTOTYPE [female] / *Bombus mendax* ssp. / *chinensis* / Skorikov, 1910 / det. PH Williams 2012'; (7) white, printed '[female] *Bombus* / (*Mendacibombus*) / *waltoni* / det. PH Williams 2012'. This specimen, which is complete, is regarded as one of Skorikov's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

Note 2 (*waltoni*). The original publication specifies that there was only one type specimen of *waltoni* by Cockerell, so the single specimen in the NHM collection labeled 'Khamba Jong' is regarded as the holotype by monotypy (ICZN, 1999: Article 73.1.2).

Note 3 (*rufitarsis*). Friese's original description of the taxon *rufitarsis* lists four workers, although the queen described here is labelled as a worker by Friese. The MNHU collection studied by Friese contains a queen that agrees with the original description and carries the labels: (1) white, printed 'Mongolei / Monda / 6. 08 / Weiske'; (2) white, handwritten by Friese '*Bombus* / *rufitarsis* / [worker] 1909 *Fr.* Det.'; (3) maroon, printed 'Type'; (4) white, handwritten by Friese '*B. ?* / *pyrosoma* / [worker] 1900 Friese *Fr.* Det.'; (5) white, handwritten by Tkalců '*LECTOTYPE* / *Bombus* / *rufitarsis Friese* / [female] *Tkalců det.*' (B. Tkalců, unpublished); (6) white, printed 'Zool. Mus. / Berlin'; (7) green, printed '*Mendacibombus* / MD# 3538 det. PHW'; (7) red, printed 'LECTOTYPE [female] / *Bombus* / *rufitarsis* / Friese, 1913 / det. PH Williams 2012'; (8) white, printed '[female] *Bombus* / (*Mendacibombus*) / *waltoni* / det. PH Williams 2012'. This specimen, which is complete, is regarded as one of Friese's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name. For the same reasons as given in note 1 on *B. superbus*, we interpret the origin of the lectotype and the type locality as most likely to have been in Qinghai. Even so, the precise type locality remains very uncertain and consequently no location for the lectotype is shown on our map.

**Etymology.** The species is named after H. Walton, the medical officer during the 1904 British expedition known as the Tibet Frontier Commission with F. Younghusband as Commissioner. According to the specimen labels, in 1904 Walton collected at least two specimens of the species between Phari and Gyangzê (NHM). In July 1903 the previous expedition of the Commission, which was also led by Younghusband, visited Gamba Dzong (Hopkirk 1982), just north of Sikkim. This is the locality where the type specimen was collected, but it is unclear who collected the holotype.

**Taxonomy and variation.** This species shows two principal colour patterns of the hair: extensively black, but with either an extensive orange tail, or with a black tail. The orange-tailed pattern matches the original description of the taxon *waltoni*. Both colour patterns are unique within the subgenus. No specimens of this species have distinct pale bands on the thorax and none has yellow hair anywhere on the body. Specimens of the species from the Kunlun (MD#3868, 3869) and Tanggula (MD#4132–4137) mountains have the hair of the thoracic dorsum and T1 black and of T2–5 orange, and are unusual for the species because the hairs are mostly not white-tipped. A specimen from the far west of the range in Ladakh (MD#4023) has no white hairs at all and T2 is predominantly orange. In the east and south, individuals of this species usually have many white-tipped hairs and often have intermixed white hairs (e.g. MD#193). Sometimes T1 has many white hairs intermixed and T2–5 may have white hairs in the posterior quarter of each tergum (e.g. MD#1284). Some males (and according to Friese's description, some workers, although we have not seen examples of these) in the northern and eastern areas of the distribution have little or no orange hair on the metasomal terga (Friese's taxon *asellus*), although all males share the same form of the genitalia and similar COI sequences (Fig. 13: the orange-tailed taxon *waltoni s. str.* MD#1482 and the black-tailed taxon *asellus* MD#300). The form of the male genitalia is diagnostic.

COI sequences show two principal groups of haplotypes, although these do not coincide with known morphological or colour-pattern differences. The majority of individuals are in one group. The second divergent group (differing in at least 12 nucleotides) of three individuals (MD#267, 1482, 1483) is from a narrow region in the south, associated with the Himalaya (from Nepal and from the Yadong region of Xizang, the region of the type of the taxon *waltoni s. str.*). The latter sequences are all short, perhaps because there are also nucleotide changes in the primer region. When fresh material becomes available from the Himalayan population and a specific primer can be developed, this group needs to be checked in case it represents a separate cryptic species.

36 waltoni

37 mendax

38 superbus

39 convexus

40 waltoni

41 convexus

**FIGURES 36–55.** Morphology of parts of the male genitalia from the dorsal aspect of the left side, anterior to the left of the image, posterior to the right, white bars indicating morphological characters referred to in the key to males: 36, *B. waltoni*; 37, *B. mendax*; 38, *B. superbus*; 39, *B. convexus*; 40, *B. waltoni*; 41, *B. convexus*; 42, *B. defector*; 43, *B. mendax*; 44, *B. mendax*; 45, *B. turkestanicus*; 46, *B. avinoviellus*; 47, *B. mendax*; 48, *B. mendax*; 49, *B. makarjini*; 50, *B. handlirschianus*; 51, *B. himalayanus*; 52, *B. turkestanicus*; 53, *B. himalayanus*; 54, *B. himalayanus*; 55, *B. marussinus*.

42 *defector*



43 *mendax*
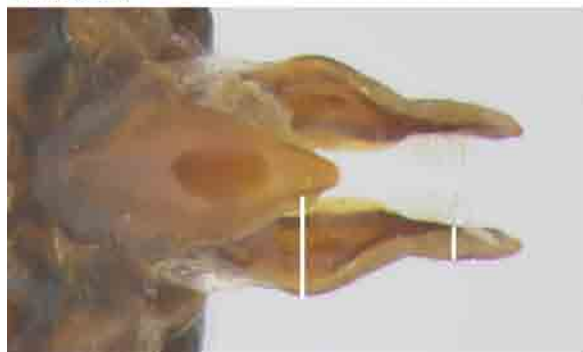


44 *mendax*



45 *turkestanicus*



46 *avinoviellus*



47 *mendax*



48 *mendax*



49 *makarjini*

**FIGURES 36–55**. (Continued)

50 *handlirschianus*

51 *himalayanus*

52 *turkestanicus*

53 *himalayanus*

54 *himalayanus*

55 *marussinus*

**FIGURES 36–55**. (Continued)

**Diagnostic description.** Wings nearly clear. Hair long, uneven and slightly sparse. *Female hair colour pattern:* generally black, but the thoracic dorsum often with many grey-white hairs intermixed with black, on the side of the thorax and on T1 and on T2 anteriorly the black hairs often have white tips (*cf.* all other *Mendacibombus* species), on T2 posteriorly and on T3–6 the predominantly orange hairs often have white tips, T6 with few black hairs. Hindleg tibia with the corbicular fringes with black and orange hairs, many with white tips. *Female morphology:* labrum with the basal depression narrow, the transverse ridge very broad and high, medially not

subsiding or interrupted and in the median third shining with very few scattered large punctures, lateral tubercles almost without punctures. T2 at most (in queens) with only a very subtle posteriorly-directed convexity of its median posterior edge (*cf. B. convexus*). *Male morphology*: beard of the mandible long, dense and black; genitalia (Fig. 25) with the volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point with a raised curved ridge, often with small teeth, just inside the inner margin, running for 0.5× the remaining distal length of the volsella; volsella distally sharply acute (pointed) and curled back dorsally and anteriorly. Gonostylus length 1.25× its greatest breadth. Penis-valve head length 0.33× the length of the penis valve distal to the broadest point of the spatha.

**Material examined.** 29 queens 296 workers 56 males, from China, India, and Nepal (Fig. 57: IAR, INHS, IZB, MNHU, MSI, NHM, NME, OLL, PW, RMNH, SC, YT, ZISP), with 14 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine grassland, at elevations 2604–(3927)–5220 m a.s.l.. A species of the east Qinghai-Tibetan plateau, in the east Himalayan, Hengduan, and Qinghai-Gansu mountains, including the Tanggula Shan, Kunlun Shan, Burhan Budai Shan, Qinghai Nan Shan, Qiliang Shan, and Min Shan, but much rarer in the western Himalaya. The lack of records in the northwest Tibetan plateau (Fig. 57) may at least in part reflect a lack of sampling (see the comments on *B. superbus*) or may reflect a true absence (P.H. Williams, Bystriakova, *et al.* 2015) from a semi-arid region (the Qiangtang plateau, although modelling climate suitability shows that areas near the centre near Siling lake might be suitable). Compared to *B. convexus*, distributions of the two species overlap broadly, but *B. waltoni* extends further to the north and west and tends to occur at higher elevation (and it is uncommon for the two species to occur together at a site). *Bombus waltoni* replaces the western *B. himalayanus* in the wetter meadows of the higher alpine zone of the eastern Himalaya, where it overlaps with *B. superbus* in the Hohxil and the Tanggula mountains. Regional distribution maps are available for Sichuan (P.H. Williams *et al.* 2009), Gansu (An *et al.* 2011; An *et al.* 2014), and Nepal (P.H. Williams *et al.* 2010).

**Food plants.** Williams *et al*. (2009), An *et al*. (2011; 2014).

**Behaviour.** Mate-searching males perch on bare patches of ground or low bushes and pursue other bees that fly past before the males return to the same perch (PW: Fig. 1, 5.viii.2002, 3764 m Aba-Hongyuan road, Sichuan, China; 29.viii.2009, 3914 m Diebu, Gansu, China).

### 3. *Bombus convexus* Wang
(Figs 2, 26, 39, 41, 58)

*<Bombus> lugubris* Morawitz 1880:339 (not of Kriechbaumer 1870:159, = *B. barbutellus* (Kirby) *s. l.*), type-locality citation 'Gan-su'. Holotype worker by monotypy ZISP examined, (Cyrillic) '[Gansu]' (but probably actually Qinghai, China). Synonymised with *Bombus convexus* Wang by Williams (1991). Note 1.
*Bombus lugubris* Morawitz; Morawitz 1881:243; Wu 1941:281.
*Mendacibombus lugubris* (Morawitz); Skorikov 1923:149; Skorikov, 1931:213.
*Bombus (Mendacibombus) lugubris* Morawitz; Bischoff 1936:17; Panfilov 1957:235; Tkalců 1961:369.
*Bombus (Mendacibombus) convexus* Wang, 1979:190, type-locality citation (Chinese) '[Xizang: Markam]'. Holotype queen by original designation IZB examined, (Chinese) '[Markam]' (Xizang, China).
*Bombus (Mendacibombus) convexus* Wang; S.-F. Wang 1982:429; Yao & Wang 2005:890; P.H. Williams 1991:42; S.-F. Wang 1992:1424; P.H. Williams 1998:100; P.H. Williams 2004:no. 26; Cameron *et al.* 2007:165; P.H. Williams *et al.* 2009:130; An *et al.* 2011:5; An *et al.* 2014.

Note 1 (*lugubris*). The original publication specifies that there was only one type (worker) specimen of the taxon *lugubris* Morawitz, so the worker in the ZISP collection is regarded as the holotype by monotypy (ICZN, 1999: Article 73.1.2).

**Etymology.** The species is named from the Latin *convexus* for 'rounded', a reference to a pronounced convexity or rounded posterior projection of the median posterior edge of metasomal T2 in the original description.

**Taxonomy and variation.** This species shows effectively a single colour pattern of the hair with little variation. This is the pattern in the original description, which is unique within the subgenus. All specimens have a white-banded and none has a yellow-banded colour pattern. The form of the female median posterior edge of T2 (although slightly variable) and of the male genitalia are diagnostic.

**Diagnostic description.** Wings nearly clear. Hair long, uneven and sparse. *Female hair colour pattern:*

generally black, but with white hair intermixed especially as short hairs on the face, intermixed in a transverse band anteriorly on the thoracic dorsum and extending laterally and ventrally without black hairs to the midleg base, in a lateral patch posteriorly on the thoracic dorsum (lateral patch on the scutellum, metanotum, and propodeum, so that the thoracic dorsum between the wing bases has the hair entirely black), on T1 and anteriorly on T2, and intermixed on T4–6 (*cf.* all other *Mendacibombus* species). Hindleg tibia with the corbicular fringes black, often with a few hairs with orange or white tips. *Female morphology:* labrum with the basal depression narrow, the transverse ridge moderately broad and high, medially not subsiding or interrupted and in the median third with scattered large punctures, lateral tubercles with a few scattered small punctures. T2 usually with a posteriorly-directed convexity of its median posterior edge, affecting a quarter of its breadth, especially pronounced in queens, for which there may be edge concavities and even slight pre-marginal depressions lateral to the convexity. *Male morphology*: beard of the mandible long, dense and black, but the short hairs and a few of the long hairs brown; T2 and sometimes T3 with posteriorly-directed convexities of their median posterior edge, affecting a quarter or less of their breadth. Genitalia (Fig. 26) with the volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point with a raised curved ridge, often with small teeth, just inside the inner margin, running for 0.3× the remaining distal length of the volsella; volsella distally sharply acute (pointed) and curled back dorsally and anteriorly. Gonostylus length 2× its greatest breadth. Penis-valve head length 0.25× the length of the penis valve distal to the broadest point of the spatha.

**Material examined**. 6 queens 296 workers 51 males, from China (Fig. 58: AMNH, IAR, IZB, NHM, PW, SC, USNM, YT, ZISP, ZX), with 6 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution**. Flower-rich alpine and subalpine grassland, at elevations 2196–(3449)–4500 m a.s.l.. A species of the east Qinghai-Tibetan plateau, in the east Himalayan, Hengduan, and Qinghai-Gansu mountains, including the Min Shan and Qilian Shan. Compared to *B. waltoni*, distributions of the two species overlap broadly, but *B. convexus* extends less far to the north and west and tends to occur at lower elevation (and the two species rarely occur together at a site). *Bombus convexus* replaces the western *B. avinoviellus* in the lower alpine zone and upper forest wet meadows of the eastern Himalaya, where it appears to be rare. Regional distribution maps are available for Sichuan (P.H. Williams *et al.* 2009) and Gansu (An *et al.* 2011; An *et al.* 2014).

**Food plants**. Williams *et al.* (2009), An *et al.* (2011; 2014).

**Behaviour**. Mate-searching males perch on bare patches of ground and pursue other bees that fly past before the males return to the same perch (PW: Fig. 2, 29.viii.2009, 3339 m Diebu, Gansu, China).

## 4. *Bombus makarjini* Skorikov
(Figs 27, 49, 59)

<*Bombus mendax*> subsp. *makarjini* Skorikov 1910b:329, type-locality citation (Cyrillic) '[East Pamir]'. **Lectotype** queen by present designation ZISP examined, (Cyrillic) '[Pamir]' (Pamir, Tajikistan). Note 1.
[*Bombus mendax macarjini* Skorikov; Reinig 1930:102; Reinig 1932b:163, incorrect subsequent spellings.]
[*Bombus mendax marcajini* Skorikov; Reinig in Bischoff 1931:862 footnote, incorrect subsequent spelling.]
[*Bombus (Mendacibombus) macarjini* Skorikov; Reinig 1932a:258, incorrect subsequent spelling.]
[*Bombus marcajini* Skorikov; Reinig 1934:172, incorrect subsequent spelling.]
[*Bombus (Mendacibombus) makaryini* Skorikov; Panfilov 1957:236, incorrect subsequent spelling.]
*Bombus (Mendacibombus) makarjini* Skorikov; Panfilov 1962:195; P.H. Williams 1991:15,40; P.H. Williams 1998:99.

Note 1 (*makarjini*). Skorikov's original description of the taxon *makarjini* cites the type locality as east Pamir. The ZISP collection studied by Skorikov contains a queen that agrees closely with the original description and carries the labels: (1) white, printed (Cryrillic) '[[pass] Koytye-zyek, / [Pamir range] 2600 mt. / *Makarin*] 19vi09.'; (2) white, printed (Cyrillic) '[*k. Skorikova*]'; (3) red, handwritten '*Lectotypus Bombus / mendax subsp. / makarjini Skor.* / design. *Podbolotsk.*' (M. Podbolotskaya, unpublished); (4) green, printed '*Mendacibombus* / MD# 3520 det. PHW'; (5) red, printed 'LECTOTYPE [female] / *Bombus mendax* ssp. / *makarjini* / Skorikov, 1910 / det. PH Williams 2012'; (6) white, printed '[female] *Bombus* / (*Mendacibombus*) / *turkestanicus* / det. PH Williams 2012'. This specimen, which lacks the last four joints of the left hindleg tarsus, is regarded as one of Skorikov's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

Another queen was examined on loan from the ZISP collection in 1984 (MD# 737), with labels: (1) white, handwritten (Cyrillic) '[[Pass] Mas 4000 m / Pamir 30.vi.09 / Makarin]'; (2) white, printed (Cyrillic) '[*k.*

*Skorikova.*]'; (3) red, part handwritten '*Paralectotypus Bombus / mendax subsp. / makarjini Sko /* design. *Podbolotsk*' (M. Podbolotskaya, unpublished). This specimen is interpreted as a syntype of the taxon *makarjini* and is designated here as a paralectotype of the taxon *makarjini*. This specimen resembles *B. defector* in the colour pattern of the hair, although *B. defector* is not known to occur in the Pamir. The specimen was unavailable for its morphology to be checked in this study.

**Etymology.** The species is named after A.G. Makarjin, who collected the lectotype specimen in the Pamir in 1909 (see also the type data for *B. defector, B. marussinus*). He collaborated with A.G. Jakobson, the brother of the G.G. Jakobson (A. Byvaltsev, in litt.) who collected other *Mendacibombus* types in the Himalaya (see below on *B. himalayanus, B. avinoviellus*).

**Taxonomy and variation.** The interpretation of this species is based here on DNA, on the form of the male genitalia, and on colour pattern. It is the least well characterized species in the subgenus because of a lack of material, especially of recent material that can be sequenced. Our concept disagrees with earlier concepts diagnosed originally in terms of the colour pattern of the hair (Skorikov, 1910b). The species appears to be more variable and less easily diagnosed by colour pattern (*cf. B. turkestanicus, B. margreiteri*) than was originally understood.

Skorikov (1910b) described queens from the Pamir (Tajikistan) with a colour pattern (corbicula framed with yellow, grey, or light rusty hairs) and with the ventral side of the metasoma (S1–4) with black hair. The lectotype queen (MD#3520) has the pale bands greyish and scarcely cream. A queen with a similar greyish colour pattern, pale corbicular fringes, and black hairs on S2–3 from Uzbekistan (but labelled 'Tadzikistan', MD#330) and another from Kazakhstan (but labelled 'Kirgyzstan', MD#4101) yielded COI sequences that differ from one another in just one base pair and which are strongly divergent from the other species (Figs 11, 12). Queens from southern Xinjiang (MD#3563, 4108) failed to sequence. Another queen (MD#3562) from the same region gave a sequence of just 96 bp, although this part of the sequence does not include any known diagnostic positions for this species (Table 5). Females show varying degrees of replacement of yellow hair with black on the lower side of the thorax near the midleg base, and on S2–3. All of these specimens are currently indistinguishable from one another in any substantial morphological characters. Associated by us with these females are three males (MD#1240, 3519, 4403) with distinctive genitalia (Fig. 27), one of which (MD#3519) has a COI sequence closely matching the COI sequences from females (MD#330, 4101). These males are broadly similar in the form of the genitalia to the genitalia ascribed to this species by Skorikov (1931: his fig. 18). Skorikov's drawing differs in showing the gonostylus as slightly broader and with the sides slightly diverging in the proximal half (more like *B. margreiteri*). However, Skorikov's illustration also shows: that (1) the spatha is broad with sinusoidal rather than straight converging sides; and that (2) the penis valve has a pronounced inner shoulder. Therefore his illustration is likely to be of *B. makarjini* as understood here.

