Abc Taxa

The Bumblebees of the Himalaya

An Identification Guide

Paul H. Williams

Volume 21 (2022)

Abc Taxa the Series of Manuals Dedicated to Capacity Building in Taxonomy and Collection Management

Editors

Yves Samyn - Zoology (non African)
Curator of Recent Invertebrate Collections
Royal Belgian Institute of Natural Sciences
Rue Vautier 29, B-1000 Brussels, Belgium
yves.samyn@sciencesnaturelles.be

Didier VandenSpiegel - Zoology (African)
Head of Biological Collection and Data Management Unit
Royal Museum for central Africa
Chaussée de Louvain 13, B-3080 Tervuren, Belgium
dvdspiegel@africamuseum.be

Jérôme Degreef - Botany
Scientific Director
Meise Botanic Garden
Nieuwelaan 38, B-1860 Meise, Belgium
jerome.degreef@botanicgardenmeise.be

Instructions to authors: http://www.abctaxa.be

Cover picture: Male bumblebees of the species *Bombus* (*Melanobombus*) *prshewalskyi* Morawitz feeding from a thistle. This is one of the most abundant bumblebee species in the moist flower-rich subalpine and alpine grassland of the eastern Himalaya. Photograph by Paul H. Williams.

Inner page photograph: The Great Himalaya mountain range in Kashmir, viewed from just below the Zoji La (pass) at 3400 m a.s.l. through the upper coniferous forest zone southwest towards the village of Baltal. Photograph by Paul H. Williams.

Volume published by the RBINS' Scientific Publication Unit
Revision and layout: Charlotte Gérard (RBINS) & Kristien Vrancken (RBINS)
Printed by Peeters (Belgium) on FSC papers

ISSN 1784-1283 (hard copy); ISSN 1784-1291 (on-line pdf)
ISBN 978-9-0732-4255-5 (hard copy); ISBN 978-9-0732-4256-2 (on-line pdf)
D/2022/0339/1 (hard copy); D/2022/0339/2 (on-line pdf); NUR 910

29 Vautierstraat, 1000 Brussels – www.naturalsciences.be

The Bumblebees of the Himalaya

An Identification Guide

Paul H. Williams
The Natural History Museum, Cromwell Road,
London SW7 5BD, United Kingdom
E-mail: p.williams@nhm.ac.uk

Preface

The subfamily Apinae is represented by 16 genera of bees In the Himalayan region, interestingly the genus *Bombus* has the highest number of species (>33%) with over 20 per cent of all species of bumblebees in the world occuring in this region. No wonder, Dr Paul Williams could not ignore the bumblebees of the Himalayas.

Being important pollinators of both wild and cultivated plants bumblebees are of high ecological significance. But, climate change, habitat loss and excessive use of pesticides are resulting in local extinctions of several species. Paul Williams' book on the Himalayan Bumblebees will go a long way in making us understand the status of bumblebee diversity and to take measures to conserve them in the Himalayas, but also beyond thanks to the excellent general introduction on the topic.

The book includes 62 species of bumblebees under ten subgenera that occur in this region. It has been written in a simple language which makes even a non-specialist to understand. Paul starts with explaining how bumblebees are different from other bees (especially the carpenter bees which are often mistaken for bumblebees!), details collecting and curating methodologies for bumblebees, and explains morphological characters useful in identification and for running the keys.

The most interesting part of the book is the systematics. Paul provides identification keys to the subgenera and species of bumblebees, including separate keys for females and males. In addition, for each species distribution maps are given. The author divides the Himalayan region into four subregions, based on altitude and vegetation – lower forest, upper forest, alpine grassland and trans-Himalayan alpine grassland. While providing the descriptions of each species, he provides an illustration of the overall distribution along with the distribution map. This in fact will be interesting for any student or scientist studying bumblebees or any other bee.

We congratulate Paul Williams and the editors of *Abc Taxa* and the Belgian Global Taxonomy Initiative for coming out with this excellent book entitled " The Bumblebees of the Himalaya: an Identification Guide". The book will be a very effective tool for capacity building in the area of bumblebee taxonomy. Taxonomic works are urgently needed to help to conserve the insect diversity in India. We hope this book will be a model for any future attempts on other groups of bees of the Indian subcontinent or of the Asian Bees.

V.V. Belavadi*
Axel Brockmann **

Indian Pollinator Initiative (InPollIn.com)
*University of Agricultural Sciences, Bangalore, India
**National Centre for Biological Sciences, Bangalore, India

Table of Contents

1. Introduction

Bumblebees are among the most abundant bees (and flower visitors) throughout the spring and summer in cool temperate environments, especially in the northern hemisphere (Williams 1998a). Their great ecological significance is that they are some of the most important pollinators in both wild and commercial ecosystems (Dias *et al.* 1999; Winter *et al.* 2006; Goulson 2010; Ollerton 2020). Unfortunately bumblebees are also widely threatened by loss of habitat, by pesticides, by the introduction of exotic competitors and pathogens, and by climate change (Williams & Osborne 2009; Cameron & Sadd 2020). To maximise our chances of mitigating the effects of the environmental changes in an uncertain world, we need to conserve as much as possible of the entire diversity of bumblebees, as an insurance policy (Williams 1998b). To do this we need to know which bumblebee species are most threatened (Williams & Osborne 2009). However, bumblebee species can be difficult to identify, while for the Himalaya some areas are difficult to access and there is no up-to-date guide to all of the species. This guide seeks to address this identification need.

The Himalaya mountains are part of one of the greatest hotspots of bumblebee species richness on Earth (Fig. 1), with more than one fifth of the world's total bumblebee species (62/288: updated from a world list by Williams 1998a). Globally, these insects are most species-rich in mountains in the cool environments of subalpine flower-rich grasslands. This contrasts with the approximately 20,000 species of other bees, which tend to be associated more generally with lowland dry Mediterranean climates (Michener 1979; Orr *et al.* 2021). In the Indian subcontinent, bumblebees are absent from the lowland plains and from the Western Ghats mountains, as well as from the Himalayan foothills below about 300 m above sea level (a.s.l.) (where bumblebees are often confused with the large carpenter bees of the genus *Xylocopa*, which are common in the lowlands). The absence of bumblebees from isolated mountains further south is probably because bumblebees, despite their strong flight, appear to be poor at dispersing across wide barriers of unsuitable warm lowland areas and then establishing new populations (Williams *et al.* 2017b).

Within the Himalaya, bumblebees are most abundant and most species-rich in flower-rich grasslands just above the tree line, at around 3000–4000 m a.s.l. (Williams 1991; Williams *et al.* 2010; Streinzer *et al.* 2019). Bumblebees continue upwards into the high mountains as high as there are flowers to support them, to elevations of at least 5640 m (Williams 2018).

One of the reasons why bumblebees are especially species-rich in the mountains of Asia around the Qinghai-Tibetan Plateau (QTP) is that bumblebees are likely to have originated in this region around 35 million years ago (Williams 1985; Kawakita *et al.* 2004; Hines 2008; Williams *et al.* 2017b), so that they have had a longer time to accumulate species here than elsewhere. Speciation rates for bumblebees also appear to be higher in mountainous areas, probably because of the interactions between the physical heterogeneity of mountain ranges and their complex histories of climate change forcing fragmentations of distributions by moving them up or down or around mountains to areas of different aspect (Williams *et al.* 2016; Williams *et al.* 2017b; Williams *et al.* 2020).