**Diagnostic description.** Wings nearly clear. *Female hair colour pattern:* generally black, but with pale hair (grey, cream-white, or yellow) over most of the face or at least in a large patch below the base of the antenna with variable amounts of black intermixed or covering the outer side of the face and above the antenna, in a small patch on the vertex of the head, in a transverse band anteriorly on the thoracic dorsum and extending laterally and ventrally from at least one third to two thirds of the way down the side of the thorax towards the midleg base (*cf. B. turkestanicus*), in a transverse band posteriorly on the thoracic dorsum (scutellum; so the thoracic dorsum between the wing bases has the hair entirely black), on T1–2, although T2 with a few black hairs intermixed along the posterior margin, orange hair on T3 as a posterior fringe, and throughout on T4–6, T6 without many obvious black hairs, with black hairs on S2–3 or rarely S1–4 (*cf. B. turkestanicus*). Hindleg tibia with the corbicular fringes extensively yellow or grey (the hairs often orange in their basal half), the fringes with a few hairs black intermixed (*cf. B. turkestanicus, B. margreiteri, B. defector*). *Female morphology:* labrum with the basal depression narrow, the transverse ridge just broader medially than the basal depression, in the median third subsiding slightly but not clearly or abruptly interrupted, with many scattered medium punctures, the lateral tubercles with only a few punctures (*cf. B. margreiteri, B. defector*). Clypeus in its central half with very few punctures but some of them large (*cf. B. margreiteri, B. defector*). *Male morphology:* genitalia (Fig. 27) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin. Gonostylus brown (Fig. 49), distally as thick as 0.25× its own breadth, the inner distal corner distinctly acute from both the inner and the dorsal aspects, in dorsal aspect long and narrow, 2× as long as its greatest breadth, the inner and outer lateral margins nearly parallel in the anterior proximal half. Penis-valve inner shoulder located at ≤ 0.5× the length of the penis valve from the distal end to the broadest point of the spatha.
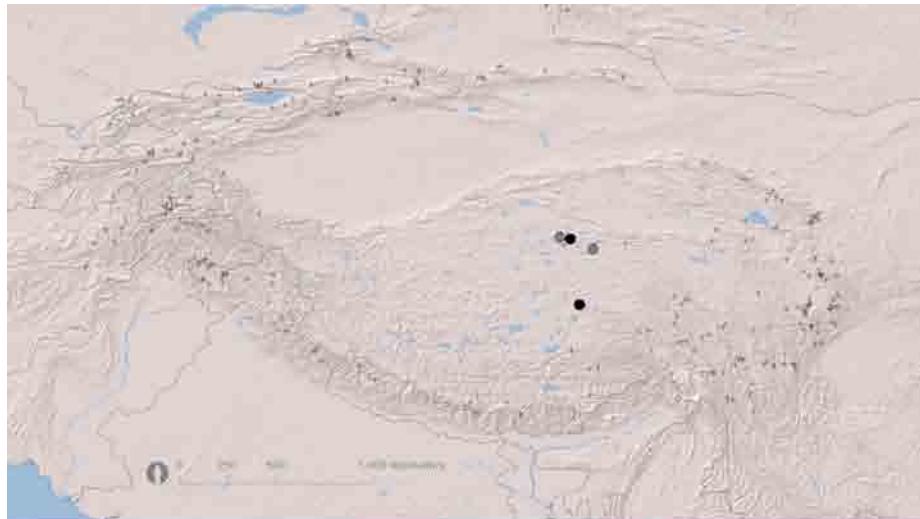
**56** *superbus*
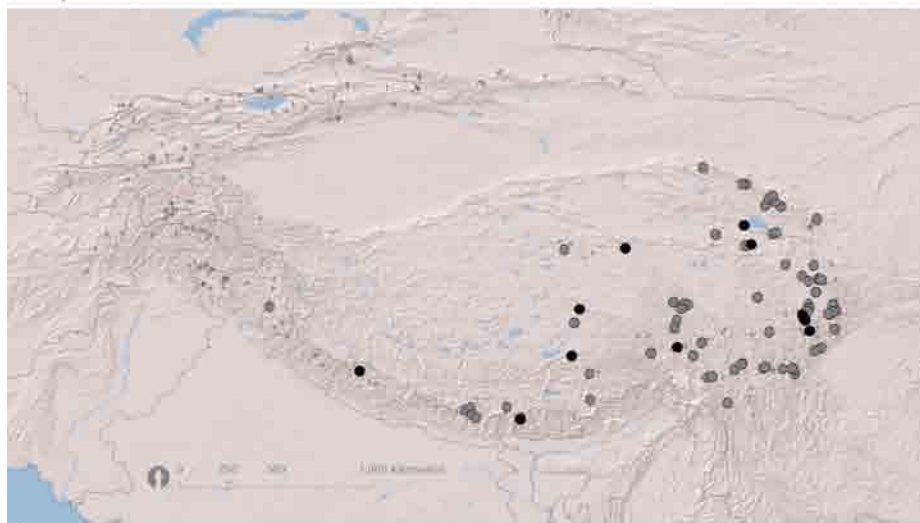


**57** *waltoni*
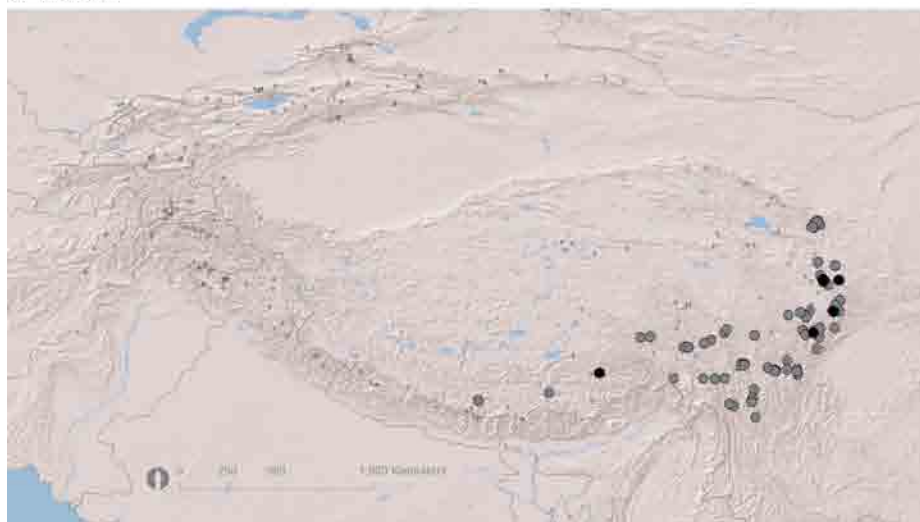


**58** *convexus*

**FIGURES 56–67**. Maps of the global distributions of species of the subgenus *Mendacibombus* from the material examined, with grey spots for specimen records and black spots for the samples with COI sequences (each species is unknown from regions outside the map boundaries shown); grey crosses for records of all species of *Mendacibombus* combined. Relief map with hill shading, Cartesian orthonormal projection, grey lines show borders to national administration according to UN maps, north at the top of the map. Image created in ArcGIS using World_Shaded_Relief basemap © 2014 Esri.
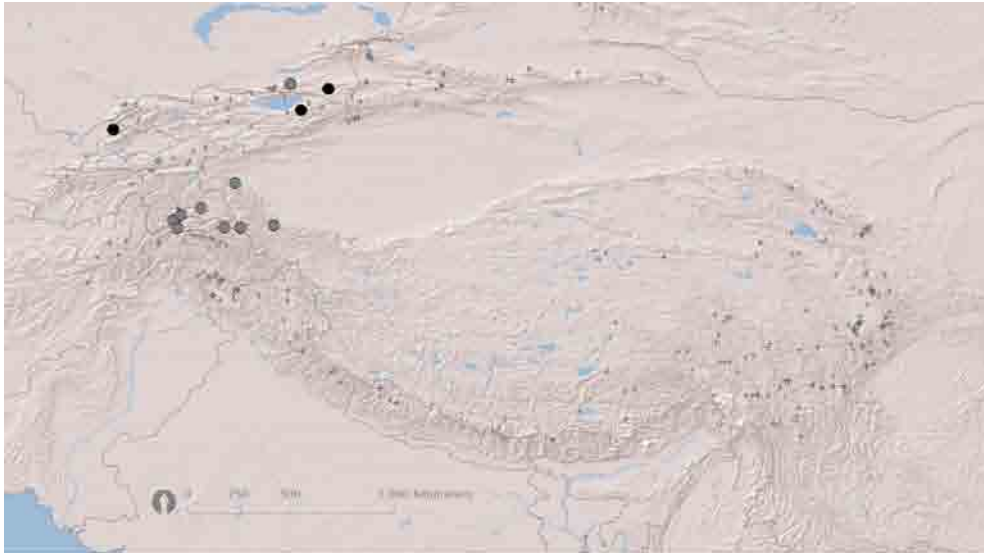
59 *makarjini*
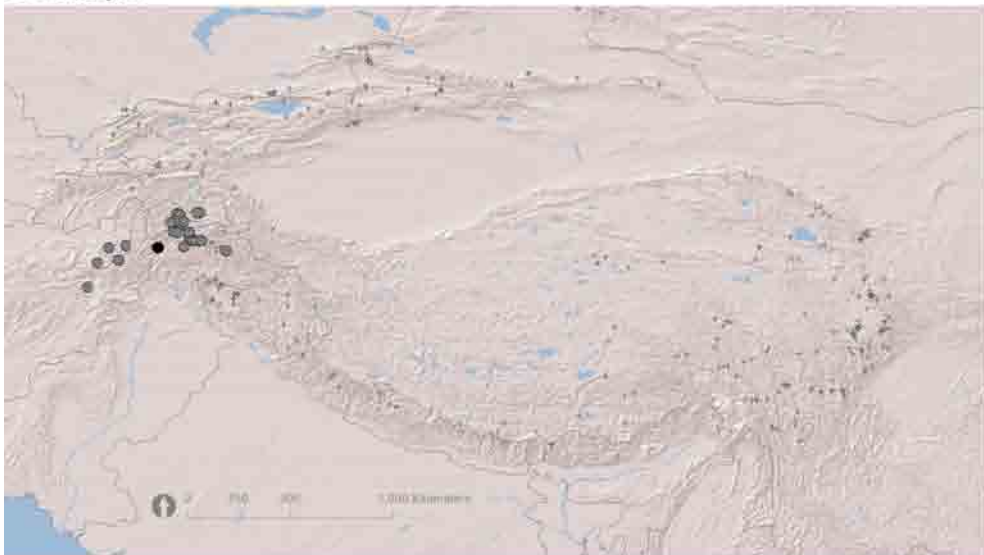


60 *marussinus*
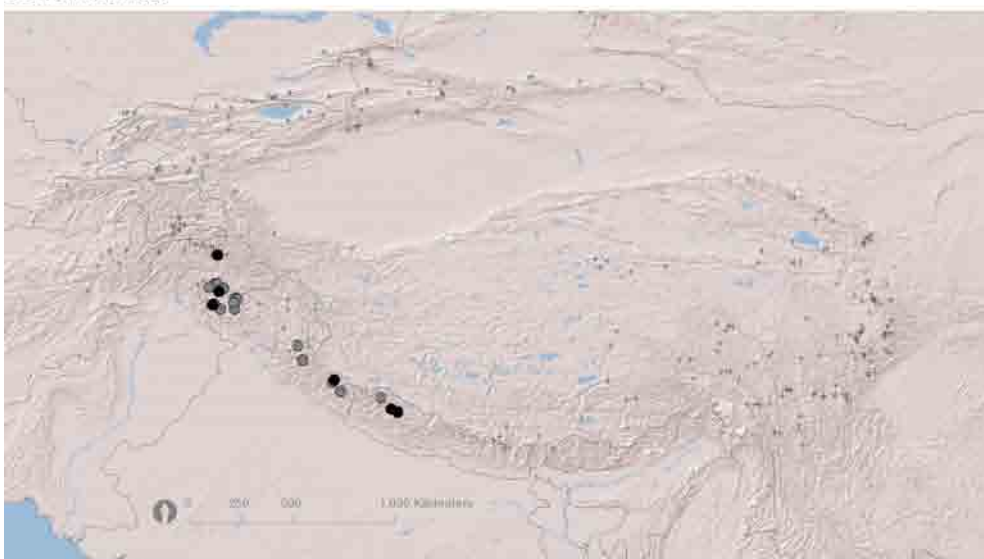


61 *avinoviellus*

**FIGURES 56–67**. (Continued)
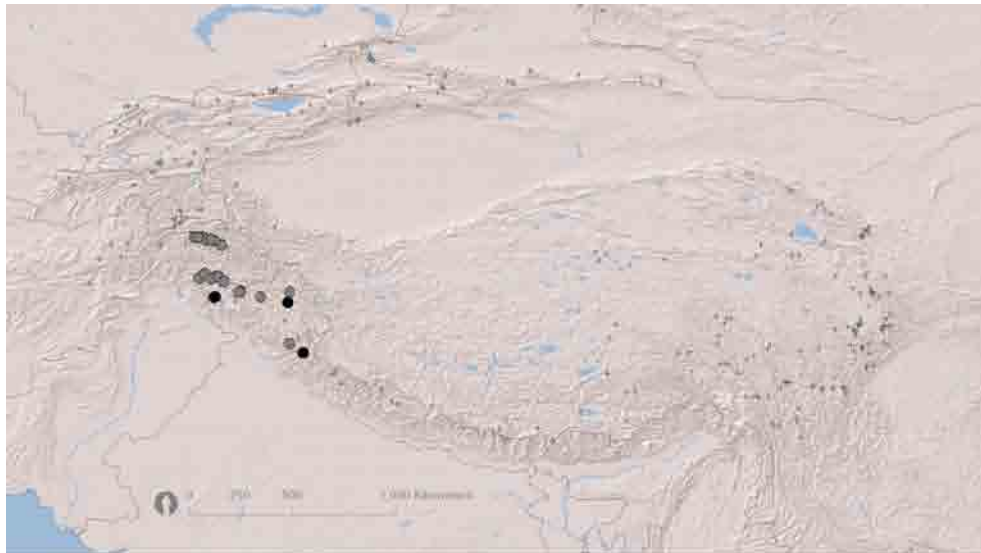
62 *himalayanus*
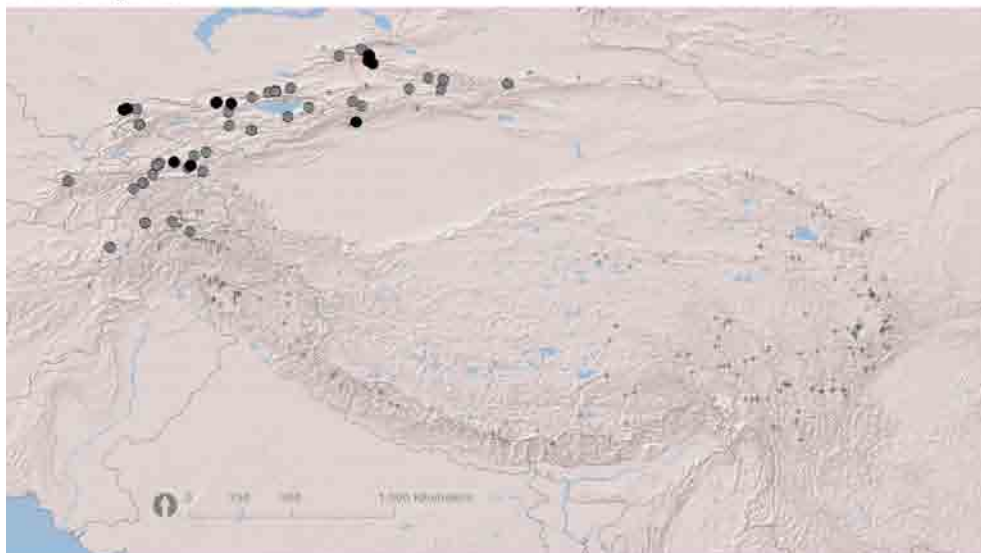


63 *turkestanicus*
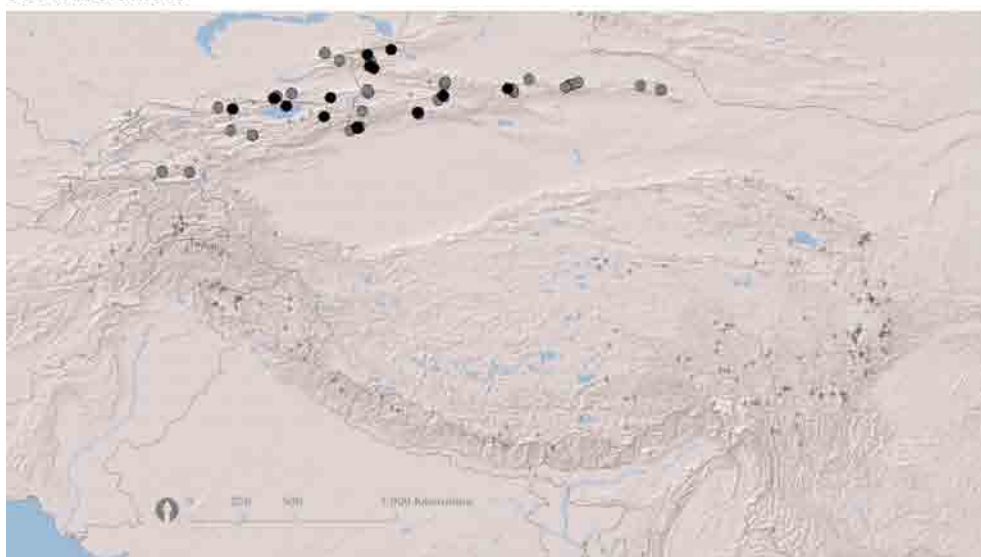


64 *defector*

**FIGURES 56–67**. (Continued)
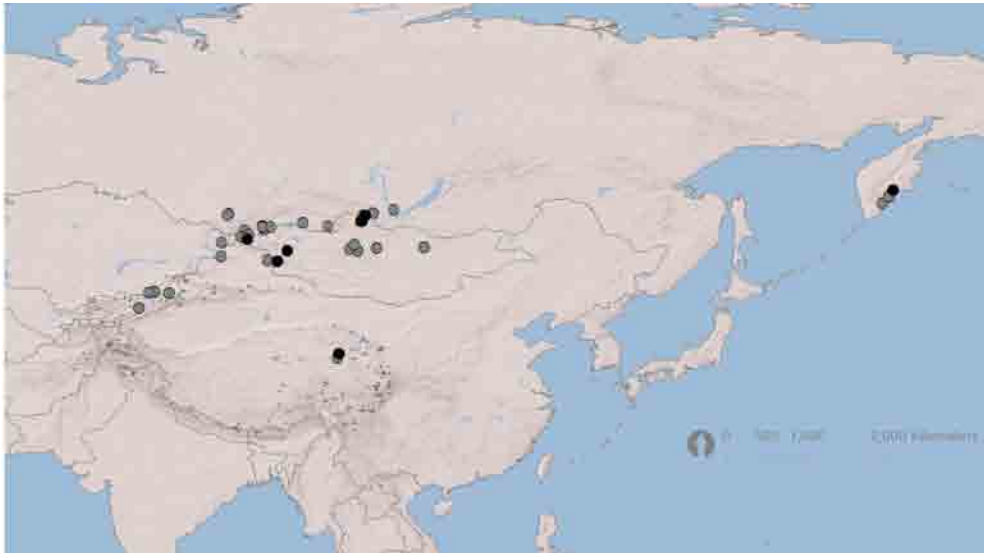
65 *margreiteri*
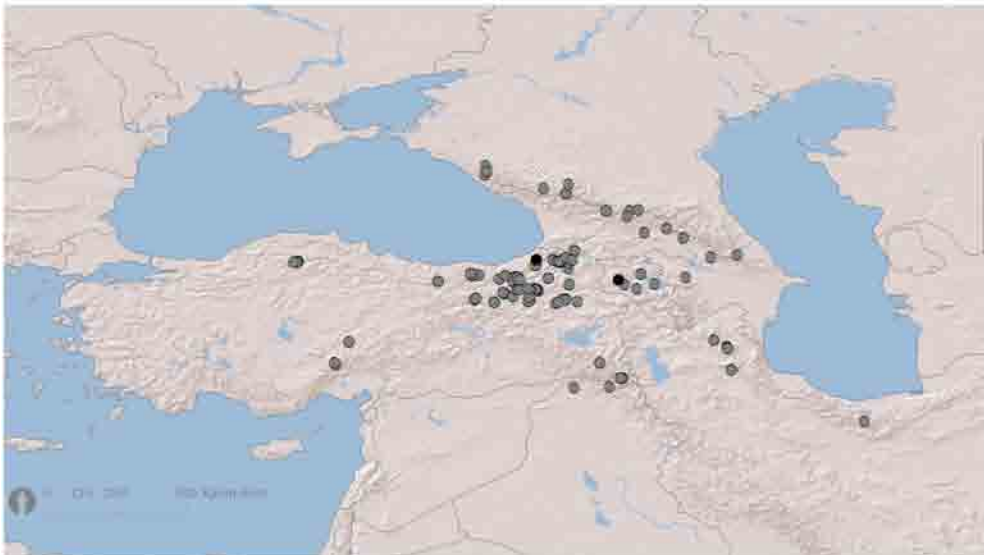
66 *handlirschianus*

67 *mendax*

**FIGURES 56–67**. (Continued)

**Material examined**. 8 queens 4 workers 3 males, from Afghanistan, China, Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan (Fig. 59: IZB, OLL, RMNH, UMONS, ZISP), with 3 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution**. Flower-rich alpine and subalpine grassland (not seen by us), at elevations 1550–(3144)–4500 m a.s.l.. A species of the Tian Shan and Pamir mountains (it is likely to occur in the Alai as well). There is overlap with *B. marussinus* in the Pamir, there is some overlap with *B. turkestanicus* in the Pamir and in the Tian Shan, and there is some overlap with *B. defector* and *B. margreiteri* in the Tian Shan, where the species may occur together.

**Food plants**. No records.

**Behaviour**. See Reinig (1930) and Reinig in Bischoff (1931), under the name *B. mendax macarjini*; Panfilov 1962.

## 5. *Bombus marussinus* Skorikov
(Figs 15, 28, 55, 60)

<*Bombus mendax*> subsp. *marussinus* Skorikov 1910b:330, type-locality citation (Cyrillic) '[East Pamir]'. **Lectotype** queen by present designation ZISP examined, (Cyrillic) '[Shugnan, Pamir]' (Pamir, Tajikistan). Note 1.
[*Bombus mendax* var. *aberrans* Skorikov 1910b:330, infrasubspecific.]
*Mendacibombus mendax* subsp. *marussinus* (Skorikov); Skorikov 1914:124.
*Mendacibombus marussinus* (Skorikov); Skorikov 1923:149; Skorikov, 1931:215; Tkalcŭ 1969:192.
[*Bombus mendax marussinus aberrans* Skorikov; Reinig 1930:100, infrasubspecific.]
[*Bombus mendax marussinus aberrans zonatus* Reinig 1930:101, infrasubspecific.]
*Bombus (Mendacibombus) mendax* Subsp. *marussinus* Skorikov; Richards 1930:634.
*Bombus mendax marussinus* Skorikov; Reinig 1932b:158.
*Bombus (Mendacibombus) marussinus* Skorikov; Reinig 1932a:258; P.H. Williams 1991:44; P.H. Williams 1998:99; P.H. Williams 2004:no. 28; Suhail *et al.* 2009:3 [not seen].
[*Bombus (Mendacibombus) marussinus* f. *aberrans* Skorikov; Reinig 1932a:258, infrasubspecific.]
[*Bombus (Mendacibombus) marussinus* f. *zonata* Reinig; Reinig 1932a:258, infrasubspecific.]
*Bombus marussinus* Skorikov; Reinig, 1934:172; Sabir *et al.* 2011:161 [not seen].
*Bombus (Mendacibombus) marussinus* <subsp.> *afghanus* Reinig 1940:230, type-locality citation 'Chodja-Mahomed' (Kwaja Muhammed, Badakhshan, Hindu Kush, Afghanistan). Syntype queen and male presumed lost by Tkalcŭ 1969.

Note 1 (*marussinus*). Skorikov's original description of the taxon *marussinus* cites the type locality as east Pamir. The ZISP collection studied by Skorikov contains a queen that agrees with the original description and carries the labels: (1) white, printed (Cryrillic) '[r. Toguz-bulak / V. Shugnan, Pam. / *Makarin*] 24/27.Ⅵ09.'; (2) white, printed (Cyrillic) '[*k. Skorikova*]'; (3) white, handwritten in pencil '[illegible] / N 14'; (4) red, handwritten '*Lectotypus Bombus* / *mendax subsp.* / *marussinus Skor.* / design. *Podbolotsk.*' (M. Podbolotskaya, unpublished); (5) green, printed '*Mendacibombus* / MD# 736 det. PHW'; (6) red, printed 'LECTOTYPE [female] / *Bombus mendax* ssp. / *marussinus* / Skorikov, 1910 / det. PH Williams 2012'; (7) white, printed '[female] *Bombus* / (*Mendacibombus*) / *marussinus* / det. PH Williams 2012'. This specimen, which is complete, is regarded as one of Skorikov's syntypes (others may have existed, it is unclear) and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

**Etymology.** The species may be named after a Russian entomologist, P. Marusin, from Tashkent (A. Byvaltsev, in litt.).

**Taxonomy and variation.** The single composite COI sequence supports this as a separate species (Fig. 11). The interpretation of this taxon as a separate species is also supported by the distinct form of the female labrum and of the male genitalia. This disagrees with earlier concepts (Tkalcŭ, 1969), diagnosed originally in terms of the colour pattern of the hair (Skorikov, 1910b), because the species appears to be not as easily diagnosable by colour (cf. *B. avinoviellus*) as originally understood.

All specimens have yellow and none has white hair on the thoracic dorsum or a black band between the wing bases. Skorikov (1910b) described females of the taxon *marussinus s. str.* from the Pamir (MD#736) as having the corbicula framed with light hairs, with T1–2 light yellow, the side of the thorax yellow above and whitish below, and the ventral side of the metasoma light (yellow). The palest specimens from the Pamir have T2 almost white (MD#1191).

For some specimens from further south in the Hindu Kush there is variation in the replacement of yellow with

black on T2 and on the lower side of the thorax (Reinig's taxon *afghanus*) although we have no COI sequences (from the taxon *marussinus s. str.*) from which to confirm this. Geographically associated males with the two colour patterns share the same diagnostic form of the male genitalia. The form of the female labrum is also diagnostic in grouping the taxa together. These specimens are interpreted as conspecific, as parts of the species *B. marussinus s. l.* (all of our COI sequences come from specimens from Pakistan with this dark colour pattern: MD#407, 408, 410).

Tkalců (1969) subsequently applied the name *Mendacibombus afghanus* to a series of specimens from the Karakorum that, in addition to the dark hair of T2, have darker wings and predominantly black hair on T6 (as opposed to predominantly orange for *B. marussinus*), treating them as a separate species. These darker Karakorum specimens (but not those with a similar colour pattern from the Hindu Kush) are interpreted here as likely to be conspecific with *B. avinoviellus* (see the comments on that species).

**Diagnostic description.** Wings nearly clear (*cf. B. avinoviellus*). *Female hair colour pattern:* generally black, but with yellow hair in a large patch below the base of the antenna, in a small patch on the vertex of the head, on the entire thoracic dorsum (at most with an obscure small round patch of black hairs between the wing bases, *cf. B. himalayanus*) and extending laterally and ventrally to half way down the side of the thorax, or to all of the way to the midleg base, on T1, on T2 anteriorly and medially or sometimes all of T2 except for a few black hairs intermixed medially along the posterior margin, T3 varying from orange only as a narrow posterior fringe to orange except for some black hairs anteriorly, and T4–6 orange, except T6 usually dominated medially by long black hairs. Hindleg tibia with the corbicular fringes often appearing double: hairs on the corbicular surface and in the adjacent fringes are usually black, sometimes with orange tips, but exterior to this, the hair in the outer fringes (anteriorly and posteriorly) may be black or yellow (*cf. B. himalayanus, B. avinoviellus*). *Female morphology:* labrum with the basal depression narrow, the transverse ridge broader medially than the basal depression, in the median third convex throughout, not subsiding completely or interrupted and with only a few scattered medium punctures, the lateral tubercles smooth with very few punctures (Fig. 15) (*cf. B. himalayanus, B. avinoviellus*). Clypeus in its central half with few scattered punctures, almost as many large as small punctures (*cf. B. avinoviellus*). *Male morphology*: genitalia (Fig. 28) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin; volsella with the apex broad, broader than the adjacent penis-valve head, but with the apex narrowly produced and finger-like. Gonostylus from the dorsal aspect almost triangular, without a distinct outer distal corner but broadly rounded. Penis-valve inner shoulder located at $\leq 0.5\times$ the length of the penis valve from the distal end to the broadest point of the spatha; penis valve proximal to the outer shoulder $< 2\times$ as broad as the penis-valve head; penis-valve breadth just proximal to penis-valve head $0.11\times$ the length of the penis valve distal to the broadest point of the spatha.

**Material examined.** 9 queens 86 workers 17 males, from Afghanistan, Pakistan, and Tajikistan (Fig. 60: NHM, PW, RMNH, UMONS, ZISP), with 3 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine grassland (not seen by us), at elevations 2800–(3787)–4500 m a.s.l.. A species of the Pamir, Hindu Kush, and Karakorum mountains. There is some overlap with *B. makarjini* in the Pamir, there is some overlap with *B. turkestanicus* in the Pamir and Hindu Kush, and there is some overlap with *B. himalayanus* in the northwestern Karakorum, but in these cases the two seldom occur together. A regional distribution map is available for Kashmir (P.H. Williams 1991).

**Food plants.** No records.

**Behaviour.** No records.


## 6. *Bombus avinoviellus* (Skorikov)
(Figs 3, 16, 29, 46, 61)

*Mendacibombus avinoviellus* Skorikov 1914:126, type-locality citation (Cyrillic) '[along the river Sind above Sonamarg, … Baltal … pass Zodji-La]'. **Lectotype** queen by present designation ZISP examined, (Cyrillic) '[along the river Sind upstream of Sonamarg]' (Great Himalaya, Kashmir, India). Note 1.
[*Mendacibombus avinoviellus* var. *eriophoroides*, var. *cremeus* Skorikov 1914:126, infrasubspecific.]
*Bombus niveatus* <subsp.> *callophenax* Cockerell 1917:122, type-locality citation 'Kashmir'. Holotype queen by monotypy USNM examined (Williams, 1991), 'Kashmir' (Kashmir, India). Synonymised with *Bombus avinoviellus* (Skorikov) by Williams (1991).

*Mendacibombus avinoviellus* Skorikov; Skorikov 1923:149; Skorikov 1933:2.

*Bombus (Mendacibombus) avinoviellus* (Skorikov); Richards 1930:635; P.H. Williams 1991:39; P.H. Williams & Cameron 1993:126; P.H. Williams 1998:99; P.H. Williams 2004:no. 25; Cameron *et al.* 2007:165; Suhail *et al.* 2009:3 [not seen]; P.H. Williams *et al.* 2010:124.

[*Bombus (Mendacibombus) avinoviellus* Var. nov. *subtunicatus* Richards, 1930:635, infrasubspecific.]

[*Mendacibombus afghanus* (Reinig); Tkalců 1969:193, misidentification: see below.]

*Bombus (Sibiricobombus) avinoviellus* (Skorikov [cited as Cockerell]); Burger *et al.* 2009:457.

*Bombus avinoviellus* (Skorikov); Sabir *et al.* 2011:160 [not seen].

Note 1 (*avinoviellus*). Skorikov's original description of several females of the taxon *avinoviellus* cites the type locality as the Sind valley above Sonamarg up to the Zoji-La pass in the Great Himalaya. The ZISP collection studied by Skorikov contains a queen that agrees with the original description and carries the labels: (1) white, handwritten (Cryrillic) '[[Along the river Sindu, upstream of] / Sonomarga, 2400–3000 mt / G. Jakobson] 9–10.VI.12'; (2) white, printed (Cyrillic) '[*k. Skorikova*]'; (3) red, printed '*Holotypus*'; (4) white, handwritten 'avinoviellus'; (5) red, handwritten '*Lectotypus Mendaci- / Bombus avinoviel- / lus Skorikov* / design. *Podbolotsk.*' (M. Podbolotskaya, unpublished); (6) green, printed '*Mendacibombus* / MD# 3528 det. PHW'; (7) red, printed 'LECTOTYPE [female] / *Mendacibombus* / *avinoviellus* / Skorikov, 1914 / det. PH Williams 2012'; (6) white, printed '[female] *Bombus* / (*Mendacibombus*) / *avinoviellus* / det. PH Williams 2012'. This specimen, which is complete, is regarded as one of Skorikov's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

A second queen collected at Baltal on the upper Sind river by Jakobson in 1912 (MD#598, NHM, sent by Skorikov as part of an exchange with the NHM in 1934), which is closely similar in morphology, is designated here as a paralectotype and is interpreted as conspecific.

**Etymology.** The species is named after A. Avinoff, a Russian entomologist who prior to 1914 had been collecting in Central Asia. After the Russian revolution he emigrated to the USA and later became Director of The Carnegie Museum.

**Taxonomy and variation.** The interpretation of this species is based here on the form of the female clypeus and labrum and of the male genitalia (and between species on DNA). This disagrees with earlier concepts (Tkalců, 1969), diagnosed originally in terms of the hair colour pattern (Skorikov, 1910b), because the species appears to be much more variable in colour pattern than was previously understood.

Skorikov (1914) described females of the taxon *avinoviellus s. str.* from the Kashmir Great Himalaya as having all of the pale bands grey-white, with an indistinctly-delimited black band between the wing bases (MD#3528). The taxon *callophenax* has a similar colour pattern with only a slightly more distinct black band between the wing bases. In the mountains around the Vale of Kashmir, the black band between the wings varies from broad and distinct (MD#405) to almost absent, as a small black spot (MD#397).

Our COI tree shows that specimens from further east in the Himalaya (Uttarakhand MD#286 and Nepal MD#265, 266) have a similar but undescribed colour pattern in which the pale bands are brownish yellow. These have very short branch lengths between them and specimens of the taxon *avinoviellus s. str.* (Fig. 13: the yellow-banded taxon 'yellowbanded' MD#265, 266, 286 and the white-banded taxon *avinoviellus s. str.* MD#3863). The yellow-banded individuals are interpreted here as conspecific, as parts of *B. avinoviellus s. l.*. Individuals from north-western Kashmir, in Pakistan, are also yellow-banded. Some individuals from Gulmarg and similar sites in the outer Pir Panjal range appear to be intermediate, with white hair on the thorax but yellow hair on T1–2. Grouping of specimens with these three colour patterns is supported by the associated males, which match in being yellow- or white-banded and in sharing the same diagnostic form of the male genitalia. For this COI group *B. avinoviellus s. l.*, the form of the female labrum and clypeus is also diagnostic.

Williams (1991) reports a specimen (MD#732) from Banidas, Pakistan (in the Karakorum mountains at the north-western end of the range), that is morphologically closely similar to *B. avinoviellus,* but which has a colour pattern of the hair similar to *B. marussinus.* This, and two further specimens from the same site with a similar colour pattern (MD#4058, 4059), were in Tkalců's collection (recently transferred to OLL) have now been examined. The darker wings, predominantly black hair of T6, and colour pattern of these specimens match the description of a series of specimens from the Karakorum by Tkalců (1969), misidentified (we believe) under the name *Mendacibombus afghanus* (see the comments on *B. marussinus*). No male specimens with this unbanded yellow colour pattern are known from this region from which to check their distinctive genital morphology. The

samples MD#4058, 4059 were sequenced, but yielded fragments with only the first 96 bp. Of the six uniquely diagnostic nucleotides for *B. avinoviellus* (Table 5), only those at positions 34(A) and 79(A) are within this fragment, but both of these samples match *B. avinoviellus* at both positions. In contrast, diagnostic nucleotides within this range for the other nine species of *Mendacibombus* show no other complete matches, with only partial matches (1/2 diagnostic nucleotides) for two species: *B. waltoni* (position 22A) and *B. margreiteri* (position 59C). Both species are morphologically distinctly different from *B. avinoviellus*. Consequently, these results are consistent with the yellow unbanded bees being parts of *B. avinoviellus*, possibly as an ancestral colour pattern shared with *B. marussinus*.

**Diagnostic description.** Wings lightly clouded with brown (*cf. B. himalayanus, B. marussinus*). Hair short, even and dense. *Female hair colour pattern:* generally black, but with pale hair (yellow and/or grey-white) intermixed especially as short hairs on the face, in a transverse band anteriorly on the thoracic dorsum and extending laterally and ventrally as white hair to the midleg base, in a transverse band posteriorly on the thoracic dorsum (scutellum; so the thoracic dorsum between the wing bases may have the hair entirely black, but usually has black and many pale hairs strongly intermixed, *cf. B. himalayanus* and *B. marussinus*, or sometimes with the pale hairs predominant), on T1, on T2 anteriorly and medially (T1 is more often yellow than T2 and the thoracic bands, so that individuals often have both yellow and white) or more rarely all of T2 pale except for a few black hairs intermixed medially along the posterior margin, T3 varying from orange only as a narrow posterior fringe to orange except for some black hairs anteriorly, and T4–6 orange, T6 medially with black hair and often entirely black. Hindleg tibia with the corbicular fringes black, often a few hairs with orange tips. *Female morphology:* labrum with the basal depression very broad, the transverse ridge narrower medially than the basal depression, in the median third consistently convex throughout, not subsiding or interrupted and with few scattered punctures, slightly angled between the lateral ends, the lateral tubercles with few punctures (Fig. 16) (*cf. B. himalayanus, B. marussinus*). Clypeus in its central half with few scattered punctures, many more small than large punctures (*cf. B. marussinus*), the small punctures spaced by about their own widths (*cf. B. himalayanus*), the anterior depressions with a broad band of dense punctures that are many punctures in breadth (*cf. B. himalayanus*). *Male morphology:* genitalia (Fig. 29) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin. Gonostylus distally strongly dorso-ventrally flattened and plate-like. Penis-valve inner shoulder located at ≤ 0.5× the length of the penis valve from the distal end to the broadest point of the spatha; penis valve proximal to the outer shoulder > 2× as broad as the penis-valve head; penis-valve head strongly laterally compressed.