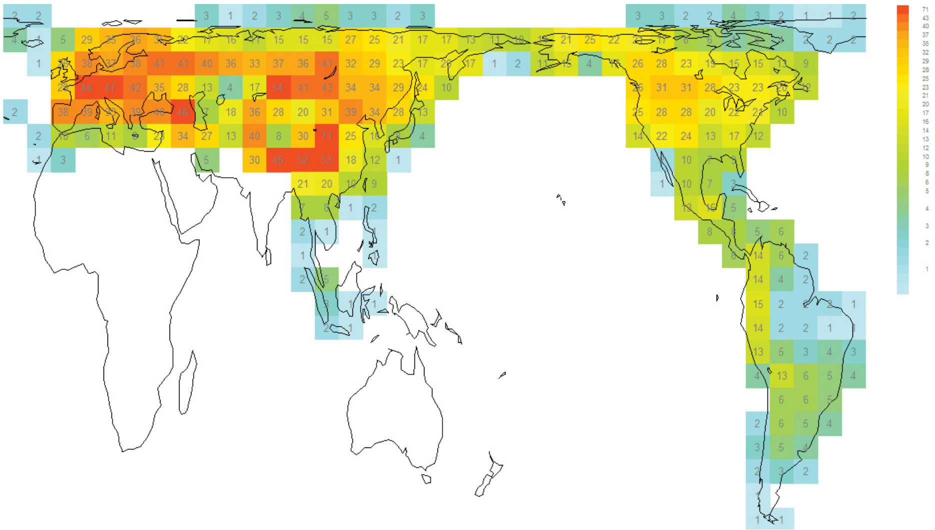


Fig. 1. Bumblebee species richness is highest in Asia, especially in the Himalaya and Hengduan mountains at the southern and eastern fringes of the Qinghai-Tibetan Plateau (updated from Williams 1998a). There are no indigenous bumblebees in sub-Saharan Africa, lowland India, or Australia. Even for a globally well-sampled group such as bumblebees, using a coarse-scale equal-area grid reduces species-area effects, reduces the effects of sampling heterogeneity (species-accumulation curves for these large grid cells are more nearly asymptotic), and smooths the effects of local habitat patchiness. The grid is based on intervals of 10° longitude, which are used to calculate graduated latitudinal intervals in order to provide equal-area cells (each cell has an area of approximately 611,000 km²). The colour scale has equal-frequency richness classes. Cylindrical orthomorphic equal-area projection (excluding Antarctica) with north at the top of the map.

This guide aims to provide an up-to-date aid for reliable species identification of Himalayan bumblebees for use in the lab. It is not a field guide and it is not a beginner's guide for those without some experience of insect identification. When using it, there are two important qualifications that must be kept in mind:

First, this guide is aimed at improving identifications to support a new survey of Himalayan bumblebees. New material from that survey will help to improve knowledge of the species, so that a revised multi-author illustrated guide is planned to follow, which will include photos of live bumblebees and high resolution distribution maps (and more images to support keys, which has been prevented during the pandemic). We have reached a time in which the majority of Himalayan bumblebee species are likely to be known already, because the rate of discovery of completely unknown species is now low. However, the status of a few taxa, either as separate species or as parts of other species, still has a degree of uncertainty. It is hoped that this guide will help to stimulate the studies that will investigate and clarify these issues.

Second, identification of many Himalayan bumblebee species can be difficult with current technology, even with DNA data (*e.g.*, COI 'barcodes'). Much as everyone would like identification to be easier, there is currently no easy way around this. This guide is designed to help identify Himalayan bumblebee species from the most recent knowledge, using the best known characters in order to increase the precision of identifications. Unfortunately, by aiming for precision this cannot then be an easy beginner's guide. Despite Himalayan bumblebees' large body size and despite their obvious characteristic of many varied colour patterns, they are in many cases not easy to identify from the colour patterns of the hair alone (see the section on what is a species?). Consequently, reaching reliable identifications still usually requires close attention to some of the finer and more subtle details of morphology. Even COI barcodes (when available), although potentially diagnostic, are not always straightforward to interpret, although this should become easier once a more complete reference library of reliably-identified sequences can be made available. Perhaps in the future new techniques will make identification easier for everyone. But in the meantime, if used with care, the finer details of morphology may at least help towards obtaining reliable and representative species occurrence data for the urgently needed studies of bumblebee ecology and conservation in the Himalaya, for which correct species identification is crucial.

2. What are bumblebees?

Apart from their bright colours and large size for insects, bumblebees (all are species of the genus *Bombus*) attract a lot of attention because they are especially important and abundant pollinators in temperate environments. They are among the most efficient pollinators for food crops including many tree fruits, berries, and nuts (Dias *et al.* 1999; Winter *et al.* 2006; Goulson 2010). While a couple of bumblebee species from Europe (*Bombus terrestris*) and North America (*B. impatiens*) are reared on a large scale for commercial pollination on those continents, in the Himalaya the use of local indigenous bumblebee species for pollination must be encouraged in order to replace the demand for the introduction of exotic bumblebees. These are very likely to compete for resources and their introduction will very likely bring with them (although inadvertently) their pathogens, both of which can seriously harm indigenous bees (Williams & Osborne 2009; Cameron & Sadd 2020).

This guide is not intended as an introduction to bumblebee general biology, foraging and pollination, or for rearing colonies, which are all large subjects already covered in depth in many books (*e.g.*, Sladen 1912; Alford 1975; Heinrich 1979; Kearns & Thomson 2001; Goulson 2010; Prys-Jones & Corbet 2011; Williams *et al.* 2014). However, in outline, most species of bumblebees world-wide are social, forming small colonies that last only for the summer months in temperate regions (Fig. 2). Females of these species have the hind tibia broadened and flattened, with long anterior and posterior hair fringes forming a pollen basket (corbicula) for collecting pollen. These social species have large females (queens) that start colonies in the spring, rearing small females (workers) and eventually males and a new generation of queens before the colonies usually die out before the winter. Because colonies often persist for several months, most species of bumblebees will collect pollen from a variety of unrelated plants (*i.e.*, are polylectic), switching choices as the most rewarding food sources change as the summer progresses and as different plants come into flower (all studies of bee-plant relationships need to ensure that both the bees and the plants have been correctly identified, an ideal that is not always attained in some published studies, so that all published records need to be checked and confirmed). In contrast, a few bumblebee species (in the Himalaya, all in the subgenus *Psithyrus*) are social parasites within colonies of the social species (the parasitic species lack pollen baskets) (Fisher 1987; Williams 2008; Goulson 2010; Lhomme & Hines 2018). Females of the parasitic species invade small colonies of the social species in late spring and have their larvae reared by the workers of the host social species, with no workers of their own. For both social species and parasites, the young females mate with males outside of the nest in summer and then the females go into hibernation in the soil. Mate-searching behaviour of male bumblebees appears to be especially diverse in the Himalaya (Williams 1991).

The origins and early diversification of bumblebees are very much associated with the high uplift of the Himalaya and of the Qinghai-Tibetan Plateau and connecting mountains (Williams *et al.* 2017b).

Fig. 2. Mature colony of *Bombus eurythorax* excavated in the western Himalaya near Gulmarg in Kashmir (2500 m a.s.l. 2.ix.1985) in the upper coniferous forest from an earth bank at the end of a 0.4 m entrance tunnel, containing the old queen and 20 young queens (large white-tailed individuals), 36 workers (small red-tailed individuals), and 31 males (the predominantly yellow individual near the centre). The large dark wax cells left of centre contain mature larvae, whereas the yellow cocoons contain pupae.

3. What are the Himalaya?

The Himalaya (plural) for the purpose of this guide include the high mountain ranges contained (from west to east) within north-eastern Pakistan, the Indian union territory of Jammu and Kashmir (including Ladakh), the Indian states of Himachal Pradesh, Uttarakhand, the country of Nepal, the Indian state of Sikkim (including here data from the mountains of Darjeeling to its south in West Bengal), the country of Bhutan, and the Indian state of Arunachal Pradesh (Fig. 3). This is broader than some definitions of the Himalaya, which extend for example from Mt Nanga Parbat (in the west) to Mt Namcha Barwa (in the east). In contrast, other definitions extend much further, for example including the Hengduan mountains region of south-west China. The bumblebee faunas of the other eastern Indian mountain states to the south of the Brahmaputra River are not treated here explicitly, although as far as is known their faunas are subsets of the fauna of Arunachal Pradesh and so the species in these eastern states should be identifiable from this guide (for species records in these states see Table 3).