**Material examined.** 31 queens 74 workers 70 males, from India, Nepal, and Pakistan (Fig. 61: NHM, NME, OLL, PW, RR, ZISP), with 8 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine and subalpine grassland, at elevations 1881–(2796)–4080 m a.s.l.. A species of the Karakorum and west Himalayan mountains. Compared to *B. himalayanus*, the distribution of *B. avinoviellus* extends slightly less far to the north but further to the east and it tends to occur at lower elevation (the two species rarely occur together). *Bombus avinoviellus* replaces the eastern *B. convexus* in the lower alpine zone and wetter upper forest meadows of the western Himalaya. Regional distribution maps are available for Kashmir (P.H. Williams 1991) and Nepal (P.H. Williams *et al.* 2010). The unbanded yellow taxon from the Karakorum appears to be very rare.

**Food plants.** Williams (1991).

**Behaviour.** Williams (1991), mate-searching male shown in Fig. 3.

## 7. *Bombus himalayanus* (Skorikov)
(Figs 4, 20, 30, 51, 53, 54, 62)

*Mendacibombus varius* Skorikov 1914:125 (not of Lepeletier de Saint-Fargeau 1832:381, = *B. campestris* (Panzer)), type-locality citation (Cyrillic) '[pass Zodji-La, … along the river Sind above Sonamarg]'. **Lectotype** queen by present designation ZISP examined, (Cyrillic) '[Zodzi-La]' (Zoji-La, Great Himalaya, India). Note 1. Synonymised with *Bombus himalayanus* (Skorikov) by Williams (1991).
[*Mendacibombus varius* var. *differens*, var. *sexfasciatus,* var. *formosulus* Skorikov 1914:126, infrasubspecific.]

*Mendacibombus mendax* subsp. *himalayanus* Skorikov 1914:127, type-locality citation (Cyrillic) '[pass Kordong]'. Holotype
　　queen by monotypy ZISP examined, (Cyrillic) '[pass Kordong]' (Khardung-La, Ladakh Range, India). Note 2.
*Mendacibombus varius* Skorikov; Skorikov 1923:149; Skorikov, 1931:213; Skorikov 1933:2.
*Bombus* (*Mendacibombus*) *mendax* Subsp. *himalayanus* (Skorikov); Richards 1930:635.
[*Mendacibombus margreiteri himalayanus* Skorikov; Skorikov 1933:2, misidentification.]
*Bombus* (*Mendacibombus*) *himalayanus varius* (Skorikov); Williams, 1991:fig. 5 male.
*Bombus* (*Mendacibombus*) *himalayanus* (Skorikov); P.H. Williams 1991:41; P.H. Williams 1998:99; P.H. Williams 2004:no.
　　27; Suhail *et al.* 2009:3 [not seen].
*Bombus himalayanus* (Skorikov); Sabir *et al.* 2011:161 [not seen].

Note 1 (*varius*). Skorikov's original description of several females of the taxon *varius* cites the type locality as the Sind valley above Sonamarg up to the Zoji-La pass in the Great Himalaya. The ZISP collection studied by Skorikov contains a queen that agrees with the original description and carries the labels: (1) white, handwritten (Cryrillic) '[[Pass] Zodzi-La, Hi- / malaya > 3000 mt. / G. Jakobson] 12–15.ⅵ.12'; (2) white, printed (Cyrillic) '[*k. Skorikova*]'; (3) red, printed '*Holotypus*'; (4) white, handwritten '*varius*'; (5) red, handwritten '*Lectotypus Mendaci- / Bombus varius Skor.* / design. *Podbolotsk.*' (M. Podbolotskaya, unpublished); (6) green, printed '*Mendacibombus* / MD# 735 det. PHW'; (7) red, printed 'LECTOTYPE [female] / *Mendacibombus* / *varius* / Skorikov, 1914 / det. PH Williams 2012'; (6) white, printed '[female] *Bombus* / (*Mendacibombus*) / *himalayanus* / det. PH Williams 2012'. This specimen, which is complete, is regarded as one of Skorikov's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

A second queen collected at the Zoji-La by Jakobson in 1912 (MD#535, NHM, sent by Skorikov as part of an exchange with the NHM in 1934), closely similar in morphology, is designated here as a paralectotype and interpreted as conspecific.

Note 2 (*himalayanus*). Skorikov's original description of the taxon *himalayanus* specifies that there was only one type specimen for the name *himalayanus*, so this specimen in the ZISP is regarded as the holotype by monotypy (ICZN, 1999: Article 73.1.2).

**Etymology.** The species is named after the Himalaya, the mountain range at the southern edge of the Qinghai-Tibetan plateau.

**Taxonomy and variation.** The interpretation of this species is based here on evidence from DNA, as well as on the form of the female labrum (and between species on the form of the male genitalia). This disagrees with earlier concepts, diagnosed originally in terms of the hair colour pattern (Skorikov, 1914), because the species appears to be much more variable in colour pattern than was originally understood.

Skorikov (1914) described a single queen of the taxon *himalayanus s. str.* (MD#731) from the Ladakh range as having the corbicula framed with black hairs, the pale bands and most of the side of the thorax lemon yellow, and the black band between the wing bases extensively intermixed with yellow hairs. One yellow-banded queen with more extensive black hair (MD#316) and a queen and a few older workers (MD#484–489, 499, 4054, 4055) with more extensive yellow hair are known from elsewhere in Kashmir (Williams, 1991). The yellow-banded dark queen from Ladakh yielded only a short COI sequence (Fig. 13: MD#316), although this is enough to support the inference from morphology by Williams (1991) that the taxon *himalayanus s. str.* and the taxon *varius* are parts of the same species. Skorikov (1914) also described a single male with a yellow thorax with black hairs between the wing bases from Kilian (Raskam range, Xinjiang) under the name *himalayanus s. str..* Unfortunately this specimen could not be found in the ZISP collection (M. Podbolotskaya in litt.). But this is likely to be the same individual that Skorikov (1931:215) later listed from the 'Raskemkette, Nordhang des Kilieng' as *Mendacibombus makarjini*.

Other specimens are known from the Great Himalaya and Pir Panjal ranges with a similar banded colour pattern, but with more extensive black between the wing bases and on the side of the thorax, and with the pale bands on the thorax and often on T2 white (Skorikov's taxon *varius*). These specimens have similar morphology of the female labrum and have been interpreted previously as conspecific (Williams, 1991). The short COI sequences available are sufficient to give support for this white-banded taxon being conspecific with the yellow-banded taxon *himalayanus s. str.* (Fig. 13: the white-banded taxon *varius* MD#675, 417 and the yellow-banded taxon *himalayanus s. str.* MD#316).

Males (known only for the white-banded taxon *varius*) usually have the hair of T3–7 orange at least in part, but occasionally the hair of T3–7 predominantly black (MD#426) or (as visible in photographs) entirely black.

**Diagnostic description.** Wings nearly clear (*cf. B. avinoviellus*). *Female hair colour pattern:* generally black, but with pale hair (yellow and/or grey-white) varying from completely absent from the head to covering most of

the face but with at most only a few pale hairs on the anterior vertex of the head, in a transverse band anteriorly on the thoracic dorsum and extending laterally and ventrally to just below the wing base (occasionally much intermixed with black hairs and almost absent), or as white hair to half way down the side of the thorax, or to all of the way to the midleg base, often but not always in a transverse band posteriorly on the thoracic dorsum (scutellum; so the thoracic dorsum between the wing bases may have the hair entirely black, or rarely may have many pale hairs intermixed), on T1–2 (T1 is more often yellow than T2 or the thoracic bands, so that individuals may have both yellow and white hair), T3 with orange hair as a posterior fringe and throughout T4–6, T3 laterally with black hair that often extends onto T4 and even T5 laterally (*cf. B. avinoviellus*), T6 medially with black hair and often entirely black. Hindleg tibia with corbicular fringes usually black, but sometimes with a few hairs in the fringes orange-tipped or rarely more extensively pale-tipped. *Female morphology:* labrum with the basal depression narrow, the transverse ridge broader medially than the basal depression, in the median third subsiding only slightly with large punctures overflowing across it from the basal depression, the lateral tubercles laterally with scattered large and medium punctures (Fig. 20) (*cf. B. avinoviellus*). Clypeus in its central half with scattered punctures, small punctures spaced sparsely by more than their own widths (*cf. B. avinoviellus*), the anterior depressions with a narrow band of dense punctures that is only one or two punctures in breadth (*cf. B. avinoviellus*). *Male morphology*: genitalia (Fig. 30) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin; volsella with the apex broad, broader than the adjacent penis-valve head, but with the apex narrowly produced and finger-like. Gonostylus from the dorsal aspect rectangular, with a distinct outer distal corner. Penis-valve inner shoulder located at $\leq 0.5\times$ the length of the penis valve from the distal end to the broadest point of the spatha; penis valve proximal to the outer shoulder $< 2\times$ as broad as the penis-valve head; penis-valve breadth just proximal to the penis-valve head $0.11\times$ the length of the penis valve distal to the broadest point of the spatha.

**Material examined.** 16 queens 72 workers 9 males, from India and Pakistan (Fig. 62: NHM, OLL, PW, ZISP), with 3 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine grassland, at elevations 2077–(3307)–4800 m a.s.l.. A species of the Karakorum and west Himalayan mountains. Compared to *B. avinoviellus*, the distribution of *B. himalayanus* extends slightly further to the north but less far to the east and it tends to occur at higher elevation (and the two species rarely occur together at precisely the same site). There is some overlap with *B. marussinus* in the northwestern Karakorum, but the two species seldom occur together. *Bombus himalayanus* replaces the eastern *B. waltoni* in the higher wet alpine zone of the western Himalaya. A regional distribution map is available for Kashmir (P.H. Williams 1991). The yellow-banded taxon *himalayanus s. str.* from Ladakh appears to be very rare.

**Food-plants.** Williams (1991).

**Behaviour.** Williams (1991), mate-searching male shown in Fig. 4.

## 8. *Bombus turkestanicus* Skorikov
(Figs 17, 23, 31, 45, 52, 63)

[*Bombus mendax* Gerstaecker; Morawitz 1875:4, misidentification.]
<*Bombus mendax*> subsp. *turkestanicus* Skorikov 1910b:329, type-locality citation (Cyrillic) '[Turkestan (Samarkand, Fergana, and Semirechensk Province)]'. **Lectotype** queen by present designation ZISP examined, (Cyrillic) '[Voru, Samarkand]' (Alai, Tajikistan). Note 1.
*Mendacibombus mendax* subsp. *turkestanicus* (Skorikov); Skorikov 1914:124.
*Mendacibombus turkestanicus* (Skorikov); Skorikov 1923:149; Skorikov, 1931:215.
*Bombus turkestanicus* Skorikov; Reinig 1934:172.
*Bombus (Mendacibombus) turkestanus* Skorikov; Panfilov 1957:237; Panfilov 1962:195; P.H. Williams 1991:15, 41; S.-F. Wang & Yao 1996:303; P.H. Williams 1998:99; P.H. Williams 2011:28.

Note 1 (*turkestanicus*). Skorikov's original description of the taxon *turkestanicus* cites the type locality as Samarkand, Fergana, and Semirechensk Province. The ZISP collection studied by Skorikov contains a queen that agrees with the original description and carries the labels: (1) white, printed (Cryrillic) '[Voru, / Samarkands. obl. / *Golbek*] 20 VI 09'; (2) white, printed (Cyrillic) '[*k. Skorikova*]'; (3) red, handwritten '*Paralectotypus Bomb. / mendax subsp. / turkestanicus Skor.* / design. *Podbolotsk.*' (M. Podbolotskaya, unpublished); (4) green, printed

'*Mendacibombus* / MD# 3525 det. PHW'; (5) red, printed 'LECTOTYPE [female] / *Bombus mendax* ssp. / *turkestanicus* / Skorikov, 1910 / det. PH Williams 2012'; (6) white, printed '[female] *Bombus* / (*Mendacibombus*) / *turkestanicus* / det. PH Williams 2012'. This specimen, which is complete, is regarded as one of Skorikov's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

A second queen collected at Voru by Golbek in 1909 (MD#320, NHM, sent by Skorikov as part of an exchange with the NHM in 1934), closely similar in morphology, is designated here as a paralectotype and interpreted as conspecific.

**Etymology.** The species is named after Russian Turkestan, which from 1867–1918 was a Governorate-General (Krai) of the Russian Empire in Central Asia.

**Taxonomy and variation.** The interpretation of this species is based here on DNA, as well as on the form of the female labrum and of the male genitalia.

Skorikov (1910b) described females of the taxon *turkestanicus s. str.* from the Alai mountains (MD#3525) as having the corbicula framed with partly light rusty and partly greyish hairs, with the pale bands light yellow, and with the entire side of the thorax and the ventral side of the metasoma (S1–4) light yellow. For the COI group of specimens with this *B. turkestanicus* colour pattern (Fig. 13), the form of the female labrum is diagnostic (Fig. 17).

Most specimens of this species are yellow-banded. For two queens from near the Kyrgyz Ata (river), Kyrgyzstan, one has a light-yellow-banded colour pattern (MD#325) and the other a cream-white-banded colour pattern (MD#324). A queen from Kyrgyzstan is white-banded and groups with *B. turkestanicus* by its COI sequence (Fig. 14: the white-banded individual labeled 'white' MD#1281 and the yellow-banded taxon *turkestanicus s. str.* MD#324). This material is interpreted as conspecific, as parts of the species *B. turkestanicus s. l.*.

**Diagnostic description.** Wings nearly clear. *Female hair colour pattern:* generally black, but with pale hair (yellow or cream-white) over most of the face (with variable amounts of black intermixed on the outer side of the face and above the antenna), in a usually small patch on the vertex of the head, in a transverse band anteriorly on the thoracic dorsum (occasionally with black hairs intermixed posteriorly) and extending laterally and ventrally all the way to the midleg base (*cf. B. makarjini*), in a transverse band posteriorly on the thoracic dorsum (scutellum; so the thoracic dorsum between the wing bases has the hair entirely black in a narrow band), on T1–2, although T2 with a few black hairs intermixed along the posterior margin, orange hair on T3 as a posterior fringe, and throughout on T4–6, T6 without obvious black hairs, S1–6 entirely pale (*cf. B. makarjini*). Hindleg tibia with the corbicular fringes usually nearly entirely yellow or grey, the long hairs in the fringes sometimes orange close to the base and with a few short orange-brown bristles along their inner edges, only rarely with a few long dark hairs intermixed (Fig. 23) (*cf. B. makarjini, B. margreiteri, B. defector*). *Female morphology:* labrum with the basal depression narrow, the transverse ridge just broader medially than the basal depression, in the median third subsiding slightly but not clearly or abruptly interrupted, with many scattered punctures, the lateral tubercles with only a few punctures (Fig. 17) (*cf. B. margreiteri, B. defector*). Clypeus in its central half with many widely spaced small and large punctures (*cf. B. margreiteri, B. defector*). *Male morphology*: genitalia (Fig. 31) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin; volsella with the apex narrowed, narrower than the adjacent penis-valve head. Penis-valve inner shoulder located at $\leq 0.5\times$ the length of the penis valve from the distal end to the broadest point of the spatha; penis valve proximal to the outer shoulder $< 2\times$ as broad as the penis-valve head; penis-valve breadth just proximal to the penis-valve head $0.11\times$ the length of the penis valve distal to the broadest point of the spatha.

**Material examined.** 21 queens 87 workers 27 males, from Afghanistan, China, Kazakhstan, Kyrgyzstan, and Tajikistan (Fig. 63: AMNH, IAR, IZB, KUK, NHM, NME, OLL, PW, RMNH, SMNS, UMONS, ZISP), with 26 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine and subalpine grassland, at elevations 950–(2146)–4350 m a.s.l.. A species of the Tian Shan, Alai, Pamir, and Hindu Kush mountains. Compared to *B. defector*, the distribution of *B. turkestanicus* extends less far to the east, overlaps broadly in the mid part of the range (and the two species often occur together), but extends further to the south in the Pamir and Hindu Kush, where it reaches higher elevations. *Bombus turkestanicus* overlaps with *B. margreiteri* in the Tian Shan, although the two seldom occur together. There is some overlap of *B. turkestanicus* with *B. marussinus* in the Pamir and Hindu Kush, although the two seldom occur together.

**Food plants.** Williams (2011).
**Behaviour.** No records.


## 9. *Bombus defector* Skorikov
(Figs 18, 22, 32, 42, 64)

[?*Bombus mendax* Gerstaecker; Morawitz 1880:340, in part, misidentification.]
<*Bombus mendax*> subsp. *defector* Skorikov 1910b:330, type-locality citation (Cyrillic) '[Fergana (Alai range)]'. **Lectotype**
    queen by present designation ZISP examined, (Cyrillic) '[Alai range]' (Alai, Kyrgyzstan). Note 1.
<*Mendacibombus mendax* subsp.> *defector* (Skorikov); Skorikov 1914:124.
*Mendacibombus defector* (Skorikov); Skorikov 1923:149; Skorikov, 1931:fig. 17.
[?*Mendacibombus turkestanicus* var. Skorikov, 1931:215, published with name incomplete.]
*Bombus mendax defector* Skorikov; Reinig 1932b:163.
*Bombus defector* Skorikov; Reinig 1934:172.
*Bombus* (*Mendacibombus*) *defector* Skorikov; Panfilov 1957:237; Panfilov 1962:195; S.-F. Wang 1985:160; Williams,
    1991:15, 42 in part; P.H. Williams 1998:99 in part.
[*Bombus* (*Mendacibombus*) *makarjini* Skorikov; P.H. Williams 2011:27, misidentification. Note 2.]


Note 1 (*defector*). Skorikov's original description of the taxon *defector* cites the type locality as Fergana (Alai range). The ZISP collection studied by Skorikov contains a queen that agrees with the original description and carries the labels: (1) white, printed (Cryrillic) '[Ak-Basaga, Alai- / skii khr. 2600–2700 mt. / *Makarin*] 29/ 30.v.09.'; (2) white, printed (Cyrillic) '[*k. Skorikova*]'; (3) red, handwritten '*Lectotypus Bombus* / *mendax subsp.* / *defector Skor.* / design. *Podbolotsk.*' (M. Podbolotskaya, unpublished); (4) green, printed '*Mendacibombus* / MD# 3524 det. PHW'; (5) red, printed 'LECTOTYPE [female] / *Bombus mendax* ssp. / *defector* / Skorikov, 1910 / det. PH Williams 2012'; (6) white, printed '[female] *Bombus* / (*Mendacibombus*) / *defector* / det. PH Williams 2012'. This specimen, which is complete, is regarded as one of Skorikov's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

A second queen collected at Ak-Basaga by Makarin in 1909 (MD#315, NHM, sent by Skorikov as part of an exchange with the NHM in 1934), closely similar in morphology, is designated here as a paralectotype and interpreted as conspecific.

Note 2 (*makarjini*). See note 1 on *B. makarjini* regarding the paralectotype. Examination of this syntype as the only type seen at the time led to the misidentification of this species in Williams (2011).

**Etymology.** The species is named from the Latin *defector* for a deserter or rebel, presumably a reference to its slight difference in colour pattern from other co-occurring related bumblebee taxa from the mountains of Central Asia (the taxon *margreiteri* is closest to it in Skorikov's original key).

**Taxonomy and variation.** The interpretation of this species is based here on DNA, as well as on the form of the female labrum and of the male genitalia. This disagrees with earlier concepts (Skorikov, 1931), diagnosed originally in terms of the hair colour pattern (Skorikov, 1910b), because the species appears to be more variable in colour pattern than was originally understood.

All specimens have yellow-banded and none has a white-banded colour pattern. Skorikov (1910b) described females of the taxon *defector* from the Alai mountains (MD#3524) as having the corbicula framed with black hairs, with the pale bands yellow, and with the hair on the lower side of the thorax and on the ventral side of the metasoma black. Our COI tree shows that similar specimens but with the hair on the lower side of the thorax yellow, and even some with yellow hair on the ventral side of the metasoma, have very short branch lengths between them and typical *defector* (with the lower side of the thorax black) and these are interpreted as conspecific (Fig. 13: the extensively yellow females labeled 'light' MD#352, 365, 373, 1246, 1285, 1344, 4024 and females of the darker taxon *defector s. str.* MD#1251, with the black hair most extensive in the worker 'dark' MD#1336). The form of the female labrum is diagnostic (Fig. 18).

Skorikov's illustration of the male genitalia of '*Mendacibombus defector*' (Skorikov 1931: his fig. 17) is correctly identified. Males usually have the hair of T3–7 orange at least in part, but occasionally the hair of T3–7 is entirely black (Fig. 13: the black-tailed male labeled 'blacktail' MD#1250, 1256 and the lighter taxon *defector s. str.* MD#1251).

**Diagnostic description.** Wings nearly clear. *Female hair colour pattern:* generally black, but with yellow hair

in a large patch below the base of the antenna, in a large patch or almost absent on the vertex of the head, in a transverse band anteriorly on the thoracic dorsum and extending laterally and ventrally to half way down the side of the thorax, or more rarely to the midleg base, in a transverse band posteriorly on the thoracic dorsum (scutellum; so the thoracic dorsum between the wing bases has the hair entirely black), on T1–2, although T2 with a few black hairs intermixed along the posterior margin, orange hair on T3 as a posterior fringe, and throughout on T4–6, except T6 dominated medially by long black hairs. Hindleg tibia with corbicular fringes usually uniformly black, but sometimes with a few hairs on the corbicular surface and in the adjacent fringes orange, or rarely the fringes predominantly orange with black hairs (Fig. 21) (*cf. B. makarjini, B. turkestanicus*). *Female morphology:* labrum with the basal depression broad, the transverse ridge narrower medially than the basal depression, in the median fifth gradually subsiding and narrowly interrupted by a longitudinal band of many dense medium punctures overflowing across it from the basal depression (*cf. B. margreiteri, B. turkestanicus*), lateral tubercles with few punctures (Fig. 18). Clypeus in its central half with many widely spaced medium punctures (*cf. B. margreiteri, B. turkestanicus*). Hindleg tibia distal edge with the broad spines (rastellum) not continuing onto the posterior edge (*cf. B. margreiteri, B. turkestanicus*). *Male morphology:* genitalia (Fig. 32) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin. Penis-valve inner shoulder located at 0.63× the length of the penis valve from the distal end to the broadest point of the spatha.

**Material examined.** 77 queens 233 workers 173 males, from China, Kazakhstan, Kyrgyzstan, and Tajikistan (Fig. 64: AMNH, IAR, ISEAN, IZB, KUK, NHM, OLL, PW, RMNH, ZISP), with 29 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine and subalpine grassland, at elevations 936–(2174)–3108 m a.s.l.. A species of the Tian Shan (including the Bogda Shan) and Alai mountains. Compared to *B. turkestanicus*, the distribution of *B. defector* extends further to the east in the Bogda Shan, overlaps broadly in the mid part of the range (the two species often occur together), but extends less far to the south. *Bombus defector* overlaps with *B. margreiteri* in the Tian Shan and the two sometimes occur together.

**Food plants.** Williams (1991, 2011), under the name *B. makarjini*.

**Behaviour.** No records (see comments on *B. turkestanicus*).


## 10. *Bombus margreiteri* Skorikov
(Figs 5, 6, 19, 21, 33, 65)

[*Bombus mendax* Gerstaecker; Morawitz 1880:340, in part; ?Morawitz 1890:352; misidentifications.]
<*Bombus mendax*> subsp. *altaicus* Skorikov 1910b:329 (not of Eversmann 1846:436, = *B. melanurus* Lepeletier), type-locality citation (Cyrillic) '[Altai (Sary-Tau)]'. **Lectotype** queen by present designation ZISP examined, 'Altai, Sary-Tau' (Altai, Kazakhstan). Note 1. Synonymised with *B. margreiteri* Skorikov (as *B. mendax* subsp. *margreiteri* Vogt) by Williams (1991), supported here.
<*Bombus mendax*> subsp. *margreiteri* [Vogt in] Skorikov 1910b:330, type-locality citation (Cyrillic) '[Semirechensk province, Altai, Zabaykalsky province]' (Zabaykalsky in 1910 = Transbaikal). **Lectotype** queen by present designation ZISP examined, 'Narynj, Turkestan' (Tian Shan, Kyrgyzstan). Note 2.
*Mendacibombus margreiteri* (Skorikov [cited as Vogt]); Skorikov 1923:149; Skorikov, 1931:215.
*Bombus* (*Mendacibombus*) *mendax* subsp. *altaicus* Skorikov; Bischoff 1930:2.
[*Mendacibombus makarjini* (Skorikov); Skorikov, 1931:fig. 18 male, misidentification.]
*Mendacibombus altaicus* (Skorikov); Skorikov, 1931:215.
*Bombus margreiteri* Skorikov [cited as Vogt]; Peters & Panfilov 1968:179.
[*Bombus* (*Mendacibombus*) *defector* Skorikov; P.H. Williams, 1991:42 in part; P.H. Williams 1998:99 in part; Ito & Kuranishi 2000:286; Kawakita *et al.* 2003:90; Cameron *et al.* 2007:165; misidentifications.]
*Bombus altaicus* Skorikov; Yefremova 2001:272.
*Bombus* (*Mendacibombus*) *altaicus* Skorikov; Proshchalykin & Kupianskaya 2005:23; Proshchalykin & Kupianskaya 2009:64.

Note 1 (*altaicus*). There is no evidence from the original publication for the number of specimens regarded as types of the taxon *altaicus* by Skorikov. Although only a single type locality (region) is given in the original description, more than one syntype may have existed.

Skorikov's original description of the taxon *altaicus* cites the type locality as Altai (Sary Tau). The ZISP collection studied by Skorikov contains a queen that agrees with the original description and carries the labels: (1)

gold disc; (2) white, printed (Cryrillic) '[k. *F Moravitsa*]'; (3) white, handwritten 'mendax / Gerst. [female].'; (4) white, hand-written '*Mont. Altai. / Sary-Tau / 9400'. Schwarz.*'; (5) red, handwritten '*Holotypus Bombus / mendax subsp. / altaicus Skor.* [female, overwritten with male]'; (6) green, printed '*Mendacibombus* / MD# 739 det. PHW'; (7) red, printed 'LECTOTYPE [female] / *Bombus mendax* ssp. / *altaicus* / Skorikov, 1910 / det. PH Williams 2012'; (8) white, printed '[female] *Bombus* / (*Mendacibombus*) / *margreiteri* / det. PH Williams 2012'. This specimen, which is complete, is regarded as one of Skorikov's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

Note 2 (*margreiteri*). The name *margreiteri* was first published by Skorikov (1910a), who described the taxon in a key couplet followed by 'subsp. margreiteri Vogt'. Later Skorikov (1931) referred to the name as 'Mendacibombus margreiteri (O. Vogt, in litt.)' [sic]. Therefore Vogt may have recognised the taxon as undescribed and may have supplied the name *margreiteri*. However, there is no evidence from Skorikov's original publication that Vogt satisfied the other minimum criterion for availability (ICZN, 1999: Article 12.1), including that Vogt supplied a description or diagnosis. Therefore the author of the nomenclatural act is deemed to be Skorikov (ICZN, 1999: Article 50.1.1), not Vogt.

Skorikov's original description of the taxon *margreiteri* cites the type localities as Semirechensk province, Altai, and Zabaykalsky (Transbaikal) province, so multiple syntypes are expected to exist. The ZISP collection studied by Skorikov contains a queen that agrees with the original description and carries the labels: (1) black disc; (2) white, handwritten probably by Vogt 'mendax / margreiteri O.V. / Cotype. / Narynj. VI.08. / Turkestan.'; (3) red, handwritten and crossed out with a large X '*Syntypus Bombus / mendax subsp. / margreiteri / Vogt* [female]'; (4) green, printed '*Mendacibombus* / MD# 738 det. PHW'; (5) red, printed 'LECTOTYPE [female] / *Bombus mendax* ssp. / *margreiteri* / Skorikov, 1910 / det. PH Williams 2012'; (6) white, printed '[female] *Bombus* / (*Mendacibombus*) / *margreiteri* / det. PH Williams 2012'. This specimen, which lacks most of the left flagellum, the left hindwing, and the last three joints of the right hindleg tarsus, is regarded as one of Skorikov's syntypes sent to him by Vogt.

Unfortunately, the location of the type locality 'Narynj' (= Naryn) is uncertain. From gazetteers, we have identified 32 geographical features associated with the name Naryn in the region of the former Turkestan. In Turkish, the adjective 'narin' translates as thin, slender, or slight, so it may have been applied frequently to narrow features in this region.

A clue to the location of the type-locality Naryn may come from many specimens in the RMNH collection (which includes most of the Vogt collection) that are labelled 'Narynj / Siebenstrom' from 1908 in the same handwriting (e.g. *B. turkestanicus*: MD#3513–3516). This is an association of names that was repeated in print by Vogt (1911): 'der Umgebung der Festung Narynj im Siebenstromgebiet und dem Boro-Chorogebirge' (p. 51) as well as 'aus der Festungswerks Narynj und dem Boro-Chorogebirge im Siebenstromgebiet' (p. 58). This appears to place the 'Narynj' on these labels in what was in 1908 the northeastern province of Turkestan, Semirechye Oblast (or in German, Siebenstrom, both derived from the Kazakh 'Zhetysu', referring to the seven rivers: Ili, Qaratal, Bien, Aksu, Lepsy, Baskan, and Sarkand). Semirechye had been given as one of the type localities in the original description.

According to Vogt's biographer, de Boer (2004), Vogt purchased these specimens from an insect dealer, Osip Emeljanovich Neshivov (1859–1919), who lived 'in Naryn, Tashkent' (an earlier reference in de Boer, 2002, to 'Naryn, Dzharkent' was incorrect: de Boer, in litt.) and who gave his address as Fortress Naryn. According to maps for the period 1899–1916, the province of Semirechye (Siebenstrom) then included an area to the south of lake Ysyk-Köl, to encompass the well-known modern (long, narrow) town of Naryn on the Naryn River, now part of central Kyrgyzstan. A. de Boer (in litt.) believes that this is where the collector Neshivov lived, although he also believes that other collecting sites like 'Schlucht Burchan' (Burchan gorge) may have been nearby (on the Burkan river upstream to the east) rather than in the Borohoroshan (as implied by Vogt handwritten labels, e.g. 'Boro-Chorogeb. / Burchan. 8.09', MD#1236), and that perhaps Neshivov mistook the location of the Borohoroshan (not a view shared here). Within this Kyrgyz Naryn there are earthworks with possible corner emplacements surrounding a compound (41.431546°N 76.016929°E). Even more convincingly, there are earthworks that might represent a town wall or enclosure (41.434177°N 75.997418°E) and which could be the fortifications (Festungswerks) mentioned by Neshivov and Vogt.

However, Siebenstrom is often shown on maps from other periods as a narrower region or governorate to the north of the Tian Shan mountains which excluded the Naryn in modern Kyrgyzstan. If we were to assume that

Siebenstrom implied somewhere in modern Kazakhstan and if we assume that within this region *Mendacibombus* species are unlikely to occur at elevations below 1000 m (and there are three species of *Mendacibombus* in the Vogt collection labelled Naryn), then from our search of the gazetteers we would have just two candidate areas left: Narynkol (42.725864°N 80.178319°E) to the south of Siebenstrom in the narrow sense; and Naryn Zhotasy (49.004339°N 84.500323°E) to the north of Siebenstrom. Vogt (1911) gives the impression that he included both Naryn and the Boro-Choro mountains (Borohoroshan) within the region of Siebenstrom. A. de Boer (in litt.) reports a Burchan gorge (in Borohoroshan) label with an addition 'Naryntal' (Naryn valley), which if it referred to the same Naryn, might imply proximity of Naryn to the Borohoroshan. C. Burgess (in litt.) has located another Naryn river, which is closer to both the centre of Siebenstrom and to the possible Neshivov collection site of Burchan gorge in the Borohoroshan. There are ruins near this river Naryn that could be another candidate for Vogt's Naryn fortifications (44.440116°N 80.106918°E).

Nevertheless, until further information is available, for the present we follow de Boer in accepting that the Naryn on the specimen labels refers to the Kyrgyz town where Neshivov lived. Unlike de Boer, we accept that Vogt's Burchan gorge is in the Borohoroshan (near 44.70342°N 79.82960°E).

The queen in the ZISP collection described above is regarded as a syntype of *B. mendax* subsp. *margreiteri* Skorikov and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

**Etymology.** The species is named after M. Margreiter, who around 1910 was a schoolteacher in Vienna, who sold or sent many Austrian bumblebees to Vogt (de Boer, in litt.). Vogt sent the type material of this species (not collected by Margreiter), and probably the manuscript name *margreiteri,* to Skorikov.

**Taxonomy and variation.** The interpretation of this species is based here on evidence from DNA, as well as on the form of the female labrum and of the male genitalia. This disagrees with earlier concepts (Skorikov, 1931), diagnosed originally in terms of the hair colour pattern (Skorikov, 1910b), because the species appears to be much more variable in colour than was originally understood.

Skorikov (1910b) described females of the taxon *margreiteri s. str.* from the Tian Shan (and Altai and Transbaikal, including MD#738) mountains as having the corbicula framed with rusty hairs, with the pale bands yellow and the hair on the lower side of the thorax and on the ventral side of the body black. Our COI tree shows that specimens of the taxon *margreiteri s. str.* and other specimens with a closely similar colour pattern (corbicula framed with rusty hairs, with the lower side of the thorax and the ventral side of the body black), but with the pale bands white or very slightly yellow (Skorikov's taxon *altaicus* from the Altai, MD#739), have very short branch lengths between them (Fig. 13: the yellow-banded taxon *margreiteri s. str.* MD#319 and the white-banded taxon *altaicus* MD#329). Some females, especially workers from Mongolia and the Tian Shan (white-banded), have most of the hair on the outer side and edges of the hind tibia orange, except at the extreme proximal end where it remains black (MD#287, 288, 307, 327). A few females from Mongolia and the Tian Shan (white-banded) have more pale hair, both on the lower side of the thorax extending to the base of the midleg (some black hair intermixed), on all three femora, and on the ventral side of the metasoma (most extreme for the 'semipale' worker MD#287 and for the queens MD#4103, 4104). All of these individuals are interpreted as conspecific, as parts of the species *B. margreiteri s. l.*.

There appears to be a disjunction between the northern Altai-Transbaikal population and the Tian Shan population. No specimens from this Tian Shan population (e.g. MD#4103, 4104) have been sequenced successfully.

The disjunct population in Kamchatka (Bischoff 1930; Ito & Kuranishi 2000) is remarkable for its wide separation from the Central Asian and Baikalian population by more than 3570 km (only slightly less if Skorikov's [1910b] record for Transbaikal, given as Troitzkosavsk [= Kyakhta] in Skorikov, 1931, is included) in combination with so little divergence in COI sequences (Fig. 13: no base-pair differences are uniquely shared by the Kamchatka samples MD#1265, 1268, compared with the Altai taxon *margreiteri s. str.* MD#319). These Kamchatka specimens are considered conspecific with *B. margreiteri.*

In another surprising and large extension of the range, a taxon with much more extensively yellow-banded hair (and less black) is recorded here perhaps for the first time (but see Morawitz 1890:352 for a possible record). The yellow hair extends onto the lower side of the thorax and onto the ventral side of the metasoma, with the corbicula orange-fringed. It was collected at only two neighbouring sites (at Heishi and Qushiang, near Dulan, in Qinghai, China) that are distantly disjunct and separated by more than 1270 km from the nearest other recorded site for the

species, in Mongolia. These two Qinghai sites are in the mountains at the southeastern end of the Qaidam depression, in a northern extension of the Burhan Budai Shan. All specimens from Dulan sequenced for COI (4/55 specimens) share the same haplotype, which differs from all other *B. margreiteri* haplotypes only at position 271 (T substituted for C) and these samples are interpreted as conspecific with *B. margreiteri* (Fig. 13: the extensively yellow samples from near Dulan labelled 'pale' MD#289, 292, 293, 294 compared with the taxon *margreiteri s. str.* MD#319). The male genitalia do not differ appreciably. We do not name this population formally (as a subspecies) because we wish to avoid adding to the many unnecessary formal names for bumblebees below the rank of species.

Throughout its range, except in Qinghai, the species *B. margreiteri s. l.* shows a dimorphism in the pale bands, with white-banded individuals (taxon *altaicus*) and yellow-banded individuals (taxon *margreiteri s. str.*) both recorded from Kamchatka, the Altai, and the Tian Shan (Fig. 13). This dimorphism may be similar to that shown by *B. handlirschianus* in Western Asia (see the comments on *B. handlirschianus*). However, for *B. margreiteri s. l.*, white-banded individuals are more frequent in Mongolia and yellow-banded individuals are more frequent in the Tian Shan and in Qinghai.

Contrary to a previous interpretation of morphology (Williams, 1991) when not all of the types could be examined, COI sequences from specimens identified from their yellow-banded colour pattern and black-fringed corbicula as Skorikov's taxon *defector* are now found to be a separate species (Figs 11–12; see the comments on *B. defector*).