It is now broadly agreed that the high uplift of the Qinghai-Tibetan Plateau (QTP) occurred before 45 million years ago (Favre *et al.* 2015; Renner 2016) as the Indian tectonic plate pushed into the Central Asian plates, before the origin and diversification of extant bumblebees (Williams *et al.* 2017b). Uplift continued

Fig. 3. The Himalayan region as considered here is shown outlined in red: it includes the Indian union territory of Jammu & Kashmir (including Ladakh), the Indian states of Himachal Pradesh, Uttarakhand, Sikkim (Darjeeling records are included here), Arunachal Pradesh, and parts of the countries of Pakistan, Nepal (with Far Western, Mid Western, Western, Central, and Eastern provinces), and Bhutan. Mapped in ArcGIS using World_Shaded_Relief basemap © 2014 ESRI and showing boundaries between countries in black as recognised by the UN.

in the peripheral mountain ranges of the QTP, even through the Pliocene and Pleistocene and to the present day (Wang *et al.* 2008; Yin 2010). The QTP and Himalaya are likely to have had an especially important role in the early evolution of bumblebees (Williams *et al.* 2017b).

While the southern limit of the region treated here is set by the physiological and ecological limits of bumblebees at low elevations at this latitude, the northern limit follows administrative boundaries. North of the western Himalaya, these administrative boundaries lie within the more arid grassland or desert interior (the Changtang) of the QTP, although north of the eastern Himalaya the boundaries lie closer to the Great Himalaya where the hinterland of the QTP is much wetter (Williams *et al.* 2015).

Consequently this guide covers not just the Great Himalaya mountain range, but also the outer mountain ranges from the Hindu Raj range in Pakistan to the Mishmi Hills in Arunachal Pradesh. In covering some of the region beyond the Himalaya to the north, it includes the Trans Himalaya of the Zanskar, Ladakh, and Karakoram ranges of India and Pakistan. This guide excludes the Hengduan mountain region of southwestern China and neighbouring states to the east, which is considered by some to be part of the Himalayan mountain system.

4. Bumblebee habitat in the Himalaya

Within the Himalaya, bumblebees are likely to occur wherever there is a sufficient density of suitable food plants (flowers) and a suitable climate (Williams *et al.* 2007). Where conditions are not too dry or too hot, and where there are enough suitable flowers all summer every year, then there will usually be at least some bumblebees, even if they are active only in the early morning and evening (Williams 1991).

Bumblebee species differ in their tongue (proboscis) lengths and this governs which flowers they can visit most profitably (Heinrich 1979). Long-tongued bumblebees (*e.g.*, *B. haemorrhoidalis*) tend to visit deep tubular flowers, whereas short-tongued bumblebees (*e.g.*, *B. tunicatus*) tend to vist shallow open flowers (or may bite holes to rob deep flowers). However, because bumblebee colonies last longer than the flowering periods of most individual plant species, colony foragers must switch food plant species during the summer as their profitability and availability changes (Heinrich 1979). Therefore a bumblebee species rarely has a specialist, dependent relationship on a particular food-plant species, unless it is at extremely high elevation where the season is very short (*e.g.*, *Caragana* may be the only food source all summer near 5000 m a.s.l. in some areas in Zanskar: Williams 1991). Prominent patches of high-reward flowers (*e.g.*, legumes, labiates, thistles, *Pedicularis*, *Rhododendron*, *Aconitum*, *Caragana*) may attract bumblebees from hundreds of metres or even kilometres away. This may even cause foragers to commute between elevational zones.

It has often been suggested that nest sites could be limiting for bumblebees, although with the flexibility they show in choosing nest sites and the general abundance even in high alpine habitats of the small mammals that provide the suitable nest cavities with insulating material that bumblebees prefer, there is little evidence yet that lack of nest sites is often a severe constraint in these areas.

With this flexibility in the choice of food-plants and nest sites, it may be unlikely that many bumblebee species show very narrow habitat specialisations that might be visible as specialisations in particularly narrow kinds of vegetation. Variation in the densities of broadly suitable flowers is likely to be more important.

Despite their strong flight, bumblebees appear to be unable to disperse unaided very effectively across unsuitable habitat and then (re-)establish easily any unoccupied but suitable areas over a distance of more than a few tens of kilometres (Williams *et al.* 2017b). Consequently, suitable conditions need to be available reliably for the entire duration of every summer over a sufficiently large area to support viable populations of multiple colonies, or else suitable habitat needs to be within a few kilometeres of other occupied areas of suitable habitat.

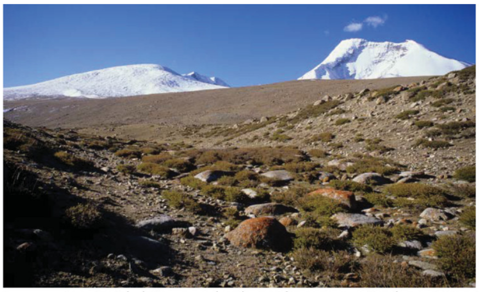
The most important factors governing bumblebee distributions are also likely to include temperature (which varies in the Himalaya especially as it decreases with increasing elevation a.s.l.) and water availability (which varies especially as it decreases from the outer monsoonal ranges of the Himalaya towards the arid interior of the QTP) as well as random chance effects (Williams *et al.* 2015a).

Very broadly, the principal pattern of habitat and faunal variation for bumblebees in the Himalaya is summarised in Fig. 4 (Williams 1991; Williams *et al.* 2010). There are many additional local complexities to this pattern, including the effects of aspect, slope, land use, and local and regional variations in vegetation. It has long been known that elevational boundaries (*e.g.*, ‘tree line’ and ‘snow line’) show great variation locally and regionally, although they are generally lower in the drier cooler western Himalaya and higher in the wetter warmer eastern Himalaya (Schweinfurth 1957).

Simple diagrams based on Fig. 4 are included in each species account to indicate what is known of each species ‘core’ habitat. These diagrams are intended as an aid to help check where species are most likely to occur. No doubt this scheme will need to be refined. It is only a very approximate indication of the zone in which a species is most abundant and species may also be recorded at lower frequencies in other zones with more sampling effort. This is a reasonable approach only because the Himalaya extend more or less east-west at similar latitudes, so that widespread species do not show pronounced changes in elevation with latitude from one end of the mountain system to the other. Some species of the semi-arid zone of the Trans Himalaya are currently known only from Zanskar and Ladakh (Kashmir, in the west), although with more sampling effort they might yet be found from other smaller semi-arid areas further east within the Himalayan region as considered here but north of the narrow Great Himalaya mountain range. Some of these species are known from neighbouring semi-arid parts of eastern Tibet (Williams *et al.* 2015a).

Among the habitat zones of the Himalaya in Fig. 4, the greatest richness of bumblebee species is concentrated above the forest in the alpine grassland and subalpine scrub (Figs 14–17). This is consistent with the global pattern of bumblebee species richness in Fig. 1.

Alpine grassland, Pir Panjal range, Mt Apharwat 4000 m



Semi-arid alpine grassland, Zanskar range, Nimaling 4800 m

Upper forest, Great Himalaya, Sind valley 2800 m

Lower forest, Great Himalaya, Harwan 1800 m

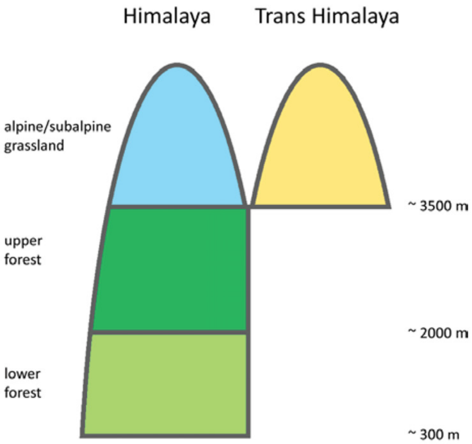


Fig. 4. Greatly simplified habitat classification for Himalayan bumblebees shown in the diagram to the lower right: a coarse-grained classification by (y axis) approximate elevation a.s.l. and (x axis) distance from the plains of India (in the south) towards the Trans Himalaya bordering the Qinghai-Tibetan Plateau (QTP, in the north), contrasting the outer ranges and Great Himalaya range that have high summer monsoonal rainfall (left of the diagram) with the semi-arid ranges in the rain-shadow hinterland of the QTP (right of the diagram). Example habitats are illustrated for the western Himalaya (Kashmir): lower forest (photo lower left) with broad-leaved trees and *Pinus*, *Cedrus*; upper forest (photo middle left) with *Pinus*, *Picea*, *Abies*; Himalayan alpine grassland (photo upper left) its lower areas with *Rhododendron*, *Betula*, *Juniperus*; Trans-Himalayan alpine grassland (photo upper right) with *Caragana*.