**Diagnostic description.** Wings nearly clear. *Female hair colour pattern*: generally black, but with pale hair (yellow or grey-white) in a large patch ventral to the base of the antenna, in a small patch or absent from the vertex of the head, in a transverse band anteriorly on the thoracic dorsum and extending laterally and ventrally to half way down the side of the thorax, or more rarely to the midleg base, in a transverse band posteriorly on the thoracic dorsum (scutellum; so the thoracic dorsum between the wing bases has the hair black, only rarely with pale hair intermixed laterally, adjacent and mesad to the tegula), on T1–2, although T2 is pale with only a few black hairs intermixed along the posterior margin, orange hair sometimes on T3 as a posterior fringe and always on T4–6, except T6 medially intermixed with short black hairs, hair of the ventral side of the metasoma usually black but sometimes pale. Hindleg tibia with the corbicular fringes often appearing double (*cf. B. defector, B. turkestanicus*): hairs on the corbicular surface and in the adjacent inner fringes usually extensively orange, but exterior to this in the outer fringes (anteriorly and posteriorly) black, or rarely with more black hairs in the inner fringes, although usually the inner fringes retaining many extensively orange hairs (Fig. 22). *Female morphology*: labrum with the basal depression narrow, the transverse ridge broader medially than the basal depression, in the median third high, consistently convex throughout and not subsiding or interrupted, with only a few scattered medium or large punctures (slightly more for individuals from Kamchatka), lateral tubercles smooth with few punctures (Fig. 19) (*cf. B. defector, B. turkestanicus*). Clypeus in its central half with few widely spaced small punctures, fewer large punctures (*cf. B. defector, B. turkestanicus*). Hindleg tibia distal edge with broad spines (rastellum) often continuing just onto the posterior edge by two or three spines (*cf. B. defector, B. turkestanicus*). *Male morphology*: genitalia (Fig. 33) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin. Gonostylus distally thick, rounded in section, and finger-like; gonostylus with the inner distal corner narrowly acute from both the inner and the dorsal aspects; gonostylus proximal half with the sides diverging (Altai, Qinghai). Penis-valve inner shoulder located at ≤ 0.5× the length of the penis valve from the distal end to the broadest point of the spatha; penis valve proximal to the outer shoulder > 2× as broad as the penis-valve head; penis-valve head laterally compressed.

**Material examined.** 56 queens 88 workers 33 males, from China, Kazakhstan, Kyrgyzstan, Mongolia, and Russia (Fig. 65: HUS, IAR, ISEAN, IZB, LP, MNHU, NHM, NME, OLL, PW, RMNH, UMONS, ZISP, ZMMU), with 19 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine and subalpine grassland, at elevations 164–(2538)–3526 m a.s.l.. A species with an unusual distribution among four distantly disjunct centres: (1) the central Tian Shan; (2) the Altai, Sayan, Mongolia and Buryatia mountains; (3) the Burhan Budai Shan; and (4) southern Kamchatka. Other genes should be checked to confirm that these are disjunctions within a single species. Individuals from Buryatia (Mondy: D. Michez, pers. comm.) and from the Burhan Budai Shan are from meadows at the upper elevational limit of trees, although there are few trees in the latter area. The population in Kamchatka is restricted to a small area where it may be associated with geothermal features (see below). This species overlaps with *B. turkestanicus* and *B. defector* in the Tian Shan, and it sometimes occurs together with one or (rarely) both of them.

The modern Kamchatka population appears now to be a relic in the warmer south-eastern coastal areas of the peninsula, where the climate is warmed by the effect of the summer southerly storms (Anonymous 2001; Newell 2004). There is another more intriguing possibility—that the Kamchatka climate is also buffered locally by strong geothermal effects. Ebmer (1996) records that the bee *Halictus rubicundus* (Christ) is a widespread holarctic species with a small northern pocket of occurrence in the same region of south-eastern Kamchatka (Kronotsky), where all of the *H. rubicundus* specimens collected (by M. Krappe, *in litt.* to Ebmer) were confined to geothermally influenced sites. Similar close association of nests of the bee *Lasioglossum nupricola* Sakagami with geothermal features has been reported from two sites on Hokkaido, Japan, where this species has been interpreted as a climate relic (Sakagami 1988).

**Food plants.** (Scrophulariaceae) pink *Pedicularis* sp. (PW: the same species as shown in Figs 5–6, 31.viii.2010, Heishi near Dulan, Qinghai, China).

**Behaviour.** Mate-searching males perch on the tops of e.g. flowering spikes of *Pedicularis* sp. and from these pursue other bees that fly past before the males return to the same perch (PW: Figs 5–6, 31.viii.2010, 3519 m at Heishi near Dulan, Qinghai, China).


## 11. *Bombus handlirschianus* Vogt
(Figs 34, 50, 66)

[*Bombus mendax* Gerstaecker; Morawitz 1881:243, in part, misidentification.]
<*Bombus mendax*> var. *Handlirschianus* Vogt 1909:49, type-locality citation 'kaukasischen'. **Lectotype** queen by present designation RMNH examined, 'Mamisson Pass' (Caucasus, Georgia/Russian border). Note 1.
[*Bombus mendax* subsp. *caucasicus* Skorikov 1910a:78, 81, published without description. Note 2.]
<*Bombus mendax*> subsp. *shaposhnikovi* Skorikov 1910b:329, type-locality citation (Cyrillic) '[Caucasus]'. **Lectotype** male by present designation ZISP examined, (Cyrillic) '[Kubanskoy Oblast]' (Caucasus, Russia). Note 3. Regarded as conspecific with *Bombus handlirschianus* Vogt by DeMeulemeester *et al*. (2010), supported here.
*Mendacibombus handlirschianus* (Vogt); Skorikov 1923:149.
*Mendacibombus shaposhnikovi* (Skorikov); Skorikov 1923:149.
*Bombias (Mendacibombus) handlirschianus* (Vogt); Rasmont 1983:10.
*Bombias (Mendacibombus) shaposhnikovi* (Skorikov); Rasmont 1983:10.
*Bombus (Mendacibombus) handlirschianus* Vogt; P.H. Williams 1998:100.
*Bombus (Mendacibombus) shaposhnikovi* Skorikov; P.H. Williams 1998:100.


Note 1 (*handlirschianus*). Vogt described his var. *handlirschianus* referring to a part of the population with both a particular area of distribution and a particular colour pattern, showing no evident intention of infrasubspecific status (e.g. without mentioning a higher rank subspecific taxon), so the taxon is deemed to be of subspecific rank (ICZN 1999: Article 45.6.4).

Vogt's original description of the taxon *handlirschianus* cites the type locality as 'kaukasischen'. The RMNH collection studied by Vogt contains a queen (and other specimens) that agrees with the original description but also carries the labels: (1) white, handwritten 'Mamisson / Pass ca 2750 / 21 VIII 03; (2) white, printed 'Collectie / C. et O. Vogt / Acq. 1960'; (3) red, printed 'Bombus / mendax Handlirschianus / Vogt 1909 / ZMAN type HYME.0112.4'; (4) red, handwritten 'B. MENDAX var. HANDLIRSCHIANUS / VOGT, 1909:43 / LECTOTYPE [female] / P. RASMONT DES. 2008' (P. Rasmont, unpublished); (5) green, printed '*Mendacibombus* / MD# 1271 det. PHW'; (6) red, printed 'LECTOTYPE [female] / *Bombus mendax* var. / *handlirschianus* / Vogt, 1909 / det. PH Williams 2012'; (7) white, printed '[female] *Bombus* / (*Mendacibombus*) / *handlirschianus* / Vogt / det. PH Williams 2012'. This queen, which lacks the right midleg, is regarded as a syntype and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

Note 2 (*caucasicus*). Skorikov's attribution of the name *caucasicus* to a subspecies of *B. mendax,* supposedly described by Vogt from the Caucasus, may have arisen from confusion with the name *B. lapidarius* 'Form (*caucasicus* RAD.)' that also appears on Vogt's (1909) page 49, in a paragraph above his description of *B. mendax* var. *handlirschianus* from the Caucasus.

Note 3 (*shaposhnikovi*). Skorikov's original description of the taxon *shaposhnikovi,* which does not specify the sex of the specimens examined, cites the type locality as the Caucasus. The ZISP collection studied by Skorikov contains a male that agrees with the original description and carries the labels: (1) white, printed (Cyrillic) '[gora Loganaky / Kubanskoy obl. / *Shaposhnik*] VII08'; (2) white, handwritten in pencil '[illegible] / N 8'; (3) white, printed '*k. Skorikova*'; (4) red, printed '*Lectotypus Bombus* / *mendax subsp.* / *shaposhnikovi Skor* / design. *Podbolotsk.*' (M. Podbolotskaya, unpublished); (5) green, printed '*Mendacibombus* / MD# 3522 det. PHW'; (6)

red, printed 'LECTOTYPE [male] / *Bombus mendax* ssp. / *shaposhnikovi* / Skorikov, 1910 / det. PH Williams 2012'; (7) white, printed '[male] *Bombus* / (*Mendacibombus*) / *handlirschianus* / Vogt / det. PH Williams 2012'. This male, which is complete, is regarded as a syntype and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

A second male collected at Mt Loganaky by Shaposhnikov in 1908 (MD#835, NHM, sent by Skorikov as part of an exchange with the NHM in 1934), closely similar in morphology, is designated here as a paralectotype and is interpreted as conspecific.

**Etymology.** The species is named after A. Handlirsch, who in 1909 was an entomologist (and later Director) at the Natural History Museum of Vienna.

**Taxonomy and variation.** The interpretation of this species is based here on DNA and the form of the male genitalia. This disagrees with earlier concepts (Skorikov, 1923, 1931), diagnosed originally in terms of the hair colour pattern (Skorikov, 1910b), because the species appears to be much more variable in colour pattern than was originally understood.

**TABLE 8.** Observed numbers of individuals of *B. handlirschianus* with each of two hue states of the pale bands of the hair, together with expected numbers from simple genetic models of inheritance, all samples combined.

| All samples (n=634) | Pale hair hue | Observed | | Expected | |
|---|---|---|---|---|---|
| | | males (haploid) | females (diploid) | females - no dominance | females - simple dominance |
| Number | yellow | 28 | 136 | 241 | 102 |
| | white | 38 | 432 | 327 | 466 |
| Frequency | yellow | 0.424 | | | (recessive) |
| Chi-square | 1-sample test (df = 1) | | | 79 | 13.8 |
| Probability that deviation of observation from expectation is due to chance | | | | << 0.0001 | < 0.001 |

**TABLE 9.** Observed numbers of individuals of *B. handlirschianus* with each of two hue states of the pale bands of the hair, together with expected numbers from simple genetic models, samples from northeast Turkey around Erzurum (39–42°N 39–43°E).

| NE Turkey (n= 485) | Pale hair hue | Observed | | Expected | |
|---|---|---|---|---|---|
| | | males (haploid) | females (diploid) | females - no dominance | females - simple dominance |
| Number | yellow | 24 | 104 | 242.5 | 121 |
| | white | 24 | 381 | 242.5 | 364 |
| Frequency | yellow | 0.500 | | | (recessive) |
| Chi-square | 1-sample test (df = 1) | | | 158 | 3.18 |
| Probability that deviation of observation from expectation is due to chance | | | | << 0.0001 | > 0.07 not significant |

Vogt (1909) described females (e.g. MD#1271) of the taxon *handlirschianus s. str.* briefly as having the pale bands white and Skorikov (1910b) described in more detail females (e.g. MD#3522) of the taxon *shaposhnikovi* as having the pale bands yellow, the corbicula framed with rusty hairs, and T3 entirely black. Our COI tree shows that specimens of these taxa can be indistinguishable in the available sequences (Fig. 13: the white-banded taxon

*handlirschianus s. str.* MD#427 and the yellow-banded taxon *shaposhnikovi* MD#3859) and are interpreted as conspecific, as parts of the species *B. handlirschianus s. l.*. Males with both colour patterns share the same diagnostic form of the male genitalia, supporting the white/yellow dimorphism in the pale bands of the females suggested for Turkish specimens from four genes by Cameron *et al.* (2007), and adding to the evidence of De Meulemeester *et al.* (2010). Both colour patterns of this species occur in Turkey, the Caucasus, and as far east as the Alborz mountains of Iran (Pittioni 1937b). Throughout this region, other species also show a similar yellow/white dimorphism (Rasmont *et al.* 2005; P.H. Williams, Byvaltsev, *et al.* 2012). The white-banded female colour pattern (taxon *handlirschianus s. str.*) is a particularly characteristic and frequent convergent colour pattern in this region (P.H. Williams 2007).

Because a relatively large sample is available, we can compare the observed yellow/white dimorphism for this species with a simple genetic model in which we assume that the two pale hue states are each determined by one of two alleles at a single gene locus (P.H. Williams 1991). We assume that there is a single homogeneous population with random interbreeding, unselective predation or other loss, and that this population has been sampled at random. Because males can be assumed usually to be haploid (Plowright & Pallett 1979), we can estimate the frequency of each allele within the population from the frequency of each colour state among the males. If the observed frequency of one colour state were much higher among the haploid males than among the diploid females, then this colour state might be coded for by a recessive allele. We could then estimate the expected frequency of the colour states among the females from the observed frequency of the alleles among the males using the Hardy-Weinberg equilibrium model. When this expected frequency is tested within the entire sample in our database, the observed frequency of colour states among the females is confirmed to differ from the frequency among the males, although it also differs from the frequency predicted among the females by the model of simple dominance at one locus, so we must reject the model (Table 8). However, we know that sampling intensity was not uniform across the entire range, and the frequency of alleles or the selectivity of sampling may also have varied geographically. Therefore we repeated the test, but restricting the sample used to the region of north-eastern Turkey around Erzurum, a small fraction of the total extent of occurrence, but reducing the sample size by only about one quarter (from 634 to 485 specimens). When the test was repeated for the geographically restricted subsample, the observed frequency of colour states among the females still differs from the frequency among the males, but the frequency predicted among the females no longer differs significantly from the model of simple dominance at one locus (Table 9). Confirmation of this model would require breeding experiments to test the pattern of inheritance (*cf.* Owen & Plowright 1980). Nonetheless, this result is consistent with both the yellow-banded and the white-banded bees being parts of a single species, *B. handlirschianus s. l.*, supporting the synonymisation of the taxon *shaposhnikovi* as part of this species.

**Diagnostic description.** Wings nearly clear. *Female hair colour pattern:* generally black, but with pale hair (yellow or grey-white) in a small patch ventral to the base of the antenna, usually absent from the vertex of the head, in a transverse band anteriorly on the thoracic dorsum and extending laterally and ventrally to from half to two-thirds the way down the side of the thorax, in a transverse band posteriorly on the thoracic dorsum (scutellum; so that the thoracic dorsum between the wing bases has the hair entirely black), on T1–2, although T2 has a few black hairs intermixed along the posterior margin, T3 with orange hair only as a very few hairs posteriorly, T4–6 always orange except T6 medially with a few short unobtrusive black hairs. Hindleg tibia with the corbicular fringes with a mixture of orange and black hairs. *Female morphology:* labrum with the basal depression narrow, the transverse ridge broad and low, in the median third subsiding only slightly and uninterrupted, with only a few scattered punctures, lateral tubercles almost without punctures. *Male morphology*: genitalia (Fig. 34) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin. Penis-valve inner shoulder located at $\leq 0.5\times$ the length of the penis valve from the distal end to the broadest point of the spatha; penis valve proximal to the outer shoulder $< 2\times$ as broad as the penis-valve head; penis-valve breadth just proximal to the penis-valve head $0.06\times$ the length of the penis valve distal to the broadest point of the spatha.

**Material examined.** 128 queens 454 workers 67 males (plus 14 with sex/caste undetermined), from Armenia, Azerbaijan, Georgia, Iran, Iraq, Russia, and Turkey (Fig. 66: AM, HH, HO, MS, NHM, OLL, PW, RMNH, UMONS, ZISP, ZSM; specimens in the UMONS database do not have individual MD# labels), with 5 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine and subalpine grassland, at elevations 472–(2338)–3982 m a.s.l.. A species of the Alborz, Caucasus, and Turkish mountains. There is no overlap in distribution with any other *Mendacibombus* species. Regional distribution maps are available for Turkey (Rasmont & Flagothier 1996; Özbek 1997) and for western Asia (Rasmont & Iserbyt 2012). Özbek (1997) reported that the species has been in decline in Turkey, although evidence for this is not apparent now (M. Aytekin, pers. com.).

**Food plants.** Özbek (1997).

**Behaviour.** De Meulemeester *et al.* (2010).

## 12. *Bombus mendax* Gerstaecker
(Figs 35, 37, 43, 44, 48, 67)

*Bomb.<us> mendax* Gerstaecker 1869:323, type-locality citation 'Königsalpen bei Kreuth (4000 Fuss)'. **Lectotype** queen by present designation ZISP examined (PR), 'Kreuth 4000' ' (Alps, Germany). Note 1.

*<Bombus mendax> latofasciatus* Vogt 1909:50, type-locality citation 'pyrenaeischen'. **Lectotype** queen by present designation RMNH examined, 'Gèdres' (Pyrenees, France). Note 2.

[*Bombus mendax* ab. *atrocaudatus* Vogt 1909:50, infrasubspecific.]

[*Bombus mendax* var. *bizonatus*, var. *friseanus,* var. *perfuga* Skorikov 1910b:328-329, infrasubspecific.]

*Bombus mendax* var. *anonymus* Friese 1911b:572, type-locality citation 'Alpen'. **Lectotype** queen by present designation MNHU examined, 'Sierre Alp.' (Alps, Switzerland). Note 3.

*Mendacibombus mendax* (Gerstaecker); Skorikov 1923:149.

[*Bombus mendax* morpha. nov. *subglacialis,* ab. nov. *flavior*, ab. nov. *feretypicus*, ab. nov. *basizonus* Pittioni 1937a:121-122, infrasubspecific.]

[*Bombus (Mendacibombus) mendax* f. *flavopleuralis*, f. *quasilatofasciatus* Pittioni 1939:103, infrasubspecific.]

*<Mendacibombus mendax>* ssp. *pyrenes* Tkalců 1975:173, unnecessary replacement name for *latofasciatus* Vogt (1909:50). Note 4.

*Bombias (Mendacibombus) mendax* (Gerstaecker); Rasmont 1983:10.

*Bombus (Mendacibombus) mendax* Gerstaecker; P.H. Williams 1998:99.

Note 1 (*mendax*). Gerstaecker's original description of the taxon *mendax* cites the type locality as 'Königsalpen bei Kreuth (4000 Fuss)'. The ZISP collection contains material studied by Gerstaecker and includes a queen that agrees with the original description and carries the labels: (1) white, handwritten 'Kreuth 4000' '; (2) white, printed 'Osnovnaya kollektsiya'; (3) white, handwritten 'mendax Gerst. Typ.'; (4) white with a black border, hand-written 'mendax Gerstäck.'; (5) red, handwritten 'Type'. No labels were added for this project. This queen, which is complete, is regarded as a syntype and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

Note 2 (*latofasciatus*). The name *latofasciatus* was used by Vogt (1909: pages 42, 49, 50) for colour-pattern-based taxa within four different species (*B. lucorum, B. mendax, B. sichelii* [as *B. sicheli*]*,* and *B. terrestris*). For the names *latofasciatus* that were used for parts of *B. lucorum* and *B. terrestris*, Vogt explicitly referred to his new names using the term 'ab.', so these taxa must remain permanently of infrasubspecific rank (ICZN 1999: Article 45.6.2). In the case of the name *latofasciatus* that was used for a part of *B. sichelii*, he related it to one of three subsets ('Grade') within the part of the population with yellow bands known from the Alps and Pyrenees (referred to by him as [subspecies] *alticola*), thereby implying infrasubspecific rank for this *latofasciatus* as well. In contrast, Vogt gave no explicit rank to the taxon *latofasciatus* of *B. mendax,* but did relate it to 'Die pyrenaeischen Exemplare', contrasting them in colour pattern with specimens from the Alps, so this characterisation by geographic distribution and colour-pattern (without a higher subspecific taxon) should be considered to imply subspecific rank as the original intention of the author (ICZN 1999: Article 45.6.1).