5. Bumblebee conservation

Bumblebees in the Himalaya not only have their own intrinsic value as part of the natural world but are economically very important to people locally for their pollination of crops (Ken *et al.* 2012; Gaira *et al.* 2016; Bhusal *et al.* 2019; Bhusal 2020). Severe declines in bumblebee populations have been seen in many parts of the world, representing a serious threat to crop pollination (Williams & Osborne 2009; Cameron & Sadd 2020). Bumblebee declines in the region of the Himalaya have been reported as likely to be driven by a combination of: (1) loss of habitat, especially food-plants (Xie *et al.* 2008); (2) use of pesticides (insecticides, herbicides, fungicides); (3) competition for resources from the introduction of non-indigenous bumblebee species, including potentially any commercial colonies of *B. terrestris* (not yet confirmed for the Himalaya); (4) introduction of exotic pathogens with the introduction of non-indigenous bumblebee species; and (5) climate change (Williams *et al.* 2015a; Lee *et al.* 2019). Reducing the intensity of these drivers or mitigating their effects is an urgent priority for research and action in the Himalaya in order to maintain and improve the pollination of the crops on which so many people depend.

People are beginning to try to assess the threats to bumblebees in the Himalaya, particularly through the work of the *International Union for the Conservation of Nature*'s (IUCN) Bumblebee Specialist Group (see regional reports by Saini *et al.* in Williams & Jepsen 2020; now a section of the IUCN Wild Bee Specialist Group). In order to conserve bumblebees, we need to know which species are threatened (Williams 1998b). Identification of the species involved has always been a bottleneck for conservation, because of the world-wide shortage of taxonomic information, gaps in taxonomic knowledge, and shortage of trained taxonomists, known as the so-called 'taxonomic impediment' (Giangrande 2003; Dar *et al.* 2012). The aim of this guide is therefore to reduce the identification problem.

6. Guides to Himalayan bumblebees

Himalayan bumblebees have attracted a lot of attention from taxonomists over the last two centuries because bumblebees are relatively large for insects and very brightly coloured (reviewed for bumblebees in general by Williams 1998). The earliest studies of Himalayan bumblebees within the tradition of Linnean taxonomy were piecemeal descriptions of individual widespread species by museum taxonomists (*e.g.*, Smith 1852a, 1852b), as these species were collected by European visitors to Asia. Especially influential collections were made by Charles Nurse, Georgiy Jacobson, and Richard Meinertzhagen, in the west, and by the expeditions to Tibet and Everest in the east, which between them yielded the specimens that were used subsequently to describe many of the new species with smaller range sizes (including Friese 1909; Cockerell 1910; Skorikov 1912b, 1914a; Friese 1918; Richards 1928a, 1928b, 1930; Tkalců 1974). For a more complete list of authors of Himalayan bumblebee species, see the lists of references under each species name.

As is the usual practice, reviews of the Himalayan bumblebee fauna to summarise and to re-assess the known species followed. In particular, Charles Bingham (1897: 24 species) presented a section summarising what was known of Himalayan bumblebees in his first volume on Hymenoptera in the series on the *Fauna of British India*, *including Ceylon and Burma* (he worked on this as a volunteer at the NHMUK after he retired from the military). No complete review was then undertaken until the prolific bumblebee specialist Borek Tkalců promised a *Monographie der Unterfamilie Bombinae des Himalaya* as in press in the reference list of his paper describing a collection of bumblebees from the Nepal Himalaya (Tkalců 1974: 18 species). Unfortunately, for reasons unknown, this Himalayan review was never published. There had been important reviews covering at least parts of the region by Skorikov (1931, 1933a), Frison (1933, 1935), and Panfilov (1957), all specialists who had studied bumblebees in detail over many years.

It has long been apparent from these accounts that the species composition of bumblebee faunas in the Himalaya varies not just with elevation but also among different regions along the length of the Himalaya. Very broadly, there are three principal regional bumblebee faunas in the Himalaya: (1) in the drier western Himalaya (which was largely covered by the review of the Kashmir fauna with keys by Williams 1991: 29 species); (2) in the wetter eastern Himalaya (largely covered by a review of the Nepalese fauna with keys by Williams *et al.* 2010: 34 species); as well as (3) in the semi-desert of the Trans-Himalayan Tibetan hinterland (largely covered by Williams 1991, with keys; Williams *et al.* 2015). A checklist of bumblebees for the entire Indian region of the Himalaya has been published (Williams 2004: 50 species for the region were covered), although this is now out of date (revised here to 62 species). Other species lists for parts of the region have been based on this 2004 Himalaya-wide list (Kumar & Chandel 2002; Burger *et al.* 2009; Suhail *et al.* 2009; Sabir *et al.* 2011; Sheik *et al.* 2015; Jaffar *et al.* 2019a; Jaffar *et al.* 2019b; Streinzer 2019; NB re-interpretations of some species identifications, where these are clear from images, are listed in the species synonymies here). Recent major contributions have been by Saini, Raina and Ghator (2015: 47 species), who brought together the Kashmir and Nepal keys above in a book on *Indian Bumblebees*, and by Streinzer *et al.* (2019: 21 species), who surveyed some of the especially poorly known eastern state of Arunachal Pradesh.

In the most recent period since most of these works were completed, there have been substantial improvements in our understanding of the bumblebee species of the Himalaya. Much new information has become available from new collections and especially from new DNA data from across Asia (Williams *et al.* 2011; Hines & Williams 2012; Williams *et al.* 2012; Huang *et al.* 2015; Williams *et al.* 2016; Williams *et al.* 2020; Williams 2021). DNA studies have begun to focus on Himalayan bumblebees alone (Pakrashi *et al.* 2020). Increasingly, we have also been gaining a better awareness of the distributions of the species in Asia more broadly as GPS data have become widely available. However, the largest obstacle to improving knowledge remains the 'taxonomic impediment' – the difficulty of identifying Asian bumblebees to species reliably.

The present guide is the result of more than 40 years of study of the bumblebees of the Himalaya. I was able to review the bumblebees of Indian Kashmir thanks to long field-work visits in the summers of 1980 and 1985–1986. This was followed with particular studies of the bumblebee faunas of Pakistan and Nepal, which also allowed an opportunity for comparison of Himalayan bumblebees within a broad Asia-wide context (Williams 1991; Williams *et al.* 2010). I have also been sent many small collections by people working in the region and had access to the remarkably rich collection of the NHMUK. Further impetus was provided by field work across more than half of the provinces of China in the years 1992, 2002, 2005, and 2007–2019, combined with opportunities to study recent collections from all of the other Chinese provinces, thanks to collaborations with many co-workers, including Prof. Wang Shufang, Prof. An Jiandong, Dr Huang Jiaxing, and Dr Ren Zongxin (Williams *et al.* 2017). Fresh material has allowed examination of much more of the variation among Asian bumblebees from their morphology and COI barcodes.

7. How to catch bumblebees

Before collecting insects, you must ensure that you have all of the permits required. This may include permissions from local landowners, for protected areas, for particular countries, and any necessary permits to move specimens or their DNA across national borders. Globally, these issues are covered by the *Nagoya Protocol* on access and benefit sharing (https://www.cbd.int/abs/). National regulations for India are covered by the *National Biodiversity Act* (http://nbaindia.org/content/25/19/1/act.html) but other regulations may apply.

With practice it may be possible to identify bumblebees of some species in the field, and sometimes even good close-up digital images can provide enough detail to identify the species. This may be especially easy when the weather is cool and the bees are moving slowly. To slow bumblebees down artificially for taking photos, they can be captured, chilled on ice in a portable cooler (for half an hour or so), and then posed to take the photos before release.

Often, however, reliable identification requires closer examination of morphology with a binocular microscope. This is because many species have closely similar colour patterns and that makes identification challenging (see the section below on what are species?). In these cases when identification is important it can be necessary to collect specimens to take back to the lab for closer examination. It is apparent from illustrations and from records from unlikely locations that even some scientific publications are likely to have suffered from misidentifications of species, probably arising from using colour patterns alone.

There are many ways to catch bumblebees, and people often have their own preferred techniques and tools. In general, catching bumblebees with an insect net while they forage on flowers works very well (Fig. 5). Insect nets can be purchased from many biological suppliers. There are two main ways to catch bumblebees using a net. You can hold the net over the bumblebee on a flower, holding the tip of the net towards the sky, and wait for the bumblebee to fly upwards (bumblebees

Fig. 5. Collecting bumblebees from flowers using a hand net in Kashmir (photo from Dr Rifat Raina).

when disturbed tend to fly up and towards light, although sometimes they will drop and escape). Alternatively, you can swipe at the bumblebee with your net, twisting your wrist mid-swipe to flip over the tip of the net and trap the bee in the folded tip (although without care this method can damage plants). Once the bumblebee is in the net, it can be held in a fold of the net while a container is inserted into the open end of the net and manipulated under the bumblebee so that the bumblebee drops into the container. If you use a clear tube, you can photograph the bumblebee from various angles before releasing it, or else keep the specimen for a collection. In some cases, you can even trap bumblebees directly from the flower using a clear tube, without a net (although the bee may see you coming and escape).

If you are visiting one or more remote sites to take samples for a survey, you may sometimes need to collect from each site a series of specimens for later careful identification or as representative (voucher) specimens as evidence of those identifications that can be checked later. A simple method for storing bumblebees in the field is to use empty clear plastic drinking water bottles (Fig. 6). You can use one bottle for each site or one bottle for groups of up to about 15 bumblebees if you need more from one site. You can add a slip of paper to each bottle with the site details to track samples. When emptied of all water, small holes just a few millimetres wide can be made with a sharp implement all over the bottle to prevent any build-up of humidity and to allow air in without letting the bumblebees out. One or two paper kitchen-towel sheets should be added inside to give the bumblebees something to hold on to and to absorb any moisture. Because the opening of the bottle is small, after removing the cap, the bottle can be inserted into the net under a bumblebee that is being held in a net fold just as with a small tube (try to keep the bottle vertical because the bumblebees cannot then climb the vertical sides). A major advantage of a large bottle containing paper is that the bumblebees will clean and groom themselves and will then remain un-matted. Keep the bottle away from direct sunlight.

If preserved 'voucher' specimens are required, and regrettably it is sometimes necessary, then it is better to kill bumblebees by placing the container in a freezer overnight. This allows dead specimens to be pinned and dried so that parts (usually legs) can still be used for DNA extraction, even after more than a decade. Do not use ethyl acetate (ethyl ethanoate) as a killing agent, because it degrades DNA severely.

A variety of traps (pan traps and blue vane traps) are sometimes used to collect bumblebees, although bumblebees are often good at flying out of interception traps such as Malaise traps. Be aware that traps may be re-purposed by local people. But beware, traps filled with liquids, such as propylene glycol or soapy water, will result in soggy, bedraggled-looking specimens with matted hair that can be difficult to identify to species.

Ideally for identification, the hair of bumblebees should be in an un-matted, un-faded, and un-abraded condition. If the hair does become matted, specimens will need to be washed and fluffed up. This can be done with a hair dryer or paint brushed before pinning. It can be very time-consuming (and if over-enthusiastic can lead to bald bees) and doesn't always work well, so it is best avoided if possible. Matted dead bees can be cleaned by immersing them in warm water with a small amount of detergent, then rinsing them in clean water. A final rinse in concentrated

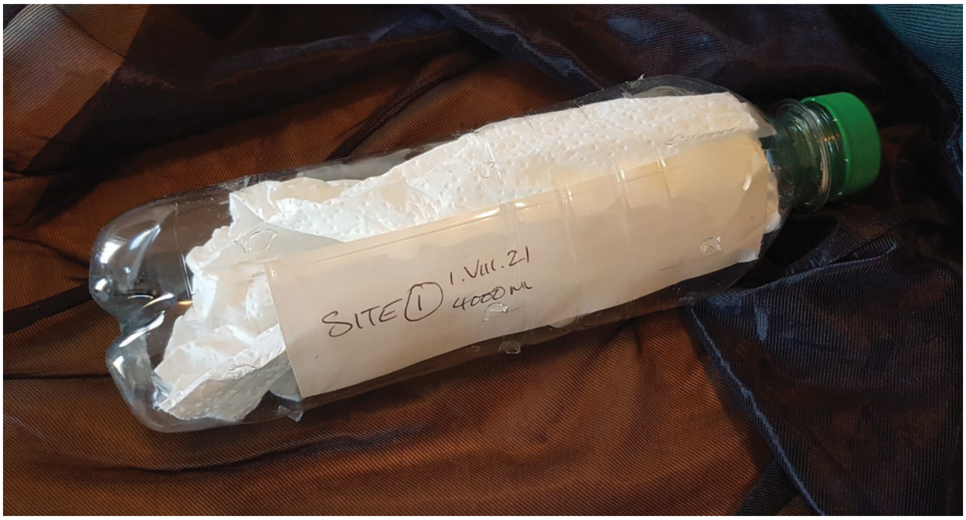


Fig. 6. Collecting bottle for sampling bumblebees at a single site re-purposed from a plastic drinking water bottle by making air holes with a knife and adding absorbent paper towel and a paper site label.

alcohol can help to dry them and reduce the surface tension so that the hair becomes erect. The hair can even be fluffed up with a fine soft brush, such as a camera-lens brush, but this must be done gently or else the hair will be abraded.

8. How to make a bumblebee collection

There may be many purposes for bumblebee collections (which may dictate different approaches), but it is assumed here that the purposes are primarily to retain 'voucher' specimens from faunal surveys for future reference and to allow for more detailed comparisons. This can help with learning to recognise difficult species and also to provide representative specimens as evidence for the subsequent checking of identifications, especially as taxonomic interpretations change.

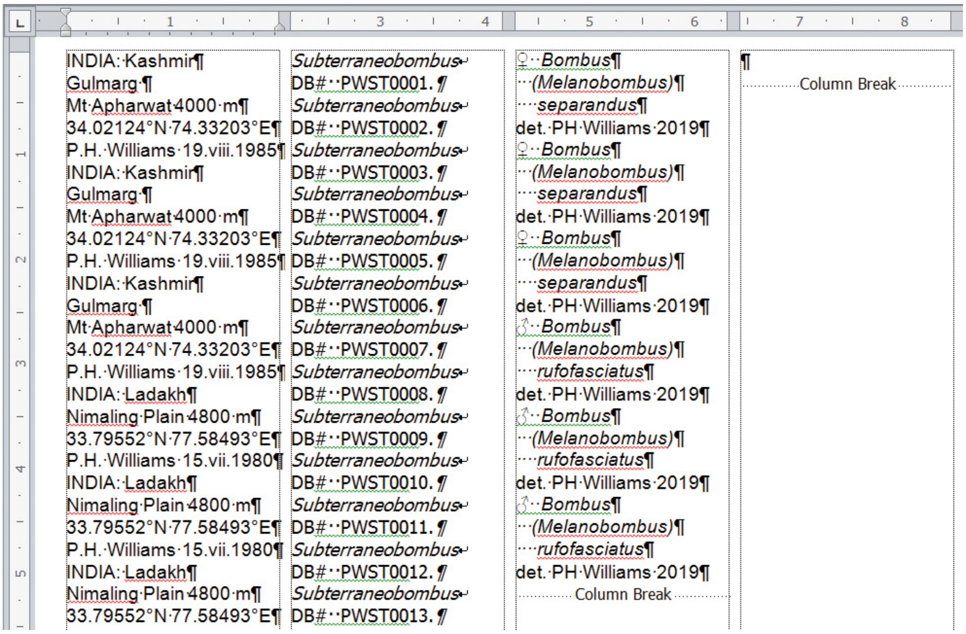
Once you have specimens, they can be preserved indefinitely by drying them on long insect pins. Pins are used: (1) to make it easier to manipulate specimens by holding the pin with forceps to avoid damaging the specimen; (2) to allow fragile specimens to be kept fixed into a sheet of expanded foam in boxes to prevent them from rolling around and becoming damaged; and (3) to carry data labels. Bumblebees should be pinned using long ('continental', ca 40 mm) stainless steel entomological pins (typically size 3) before drying out the specimen. They are pinned through the right-hand side of the thorax, with the bee about 2/3 the way up the pin. Humidity must not be allowed to build up inside store boxes or else specimens may be obscured or damaged by fungi. For this reason, cardboard or wooden boxes may be better than plastic boxes and desiccant materials and anti-fungal agents (thymol crystals) may need to be added in appropriate small containers within the boxes.