Vogt's original description of the taxon *latofasciatus* cites the type locality as 'pyrenaeischen'. The RMNH collection studied by Vogt contains a queen that agrees with the original description and carries the labels (1) green, printed in red 'Gèdres'; (2) white, printed 'Collectie / C. et O. Vogt / Acq. 1960'; (3) red, printed 'Bombus / mendax latofasciatus / Vogt 1909 / ZMAN type HYME.0146.9'; (4) green, printed '*Mendacibombus* / MD# 1239 det. PHW'; (5) red, printed 'LECTOTYPE [female] / *Bombus mendax* / *latofasciatus* / Vogt, 1909 / det. PH Williams 2012'; (6) white, printed '[female] *Bombus* / (*Mendacibombus*) / *mendax* / Gerstaecker / det. PH Williams 2012'. This queen, which is complete, is regarded as one of Vogt's syntypes and is designated here as the lectotype in order to reduce uncertainty in the identity and application of the name.

Note 3 (*anonymus*). Friese's original description of the taxon *anonymus* cites the type locality as 'Alpen' for a queen, worker, and male. The MNHU collection studied by Friese contains a queen that agrees with the original description and carries the labels (1) white, printed 'Sierre Alp. / 19. 6. 84 / Friese'; (2) white, handwritten by Friese '*B. mendax*. / *v.* / *anonymus* / [female] 1909 Friese *Fr.* Det.'; (3) maroon, printed 'Type'; (4) white, printed 'Zool. Mus. / Berlin'; (5) green, printed '*Mendacibombus* / MD# 3540 det. PHW'; (6) red, printed 'LECTOTYPE [female] / *Bombus mendax* var. / *anonymus* / Friese, 1911 / det. PH Williams 2012'; (7) white, printed '[female] *Bombus* / (*Mendacibombus*) / *mendax* / Gerstaecker / det. PH Williams 2012'. This queen, which is complete, is regarded as one of Friese's syntypes and is designated here as lectotype in order to reduce uncertainty in the identity and application of the name.

Note 4 (*pyrenes*). The absence of homonyms for the name *latofasciatus* Vogt (1909: page 50) available from the same date or older (see note 2) makes Tkalcŭ's (1975) replacement name unnecessary.

**Etymology.** The species is named from the Latin *mendax* for liar, presumably a reference to its close resemblance to other orange-tailed bumblebee species in the mountains of southern Germany.

**Taxonomy and variation.** The interpretation of this species here is based on DNA and the form of the male genitalia. It agrees with earlier interpretations, which include the substantial variation in the colour pattern of the hair.

This species shows unbanded (taxon *mendax s. str.*) or narrowly yellow-grey-banded (taxon *anonymus* MD#3540) colour patterns in the Alps (Pittioni 1937a), with more broadly yellow-banded colour patterns (taxon *latofasciatus* MD#1239) further west in the Pyrenees and in Santander in northern Spain (Vogt 1909; Kruseman 1958: his fig. 6). Our COI tree shows that specimens with these colour patterns can be indistinguishable in the available sequences and are interpreted as conspecific (Fig. 13: the unbanded taxon *mendax s. str.* from the Alps MD#301, the narrow-banded taxon *anonymus* from the Alps MD#303, and the broad-banded taxon *latofasciatus* from the Pyrenees MD#3857), as parts of *B. mendax s. l.*.

The distribution of this species is interrupted by two relatively small disjunctions (*cf. B. margreiteri*): between the Alps and Pyrenees (> 500 km); and between the Pyrenees and the Picos de Europa in Santander (> 300 km).

The RMNH collection includes at least two queens each with a label printed with 'Tunkun / Sayan' and a handwritten label *mendax*. One is a queen of *B. margreiteri* (MD#1144), for which the Tunkin mountains are consistent with its known distribution (Fig. 65). However, the other queen (MD#1280) appears from its morphology and colour pattern to be a genuine queen of *B. mendax*. This specimen has the hair of the thoracic dorsum anteriorly with a narrow pale greyish band with black intermixed, whereas the side of the thorax, the scutellum, T2, and the foreleg and midleg basitarsi are predominantly black, like many *B. mendax* from the Alps (Pittioni 1937a). Without COI data we cannot at present make a definitive determination. Therefore the apparent Tunkin location is likely to be the result of mislabeling and this record is not included on the map for *B. mendax* (mislabelling is not unknown: see the note on the holotype of *B. superbus*).

**Diagnostic description.** Wings nearly clear. *Female hair colour pattern:* generally black, but with yellow hair varying from completely absent from the entire body to present over most of the face and in a small patch on the vertex of the head, a transverse band anteriorly on the thoracic dorsum and extending laterally and ventrally almost to the midleg base, in a transverse band posteriorly on the thoracic dorsum (scutellum; so the thoracic dorsum between the wing bases has the hair entirely black, sometimes the yellow bands with black hairs intermixed), often on T1, sometimes on T2 pale in the anterior half, always orange hair on T3 as a posterior fringe and throughout T4–6, except T6 medially with black hair. Hindleg tibia with the corbicular fringes extensively orange. *Female morphology:* labrum with the basal depression broad, the transverse ridge in the median third narrowed but not interrupted or subsiding, or subsiding only slightly, with only a few scattered punctures, the lateral tubercles with few punctures. *Male morphology:* genitalia (Fig. 35) with the volsella distally rounded (finger-shaped) and curled back dorsally but not anteriorly; volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved ridge just inside the inner margin. Gonostylus distally thick, rounded in section, and finger-like; gonostylus with the inner distal corner almost a right angle from both the inner and dorsal aspects. Penis-valve inner shoulder located at $\leq 0.5\times$ the length of the penis valve from the distal end to the broadest point of the spatha; penis valve proximal to the outer shoulder $> 2\times$ as broad as the penis-valve head; penis-valve head dorso-ventrally compressed.

**Material examined.** 383 queens 1249 workers 142 males (plus 6 with sex/caste undetermined), from Andorra, Austria, France, Germany, Italy, Spain, and Switzerland (Fig. 67: AA, AS, ENAM, LC, MNHN, MNHU, NHM, PW, RBIN, RMNH, UMONS, ZIUB, ZSM; specimens in the UMONS database have not had individual MD# labels added), with 7 specimens sequenced (interpretable sequences listed in Figs. 11–13).

**Habitat and distribution.** Flower-rich alpine and subalpine grassland, at elevations 655–(2111)–3098 m a.s.l.. A species distributed in three principal disjunct centres, in the Alps, the Pyrenees, and the Cantabrian mountains. There is no overlap in distribution with any other *Mendacibombus* species. Distribution maps are available for France (Rasmont 1988), Spain (Ornosa & Torres 2010), and Europe (Rasmont & Iserbyt 2012; Rasmont *et al.* 2015).

So far, this is the only species of the subgenus *Mendacibombus* to have been assessed for Red List threat status using the IUCN criteria (2001). Cederberg *et al*. (2013) listed it as 'Near Threatened' because its known area of occupancy (AOO) is small (2,236 km²), the species' distribution is considered severely fragmented, and they believe that the number of individuals has been declining due to climate change, putting the species close to qualifying for the IUCN category 'Vulnerable' (Criterion B2). Rasmont *et al*. (2015) use climate-change models to assess this species as having a high risk of extinction from climate change by 2100.

**Food plants.** Pittioni (1937a), Aichhorn (1976), Haas (1976), Rasmont (1988), von Hagen & Aichhorn (2003).

**Behaviour.** Aichhorn (1976), Haas (1976), von Hagen & Aichhorn (2003).


## Discussion

This study changes concepts of *Mendacibombus* species and the names applied to them from the interpretation in previous reviews (Table 7).

**Sources of uncertainty.** Potential sources of uncertainty in this study include: (1) insufficient sampling; (2) problems in estimating and dating phylogeny; and (3) problems in recognising and naming species. We consider these below.

First, we recognise that for a taxonomic revision it is of paramount importance to sample all of the species from across their entire distribution ranges and that partial, regional treatments can give misleading results (Bolton 2007; P.H. Williams, Byvaltsev, *et al.* 2015). Global sampling of the bumblebees of the subgenus *Mendacibombus* has inevitably been uneven. The majority of specimens are from Europe (Fig. 71), because this region has been more accessible to the most active collectors. We have chosen not to use rarefaction (Colwell 2005) to estimate the species richness that would be expected from similar sample sizes from all regions because at this coarse spatial scale the assumptions are violated by patchy distributions and sampling (Heck *et al.* 1975). However, our results show that regional richness in the species we recognise (Fig. 72) is not a simple function of sample size (Fig. 71; there is no significant Spearman rank correlation $\rho = 0.23$, $p > 0.05$), so that spatial bias in sampling has not had an overwhelming effect on species recognition. Where our knowledge is still most lacking is of the fauna of the central and northern Qinghai-Tibetan plateau, where little is known of the fauna of most of the higher parts of the western Kunlun Shan and of the Altun Shan (Altyn Tagh) (Fig. 9). These are large regions of very high arid mountains where access is still extremely difficult and where *Mendacibombus* bumblebees are expected to occur only in small, isolated, flower-rich habitat patches, for example where there is reliable water from glacial outflows (P.H. Williams, Bystriakova, *et al.* 2015). Similarly, our COI data are unlikely to sample enough individuals to represent all of the haplotypes of extant *Mendacibombus* species. Of the unique haplotypes identified by the Collapse procedure, the rarest haplotypes of most species remain represented by single sequences without duplicates (Table 10). Unduplicated sequences of a haplotype have been interpreted as evidence of under-sampling of the true haplotype diversity within species (Phillips *et al.* 2015). In addition, it has not been possible to obtain fresh material of some species that would yield longer sequences (especially for *B. makarjini, B. marussinus,* and *B. himalayanus*). However, our sampling broadly across the geographical ranges of the species, where practical (Figs 56–67), should have improved the representation of variation.

Second, we recognise that there are many potential pitfalls in estimating phylogenetic relationships from genes (Baum & Smith 2012). But as yet, there is little evidence that these problems have affected substantially the studies seeking to recognise bumblebee species (Bertsch 2010; P.H. Williams *et al.* 2011; P.H. Williams, Brown, *et al.* 2012; Lecocq *et al.* 2013; P.H. Williams, Byvaltsev, *et al.* 2015). Reliable estimates of phylogeny for the 12 species of the subgenus *Mendacibombus* were not easily obtained and many analyses were run refining the data and models before the results showed stability. BEAST analyses for both the COI tree and the linked tree for four genes still require two billion generations of the MCMC algorithm in order to achieve effective sample sizes close to or exceeding 100 according to Tracer. Successive BEAST analyses eventually converged on closely similar trees as evidence that adequate searching (or 'mixing') across the parameter space was attained (Baum & Smith 2012). Among these trees, consistently low support for some nodes (Figs 11, 12, 68) indicates points of conflict among alternative trees. For the poorly resolved relationships among species within the *marussinus-defector*-group, successive speciation events are likely to have occurred close together in time, so that it is difficult to find sufficient

nucleotide changes to provide definitive evidence. In this case, even the faster COI gene did not resolve relationships reliably (Figs 11, 12), although more complete 16S (or other fast-gene) data might help in the future. Nonetheless, it is encouraging that for the species shared in common, our results from four genes (Fig. 68) are consistent with those obtained by Cameron *et al*. (2007) from five genes.

Third, we accept that coalescent-based approaches to recognising species have a stronger theoretical justification in comparison with genetic-distance-based approaches because they are based most directly on the concept of species as evolutionarily independent lineages (P.H. Williams, Byvaltsev, *et al.* 2015). However, coalescent-based approaches can have potential pitfalls and have to be applied with care (Reid & Carstens 2012; Fujisawa & Barraclough 2013; Talavera *et al.* 2013; Zhang *et al.* 2013; Leliaert *et al.* 2014). In particular, coalescent-based approaches may not work well when there has been unrepresentative sampling (P.H. Williams, Byvaltsev, *et al.* 2015). For *Mendacibombus*, our results using coalescent-based approaches are corroborated because the putative species are also supported by diagnostic morphological characters (see the keys and the discussion of variation below).

Naming of species in our results (Fig. 13) would be subject to error if we have failed to associate correctly our COI-sequence proxy types with the original type specimens (Table 1), a subjective process. Previously, associating specimens within taxa of the subgenus *Mendacibombus* has been a problem even for the original author of many of the taxa (Skorikov, 1931). This could be a particular problem for this group because morphological characters are sometimes subtle and because of the difficulty in obtaining fresh material from type localities to sequence. In some cases this difficulty has resulted in us having to select COI-sequence proxy types from sites that are distant from the original type localities. The severity of the effect of this problem is difficult to assess here from within our study.

Dating of events in our estimate of *Mendacibombus* phylogeny depends on just one date estimate, obtained using models of DNA evolution in another study (Hines, 2008). Therefore estimates of dates will compound uncertainties and errors will depend in part on errors in that study. A recent interpretation of a bumblebee fossil has led to a re-appraisal of the age for another group of bumblebees (*Bombus s. str.*), which suggested that that particular group is older and possibly twice as old as suggested from the earlier molecular estimate (Wappler *et al.* 2012). Even if the estimated age of the divergence of the subgenus *Mendacibombus* from the other bumblebees were treated as though precisely known, all of the mean estimates of divergence events obtained by BEAST have broad 95% confidence intervals (of 2.9–7.5 Myr, Fig. 68). Consequently, associations with historical events must be treated with caution.

**Variation among and within species.** COI sequences provide many new characters within the subgenus *Mendacibombus* (Table 5), which provide strong support for groups near the species level (Figs 11, 12). The GMYC and PTP methods have given a clearer and more accountable foundation for the concepts of the different species than was hitherto available, based on gene coalescents. Changes from earlier concepts of these species (Table 7) result especially in changes from the earlier interpretations based on differences in colour patterns.

For the species we recognise from gene coalescents (Fig. 13), we can examine mismatches with groups based on colour patterns and with groups based on external morphology. Within bumblebees generally, pronounced colour-pattern variation is familiar and heterogeneity within species has been inferred to be common (Vogt 1909; P.H. Williams 1998, 2007; Owen *et al.* 2010; Carolan *et al.* 2012; Duennes *et al.* 2012; Hines & Williams 2012; P.H. Williams, An, *et al.* 2012; P.H. Williams, Byvaltsev, *et al.* 2012; Lecocq *et al.* 2013; P.H. Williams, Byvaltsev, *et al.* 2015). In contrast, pronounced morphological variation within bumblebee species is less common, so that a strong mismatch of morphological variation with patterns of COI variation might instead indicate either: (1) COI variation within morphologically homogeneous bumblebee species (P.H. Williams *et al.* 2011); or (2) species undifferentiated in COI (Kuhlmann *et al.* 2007); or (3) COI introgression between species (Ballard & Whitlock 2004; Monaghan *et al.* 2005).

We infer that colour patterns of the hair vary substantially within the species of the subgenus *Mendacibombus* as we recognise them from gene coalescents. In the original descriptions of many of the taxa (Skorikov 1910b) that were subsequently interpreted as separate species (Skorikov 1923, 1931), the hue of the pale hair and the relative extent of the pale and black hair (e.g. on the side of the thorax or on the metasomal sterna) were used as some of the principal diagnostic characters. However, first, considering the hue of the pale bands, 6/12 of the species that we recognise (*B. makarjini, B. avinoviellus, B. himalayanus, B. turkestanicus, B. margreiteri, B. handlirschianus*) have both some individuals with the pale hair yellow and some individuals with the pale hair white. For the single colour-dimorphic species with the largest sample, *B. handlirschianus*, we show that in the best-sampled part of its range, the pattern of yellow/white dimorphism fits a simple dominance model between two alleles (Table 9), again supporting the interpretation that these bees are parts of a single species. Second, considering the extent of the black hair, at least 7/12 of the species that we recognise (*B. waltoni, B. marussinus, B. avinoviellus, B.*

*himalayanus, B. defector, B. margreiteri, B. mendax*) show substantial variation within species in the relative extent of the pale and black hair, particularly on the side of the thorax and on the metasomal sterna. So although these colour-pattern differences were used originally by Skorikov (1910b, 1914) to describe taxa and later species, our results show that they are variable within species and do not diagnose species as we recognise them from gene coalescents. This difficulty in diagnosing species from colour patterns alone has resulted in the splitting and misidentification of polymorphic species (Table 7).
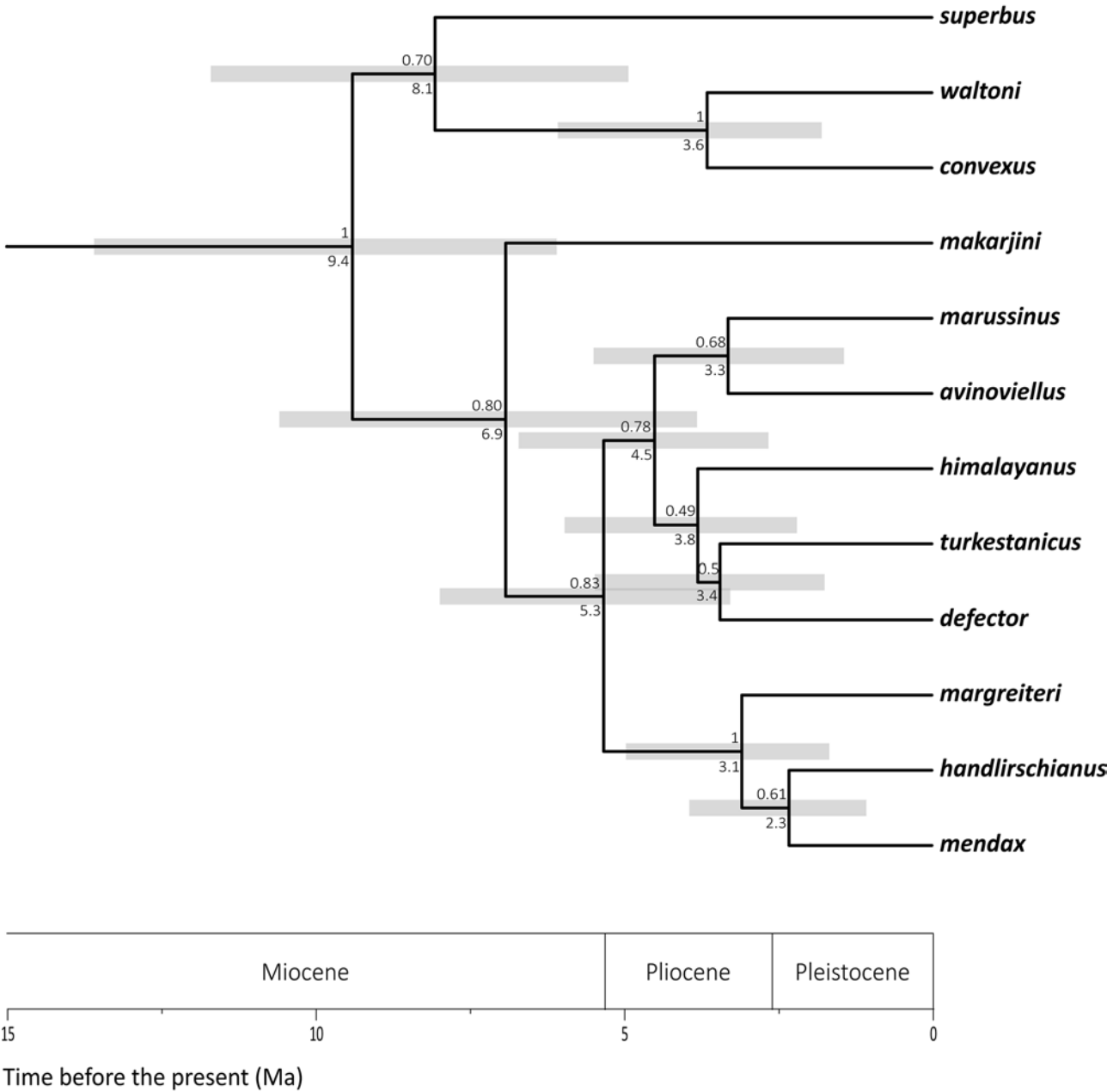


**FIGURE 68.** Best estimate of phylogeny and absolute chronogram for the species of the subgenus *Mendacibombus* (as recognised in Figs 11, 12), from a linked-tree BEAST analysis of COI, 16S, PEPCK and opsin genes. Values above nodes of the maximum clade-credibility tree are Bayesian posterior probabilities showing branch support. Numbers below nodes are the estimated ages of events in Ma (millions of years before the present) based on the *Mendacibombus* root-date estimate of 34 (25–40) Ma from Hines (2008). The grey bars represent the 95% confidence intervals for the estimates of the age of events.
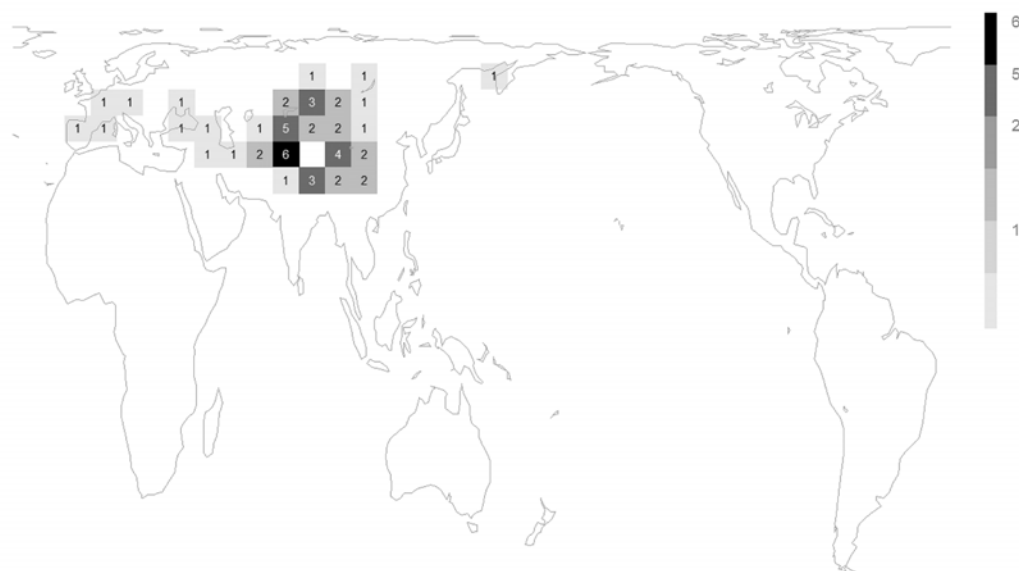
**FIGURES 69–70.** Photos of (69) a worker of *B. superbus* (MD#4123) from (left) the dorsal and (right) the left lateral aspect (scale bar 10 mm), from the sample site (70) in the Tanggula mountains, Xizang, China (16.viii.2014, 32.86142°N 91.91739°E, GPS elevation *ca* 5220 m). Photos by (69) NHM digital imaging unit and (70) Z.-Y. Miao.
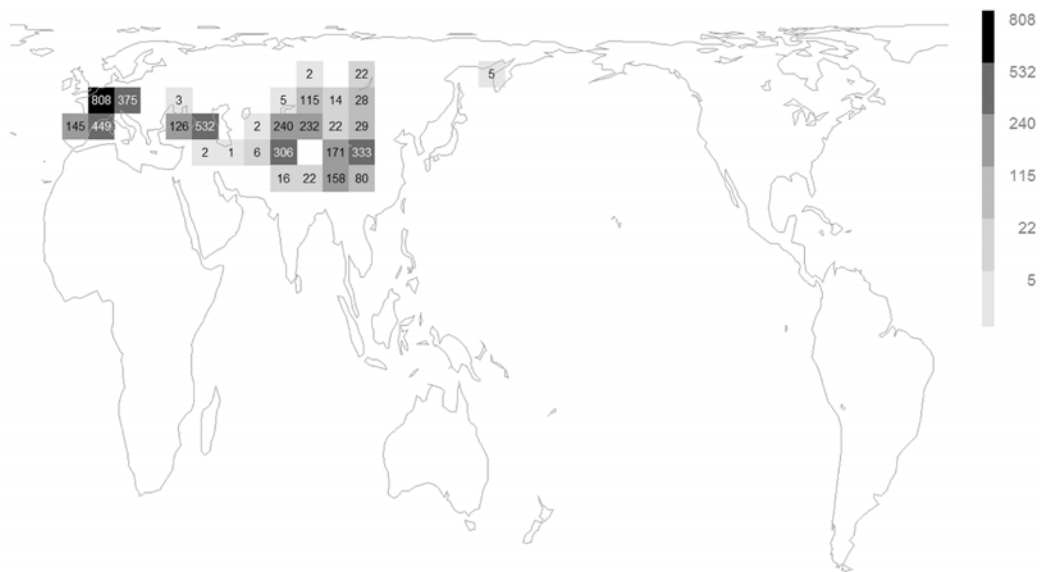
71 specimen richness



72 species richness

**FIGURES 71–72**. Maps of (71) specimen richness and (72) species richness for the subgenus *Mendacibombus* among equal-area grid cells recorded from geo-referenced specimens in the database. The grid is based on longitudinal intervals of 10°, which are used to calculate graduated latitudinal intervals to provide equal-area cells (each cell of area approximately 611,000 km²). Grey scale (right) with equal-frequency richness classes, maximum value in a separate class. Cylindrical orthomorphic equal-area projection (excluding Antarctica) with north at the top of the map.
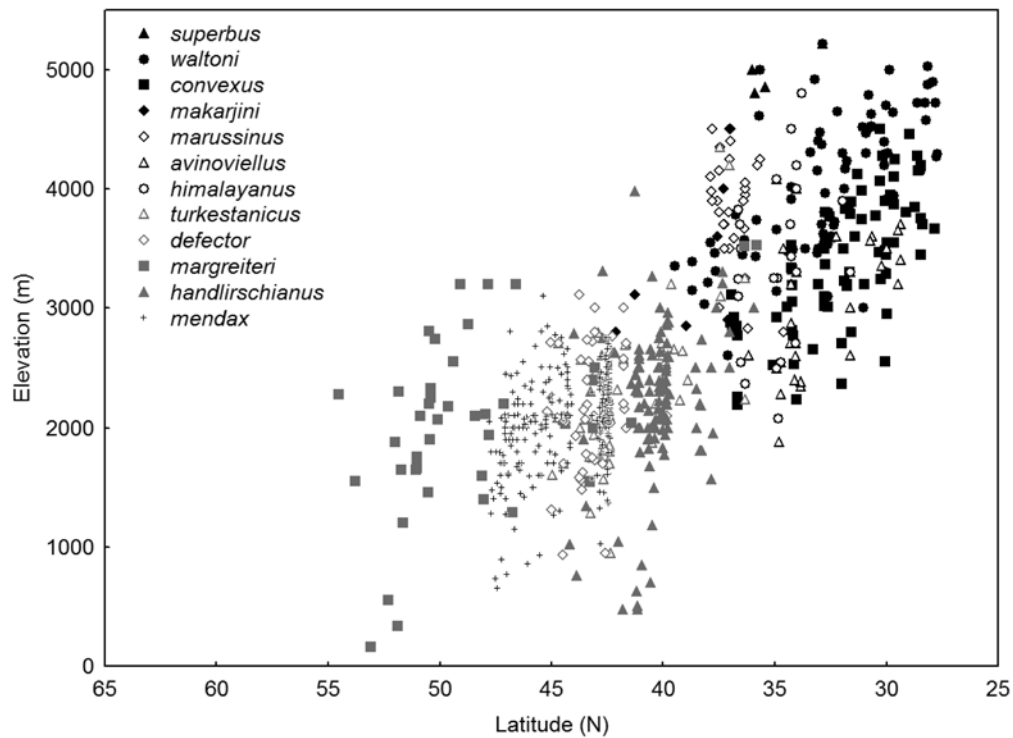
**FIGURE 73.** Plot of elevation (*y*-axis) against latitude (*x*-axis) for the 4413 records of all species of the subgenus *Mendacibombus* world-wide. A key to the symbols identifying species is shown at the upper left.
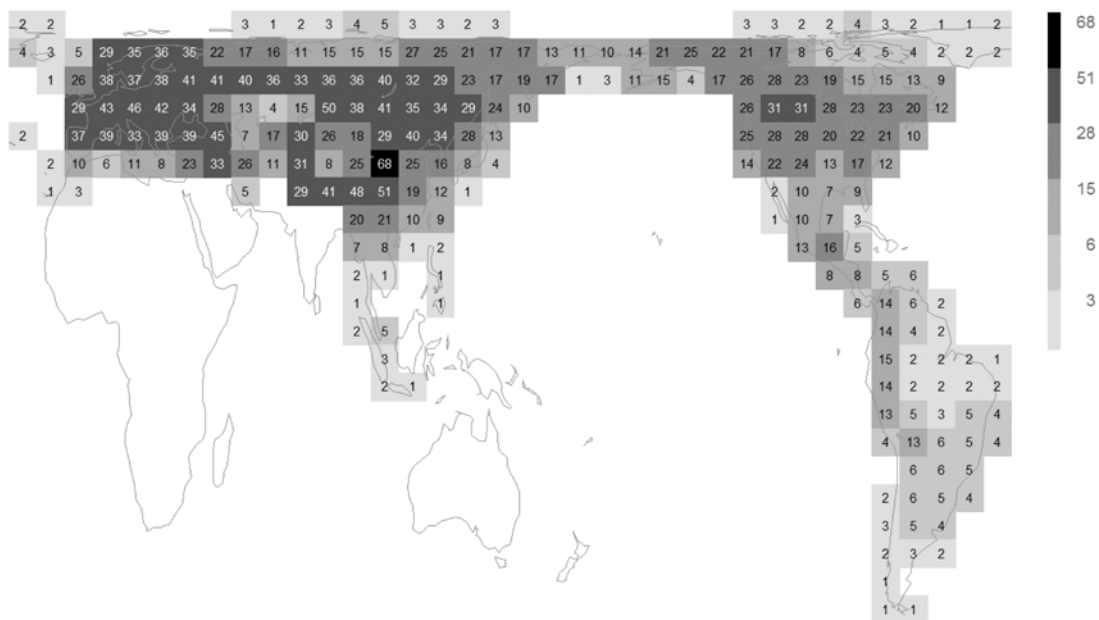


**FIGURE 74**. Map of richness in indigenous species of all bumblebees excluding the subgenus *Mendacibombus* among equal-area grid cells. Map, grid, and grey scale as in Figs 71, 72.

**TABLE 10**. Sampling of species of the subgenus *Mendacibombus* in numbers of specimens, COI sequences, and COI haplotypes from the Collapse analysis.

| Species | Specimens | Specimens < 10 years old | COI sequences | COI unique haplotypes | Matching conspecific COI sequences per rarest haplotype |
|---|---|---|---|---|---|
| *mendax* | 1780 | 70 | 7 | 3 | 1 |
| *handlirschianus* | 663 | 23 | 5 | 3 | 1 |
| *defector* | 483 | 365 | 29 | 6 | 1 |
| *waltoni* | 381 | 224 | 14 | 6 | 1 |
| *convexus* | 353 | 189 | 6 | 3 | 1 |
| *margreiteri* | 177 | 77 | 19 | 6 | 1 |
| *avinoviellus* | 175 | 7 | 8 | 2 | 3 |
| *turkestanicus* | 135 | 63 | 26 | 4 | 1 |
| *marussinus* | 112 | 0 | 3 | 2 | 2 |
| *himalayanus* | 97 | 0 | 3 | 2 | 2 |
| *superbus* | 27 | 22 | 7 | 2 | 1 |
| *makarjini* | 15 | 0 | 3 | 2 | 1 |

In contrast to colour, generally we do not find strong morphological variation within each of the species as we recognise them from gene coalescents. So far the species' limits from gene coalescents appear to be coincident with differences in morphological character states of the male genitalia. This has two consequences. First, absence of the same haplotypes occurring within multiple morphotypes shows no evidence of introgression. Second, it shows that our new morphological characters that correspond with our species recognised from gene coalescents can in practice be used to diagnose these species more easily, especially for males and for older specimens that are difficult to sequence (see the keys).

**Patterns and processes of speciation and extinction.** Divergence between the ancestor of the subgenus *Mendacibombus* and the ancestor of all other bumblebees is believed to have coincided (P.H. Williams 1985; Hines 2008) with a rapid and pronounced cooling in global climate at the beginning of the Oligocene, at *ca* 34 Ma (Zachos *et al.* 2008). This *extrinsic* factor of global climate cooling (Nürk *et al.* 2015) may have favoured the spread of early bumblebees, because it favoured the *intrinsic* factor that both of the early sister-lineages of bumblebees were apparently already better adapted to cool climates than most other bees. In part, this is because bumblebees have an unusually well-developed ability for facultative thermoregulation involving control of the circulatory system (Heinrich 1979). More obviously, the thermal insulation of the long dense pubescence over much of the body surface is combined with bumblebees' frequent use of nest sites that are also well-insulated, both because the nests for the early-diverging species are underground and because the nest sites contain insulating nest material adopted from their previous small-mammal occupants (P.H. Williams *et al.* 2008, their table III). And in contrast to other social bees, bumblebees are unique in being able to hibernate—to pass long, predictable annual seasons of adverse climate (usually winters) at relatively low cost in terms of food requirements (*cf.* the large honey stores required by high-latitude *Apis* colonies to overwinter successfully).

The first divergence among extant bumblebees between the ancestor of the subgenus *Mendacibombus* and the ancestor of all other extant bumblebees (Cameron *et al.* 2007) is asymmetric in its modern diversity, with 12 species of *Mendacibombus* and the current estimate of 253 species of other bumblebees (updated online from P.H. Williams 1998). Even with constant rates of diversification (Markov model: Simberloff *et al.* 1981), phylogenetic trees are expected to be asymmetric, although such a strong asymmetry in this case has a low probability, if diversification rates were uniform ($p= 24/264= 0.09$: Farris 1976). Comparison of sister groups such as these is well suited to studying the factors affecting relative speciation rates (Barraclough *et al.* 1998).

The relative species' diversity in these sister groups may have been affected by their relative diversity of climate niches. For many terrestrial organisms, individuals within any one species are usually considered to share similar climate requirements, which explains the characteristic shift in the elevations that a species inhabits when it occurs at different latitudes, as it tracks similar climates (Cogbill & White 1991). As expected, *Mendacibombus*

bumblebees show this pattern within species, but they also show a similar pattern among species (Fig. 73), with most species at any particular latitude often overlapping broadly (if not always completely) in elevation. This similarity implies that, despite a trend towards spreading northwards in their current distributions for the more recent species (Fig. 73), there is a lack of major evolutionary shifts in species' climate niches, with only small elevational shifts between sister species (Fig. 73). Consequently *Mendacibombus* species can be regarded as showing a degree of relative (if not complete) evolutionary conservatism in their alpine/subalpine climate niches. This contrasts strongly with the sister group of all other extant bumblebees, which show a much greater diversification of climate niches over the same period, spanning the whole range of habitats from high alpine meadows and arctic tundra on the one hand, to tropical lowland wet forest and lowland desert edges on the other (P.H. Williams 1998). It is likely that this broad diversification of climate niches among the other bumblebees may be linked to their faster diversification into more than twenty times as many species that are now far more widespread globally in these more diverse habitats (Fig. 74). Intriguingly, a lower diversification rate for the extreme alpine/subalpine *Mendacibombus* species goes against a trend towards higher speciation rates reported for montane species generally, which is suggested to be driven by the greater isolation among high mountain populations (Steinbauer *et al.* 2016). The alpine/subalpine climate niches of *Mendacibombus* species (Figs 9, 73) are likely to put their species individually and on average at a higher risk of extinction than for many of the other bumblebee species, most of which are associated with more temperate climates (Fig. 74). The relatively narrow range of climate niches among *Mendacibombus* species and the relatively small number of species is likely to put the entire *Mendacibombus* group at a higher risk of extinction than the large, more climatically-diverse, and often more climatically-generalist sister group of all other bumblebees.

Although the ancestor of the subgenus *Mendacibombus* diverged at the crown diversification in the history of extant bumblebees (Cameron *et al.* 2007), estimated at *ca* 34 Ma (Hines 2008), the most recent common ancestor of all of the extant *Mendacibombus* species is relatively young at *ca* 9 Ma (Fig. 68). This implies that for a period of *ca* 25 Myr, more than half of the age of the group, only a single lineage of *Mendacibombus* has descendants that survive to the present. During this 25 Myr period, global temperatures became warmer than at present (Zachos *et al.* 2001; Zachos *et al.* 2008). Consequently the early *Mendacibombus* may have become even more restricted to the higher mountains than at present.

By 9 Ma (late Miocene), global temperatures had declined again to near where they are now (Zachos *et al.* 2001; Zachos *et al.* 2008). This was associated in Europe with major regional extinctions of thermophilic mammal fauna (Boehme 2003). It was also followed closely by the first diversification of the extant species groups within the subgenus *Mendacibombus*, in which the *waltoni*-group, in the mountains of the east Qinghai-Tibetan plateau, diverged from the *makarjini-mendax*-group, with an ancestral distribution to the west, in the mountains around the Pamir massif.

In summary, our results show a pattern in which both the first divergence among extant bumblebees and the diversification of the crown group of *Mendacibombus* appear to have been associated with periods of pronounced climate cooling. The process by which this may have acted is less clear. Cooler climates are likely to have forced *Mendacibombus* populations to lower elevations, where because mountains are approximately conical and often located in linear ranges, the habitat connectivity becomes greater, thereby facilitating the spread of these bumblebees to new areas. But in contrast, rapid cooling or much cooler climates could also have caused *Mendacibombus* populations at the highest elevations to have become temporarily more fragmented among mountains in the short term, if rates of species' spread to lower elevations were relatively low, which could facilitate allopatric speciation. Modelling techniques may eventually be able to assess the likely roles of such processes. Patterns of increased diversification in ancestral *Mendacibombus* species during cooling or during cooler periods are consistent with the current distributions of the species of this group as high mountain specialists.

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