There is no need to 'set' specimens by drying them with the wings and legs arranged perfectly symmetrically in one plane. However, it is useful to extend the legs and hold the wings away from the body so that details of the colour pattern and surface sculpturing are clearly visible. What is especially valuable for males is to use a pin to extract the genital capsule so that it can be examined under a lens or microscope. This can usually be done for a fresh specimen by hooking the genitalia out with the tip of a pin. There should be no need to detach the genitalia because the basal part of the genitalia (the gonobase) can be held in an extended position while the specimen dries by hooking it over tergum 7 (Fig. 7). Keeping the genitalia attached to the specimen prevents it from becoming separated and lost. If the specimen is already dry, it can be 'relaxed' by pinning it into a small sheet of entomological foam in a sealed box (such as a transparent plastic lunch box) with some warm water in the bottom (the foam floats) to provide high humidity to allow the specimen to hydrate so that the genitalia can be extracted the next day when the specimen will have become flexible. The specimen can then be dried again quickly to prevent decomposition. Anti-fungal agents may be necessary.

Make sure that every specimen is given small labels of thin card or stiff paper that have at least minimal data for the collecting event (Fig. 8), including: date, name of the collector, and details of the location where they were collected, ideally with country name, province name, site name, as well as decimal latitude, longitude,

Figs 7–8. (Fig. 7: left) Preparing a male specimen (*Bombus rufofasciatus*) for a collection by extruding the genital capsule with the tip of a pin (inserted to the side in the aperture between T7 and S6 to hook the capsule out) and retaining the capsule extended beyond the posterior edge of metasomal T7. (Fig. 8: right) Preparing a specimen (*B. separandus*) for a collection by pinning it with labels carrying data for: (1) the collecting event and collector; (2) the unique specimen identifier; and (3) a taxon identification with the name of the identifier and the date on which the identification was made. Both specimens are pinned into an expanded plastic entomological foam that grips the pins (unlike expanded polystyrene) available from commercial suppliers.

and elevation data from a GPS unit (coordinates alone are not advised in case of mistakes that can then not be cross-checked). Decimal coordinates have a more standard format (compared to formats for degrees, minutes, and seconds), which makes them easier and more reliable to use in later analyses. Many of these data can now be provided using mobile phones, even in remote locations within many countries. Ideally any food-plant identification (only if certain) should also be added to labels, as well as any codes to identify DNA sequences within databases like BOLD or GenBank. Separate species identification labels with the identifier's name and date can also be added, always to the bottom of the pin. These labels should never normally be removed because old superseded labels (higher up the pin) can be used to track the history of identifications for a specimen. All data should be written or printed in permanent (non-water-soluble) ink. Labels can be designed using small fonts, copied within multiple narrow columns, and printed using standard word-processing programs from computers (Fig. 9). If the labels do ever need to be removed from a specimen, then this should be done for only



INDIA: Kashmir
Gulmarg
Mt Apharwat 4000 m
34.02124°N 74.33203°E
P.H. Williams 19.viii.1985
INDIA: Kashmir
Gulmarg
Mt Apharwat 4000 m
34.02124°N 74.33203°E
P.H. Williams 19.viii.1985
INDIA: Kashmir
Gulmarg
Mt Apharwat 4000 m
34.02124°N 74.33203°E
P.H. Williams 19.viii.1985
INDIA: Ladakh
Nimaling Plain 4800 m
33.79552°N 77.58493°E
P.H. Williams 15.vii.1980
INDIA: Ladakh
Nimaling Plain 4800 m
33.79552°N 77.58493°E
P.H. Williams 15.vii.1980
INDIA: Ladakh
Nimaling Plain 4800 m
33.79552°N 77.58493°E

Subterraneobombus
DB# PWST0001.
Subterraneobombus
DB# PWST0002.
Subterraneobombus
DB# PWST0003.
Subterraneobombus
DB# PWST0004.
Subterraneobombus
DB# PWST0005.
Subterraneobombus
DB# PWST0006.
Subterraneobombus
DB# PWST0007.
Subterraneobombus
DB# PWST0008.
Subterraneobombus
DB# PWST0009.
Subterraneobombus
DB# PWST0010.
Subterraneobombus
DB# PWST0011.
Subterraneobombus
DB# PWST0012.
Subterraneobombus
DB# PWST0013.

♀ *Bombus*
(Melanobombus)
separandus
det. PH Williams 2019
♀ *Bombus*
(Melanobombus)
separandus
det. PH Williams 2019
♀ *Bombus*
(Melanobombus)
separandus
det. PH Williams 2019
♂ *Bombus*
(Melanobombus)
rufofasciatus
det. PH Williams 2019
♂ *Bombus*
(Melanobombus)
rufofasciatus
det. PH Williams 2019
♂ *Bombus*
(Melanobombus)
rufofasciatus
det. PH Williams 2019
Column Break

Column Break

Fig. 9. Composing specimen labels in a word-processor: (left) locality labels; (centre) unique identifier codes with automated numbers; (right) determination labels.

one specimen at a time and the labels should be placed in the same order on a separate pin (to prevent losses or changing their order) and returned to the original specimen pin as soon as possible.

Ideally each specimen should have a label carrying a unique identifier – a number or code that can be used to track every single specimen (https://www.gbif.org/grscicoll). This code can be arbitrary as long as it is unique. It often starts with a code identifying the institution storing the collection. Collections and individual research projects are now expected to keep track of specimens and any data associated with them by using these codes. A simple way of doing this is by listing the specimens in a spreadsheet file on a computer. Alternatively, for greater efficiency and flexibility in answering questions from the data, a relational database can be used. Recording data in a database is also needed for registering proof of legal ownership for a collection when required for collecting and associated permits. It facilitates linking to records of subsequent use, including the history of identification, imaging, DNA sequencing, loans, analyses, mapping, and publications.

Boxes used to store pinned insects must have tightly fitting lids and be kept in a cool, dry (low humidity) place, shielded from pests, dust, and sunlight (light will cause colours to fade). Especially if the collection is small and is kept in an ordinary building, then the store box should be kept in a re-sealable plastic bag to exclude pests (Fig. 10). If pests were ever detected, then the entire store box should be placed in its bag in a freezer (< -20°C) for a week to kill the pests. Once removed from the freezer, the bag should not be opened until the temperature has

Fig. 10. Collections of pinned specimens stored in: (right) a wooden store box; or (left) in a card store box protected from pests in a re-sealable plastic bag. Ideally, modern collections use smaller cardboard 'unit trays' within the larger wooden drawers with sealed glass lids, because the smaller trays are easily re-arranged (or removed for posting) and also help to constrain any parts of specimens that become detached.

equilibrated in order to avoid condensation forming on the specimens or warping of drawers.

If the collection is larger and is maintained by an institution, then a long-term commitment is essential to continue to provide safe storage in appropriate pest-proof cabinets at a suitable temperature and humidity. For more information on resisting agents of deterioration in collections see museumpests.net.

9. Bumblebee names and classification

The aim of this guide is to help in the identification of bumblebees to species: that is, to find their correct species names. Species names are crucial because they function as the principal index labels ('handles') that are used for retrieving from the literature all of the information that is known on the properties and behaviour of those species. Put simply, names are essential because they enable people to tell others which kind of animal they have seen and to find out more about those animals.

For names to work for information retrieval, they have to be standardized. This is the purpose and advantage of formal names. People have always given organisms 'common' names, but these names are inconsistent in different languages and sometimes even in different places with the same language (the 'Yellow bumblebee' is used for different species in Europe and North America).

Table 1. The type material upon which this study is based is located in the following institutions (CAS, Chinese Academy of Sciences; CAAS, Chinese Academy of Agricultural Sciences; RAS, Russian Academy of Science)

IOZ	Institute of Zoology, CAS, Beijing, China
ISEAK	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland
KU	Christian-Albrechts-Uiniversität, Kiel, Germany
LSL	Linnean Society, London, UK
MCSN	Museo Civico di Storia Naturale, Genova, Italy
NHMUK	Natural History Museum, London, UK
NHMW	Natural History Museum, Wien, Austria
NMS	Natur-Museum Senckenberg, Frankfurt, Germany
OLML	Oberösterreichisches Landesmuseum, Linz, Austria
OUMNH	University Museum of Natural History, Oxford, UK
RMNH	National Museum of Natural History, Leiden, Netherlands
USNM	US National Museum of Natural History, Washington DC, USA
ZIN	RAS Zoological Institute, St Petersburg, Russia
ZMHB	Museum für Naturkunde an der Humboldt-Universität, Berlin, Germany
ZSC	Zoological Survey of India, Kolkata, India
ZSM	Zoologische Staatssammlung, München, Germany

To solve the problem of standardisation, in the eighteenth century the Swede Carl Linnaeus developed the system that is now used throughout the world, with names usually based on classical Latin or Greek (which makes the names international and independent of any particular current nation). For example, most children already know the dinosaur name *Tyrannosaurus rex*, demonstrating that the system is not inherently difficult. Names in this Linnean system consist of a generic group name (*Bombus* for all bumblebees), followed by a specific name (*e.g.*, *tunicatus*) and preferably a reference to the original publication in which the name was first made available (*e.g.*, Smith, 1852) (to avoid confusion in some cases of otherwise similar names). More than one name may have been applied to the same species (synonyms), or names that look the same may have been applied to different species (homonyms) (see the section below on a checklist of names). To keep the system standardised, a set of rules has been agreed internationally (the most recent version of the *International Code of Zoological Nomenclature*, ICZN

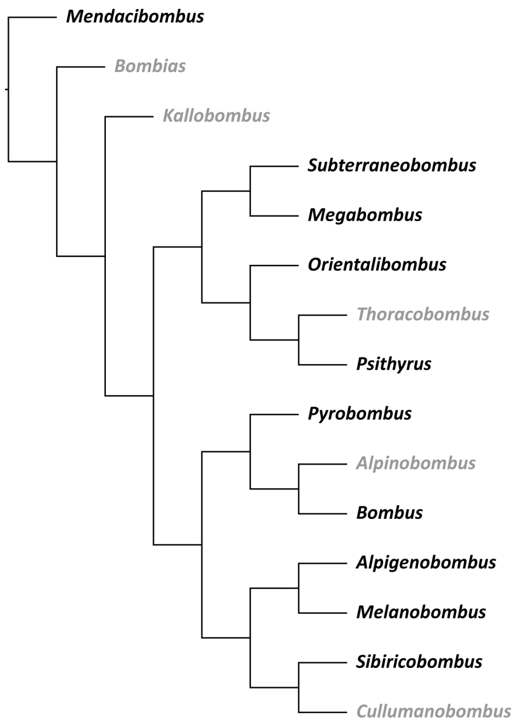


Fig. 11. Bumblebee subgenera world-wide as revised (Williams *et al.* 2008) based on the estimate of phylogeny by Cameron *et al*. (Cameron *et al.* 2007), although here the estimate of phylogeny is updated and re-drawn from the results of a recent analysis of much richer genomic data by Sun *et al*. (Sun *et al*. 2020). Subgenera not represented in the Himalaya are shown in grey. All bumblebees belong to the genus *Bombus s.l.* (in the broad sense), but within this must be a subgenus Bombus *s.str.* (in the narrow sense) that includes the generic type species, *Bombus terrestris*.

1999: see www.iczn.org/code). Examples of some common problems are given by Samyn *et al.* (2010).

Each name in the 'species group' (*i.e.*, species and subspecies in the sense of the *International Commission on Zoological Nomenclature*, ICZN) is attached to a primary 'type' specimen and it is this specimen that acts as the reference standard. This means that in order to know what is meant by a species name, it is important to examine the primary type specimen. A particular problem for people in Asia is that many of the type specimens for Asian bumblebee names are in European, Russian, or North American institutions, making access difficult. The depositories (permanent institutional collections) of all type specimens referred to in this guide are given using the acronyms listed in Table 1 to make it easier for people to seek out and compare types for themselves. At the NHMUK in London, all of the bumblebee type specimens have been photographed, so that images of them and of their data can be seen online (https://data.nhm.ac.uk/ see also https://www.si.edu/openaccess).

All bumblebee species are now widely accepted to be included in a single genus, *Bombus* (Latreille, 1802). This group includes not just the majority of social species but also the socially parasitic, inquiline, or 'cuckoo' bumblebees that were previously placed in a separate genus *Psithyrus* (Lepeletier de Saint-Fargeau, 1832). Evidence from morphology (Williams 1985, 1998a) and genes (Cameron *et al.* 2007; Sun *et al.* 2020) supports the inclusion of *Psithyrus* as a subgenus within the genus *Bombus* (*s. l*., or in the broad sense) in order to make the genus *Bombus* a natural, monophyletic group (including all extant descendants of a most recent common ancestor).

Some groups of bumblebee species share particular morphology or behaviour. These shared characteristics are often predictable from the ancestral relationships among the species, because of the fundamental evolutionary model of descent with modification. Currently the best estimates of these relationships (in the sense that they have the most supporting evidence) come from using DNA-sequence data, because these data are especially rich in informative differences. These estimates can be represented as 'family trees' of evolutionary relationships or phylogeny among species. For bumblebees, the larger groups of species within these trees have been labelled with names for groups called subgenera, of which there are 15 world-wide (Fig. 11).

As research progresses and new evidence becomes available, our understanding of the species and of their ancestral relationships changes. As a result, both the best estimates of the phylogenetic trees and the names of the species sometimes need to change. This may appear to be unhelpful, but it is actually a strength, showing that we can update the system of names to reflect improvements in our knowledge and understanding.

10. What are species?

People find it convenient to discuss the variety of nature by referring to named species as the principal recognisable units or component parts within this variety. However, even after more than two and a half centuries since Linnaeus (1758), there is still no entirely shared agreement about either what 'species' are in theory, or how they can be recognised in practice (Mallet 2013a). Recognising that this is a problem is not new. More than a century ago, Vogt (Vogt 1909, 1911) explicitly discussed what he called the 'species problem' for bumblebees.

Species are particularly problematic for the taxonomy of bumblebees. This is because bumblebees display such obvious and complex variation in the colour patterns of their hair that it has often led to quite different interpretations of species by different people. Colour-pattern variation includes not only: (1) local variations within one species population in one small area (Vogt 1909, 1911); but also (2) broad geographical variation within one (polytypic) species among different regions (Vogt 1909, 1911; Reinig 1935, 1939; Tkalců 1968b, 1989;

Hines & Williams 2012); often combined with (3) convergences in colour pattern among sometimes distantly related species within one region (Reinig 1935; Tkalců 1968b, 1989; Williams 2007; Hines & Williams 2012); and, occasionally at least, also combined with (4) ancestral polymorphisms that are inherited and shared by several closely related species (Williams *et al.* 2015b). These variations all have some genetic basis, but super-imposed upon them are variations caused by: fading of colours with exposure to sunlight with age; loss of hair by abrasion; and sometimes failure of the normal hair colour to develop, for example because of thermal or other shocks to the pupae during development. As a consequence of this complexity (which is paralleled to varying extents by variation in morphology and gene sequences), bumblebee specialists have long disagreed on which criteria should be used to recognise species (*e.g.*, Radoszkowski 1884) and on the resulting concepts of particular species (*e.g.*, Williams *et al.* 2015b), which explains in part why on average there are more than ten published names for each bumblebee species (Williams 1998a).

One aim in reviewing the Himalayan bumblebee fauna is to seek to apply appropriate and consistent ideas of the nature of species across the entire fauna. Within the four decades spanned by this project, emphasis for species concepts has shifted away from interbreeding (following Poulton 1904) and the so-called 'Biological Species Concept' (Mayr 1963), and in particular from Paterson's (Paterson 1985) 'Recognition Concept' of species (considered for Himalayan bumblebees in Williams 1991, 1998a), and towards de Queiroz's (de Queiroz 2007) unified concept of species as 'Evolutionarily Independent Lineages' (EILs; considered for bumblebees in Williams *et al.* 2020). Although by no means a panacea (Mallet 2013a), the EIL concept accommodates a consideration of multiple criteria for recognising species in practice within a reasonably practical integrative framework (Schlick-Steiner *et al.* 2010). This framework encourages results from different sources of diagnostic characters for species to be compared in order to assess whether there is corroboration among them to strengthen support for a particular interpretation.

All bumblebee species have been revised here in the context of considering all of the taxa available world-wide within each of the subgenera (Fig. 11). The list of bumblebee species used is updated from the previous global checklist of species that were distinguished primarily using morphology (Williams 1998) and by using new DNA evidence. Because morphology can be slow to evolve, it tends to support a more conservative estimate of the numbers of species, as in the earlier checklist. Our understanding of species is expected to have improved as new evidence has been added from analyses of variation in gene sequences. With genes, as with morphology, it is crucial that analyses are based on global revisions that include all of the known variation within each of the major monophyletic groups being treated, so that interpretations of the degrees of divergence can be calibrated for analyses of species coalescents.

Global revisions or analyses over the last decade are now available for the subgenera: *Mendacibmbus* (Williams *et al.* 2016), *Subterraneobombus* (Williams *et al.* 2011), *Megabombus* (Huang *et al.* 2015), *Bombus s.str.* (Williams *et al.*

2012; Williams 2021), and *Melanobombus* (Williams *et al.* 2020). This guide is necessarily very much a work in progress because revisionary work is never complete as long as new information is still being discovered, which is likely to continue because of the geographical scale of the project. For example, there have been recent continuing analyses of DNA-barcode variation for all of the species world-wide of the *lepidus*-group of the subgenus *Pyrobombus*, as well as for the entire subgenera *Alpigenobombus* and *Sibiricobombus* (using the methods from Williams *et al.* 2020).

Subspecies (as well as 'varieties' and 'forms') are not recognised here. Despite the acceptance of the idea of polytypic species (Mallet 2013a) and despite some recent arguments in favour of the use of subspecies (Mallet 2013b), there are serious problems in practice with the application of taxa at the rank of subspecies (Wilson & Brown 1953; Zink 2004). Over the last century the term subspecies has frequently been applied in studies of bumblebees, although in practice subspecies have often included entities of different 'kind', which are therefore not directly comparable (Williams *et al.* 2015b). For example, within the particularly well-known bumblebee species *B. terrestris* in Europe, several subspecies have been advocated (Rasmont *et al.* 2008). However, while some are discrete island populations with discrete diagnostic characters, others are merely parts of the widespread mainland population, which shows clines of continuous and graduated variation in these characters between different regions (Estoup *et al.* 1996; Rasmont *et al.* 2008). Because the consequences of this confounding of different 'kinds' of entity is not always explicit and could be misleading (especially when it is assumed that varying colour patterns correlate with other but unmeasured characteristics of *e.g.*, behaviour, especially when these differences may be local, plastic responses), the use of subspecies is not continued here. Covariation in characters of colour, behaviour, and ecology needs to be demonstrated and not just assumed. It is considered better to describe directly the variation that is actually observed, rather than imposing subspecific groupings that are usually of unknown biological significance.

An important practical aim of this guide is to share information which will encourage further research into Himalayan bumblebees, beginning with the known species. As more samples become available, it should become possible to examine variation more thoroughly in order to achieve a better understanding of the species present. It is just as important that appropriate methods are used. For a summary of the methods used recently to recognise species for this guide and why these methods were chosen, see Williams *et al.* (2020).

11. Checklist of Himalayan bumblebee species

This guide is a review of the fauna of a region rather than a formal taxonomic revision, so a full list and resolution of all synonyms of names for species is not included. Instead, there is emphasis on including references only to those names that have been used previously for bumblebees from the Himalayan region or from its immediately neighbouring areas.

Table 2 lists the 62 species of bumblebees currently known and recognised from the Himalaya within their ten subgenera of *Bombus*. This list places the species most closely related by ancestry (as currently understood) close together within the order, according to best current estimates from genes (Fig. 11), because these species are expected to have the most similar morphology and behaviour (an alphabetical index of names is also included at the end of the guide). After the current valid name for each species (in bold) is a list of synonyms. These are names for bumblebees often previously considered to be separate species or subspecies, but now interpreted as parts of the same species. This process of discovery continues with this guide, which applies changes to the names for a few species ('stat. rev.', indicating revised status) and describes one new species ('sp. nov.'). In several cases new evidence from DNA barcodes (from the fast-evolving COI gene) provides stronger support for new interpretations of species status as separate from other species elsewhere in the world.

Table 2. Species are grouped into subgenera and ordered within subgenera based on estimates of their evolutionary relationships (Fig. 11). Valid names of species are shown in bold with some of the more frequently encountered synonyms from the literature on Himalayan bumblebees indented below them. In cases where a name was published originally in another genus, the author reference is placed in parentheses. In some cases names cannot be used for these species because the same spelling of a name was published earlier for another species (a homonym, indicated by 'not of'). Misidentifications are not listed here but selected examples are listed in the main text.

SUBGENUS	SPECIES and synonyms
MENDACIBOMBUS	***Bombus waltoni*** Cockerell, 1910 ***Bombus marussinus*** Skorikov, 1910 ***Bombus avinoviellus*** (Skorikov, 1914) *callophenax* Cockerell, 1917 ***Bombus himalayanus*** (Skorikov, 1914) *varius* (Skorikov, 1914) (not of Lepeletier, 1832)
SUBTERRANEOBOMBUS	***Bombus personatus*** Smith, 1879 *roborowskyi* Morawitz, 1887 ***Bombus melanurus*** Lepeletier, 1835 *tschitscherini* Radoszkowski, 1862 *subdistinctus* Richards, 1928 ***Bombus difficillimus*** Skorikov, 1912
MEGABOMBUS	***Bombus montivagus*** Smith, 1878 ***Bombus albopleuralis*** Friese, 1916 *mimeticus* Richards, 1931
ORIENTALIBOMBUS	***Bombus funerarius*** Smith, 1852 *priscus* (Frison, 1935) ***Bombus haemorrhoidalis*** Smith, 1852 *orientalis* Smith, 1854 *assamensis* Bingham, 1897
PSITHYRUS	***Bombus cornutus*** (Frison, 1933) *pyramideus* (Maa, 1948) *acutisquameus* (Maa, 1948) *klapperichi* (Pittioni, 1949) *canus* (Tkalců, 1989) ***Bombus turneri*** (Richards, 1929) *decoomani* (Maa, 1948) *martensi* (Tkalců, 1974) ***Bombus novus*** (Frison, 1933) *nepalensis* (Tkalců, 1974) ***Bombus branickii*** (Radoszkowski, 1893) *chloronotus* (Morawitz, 1893)

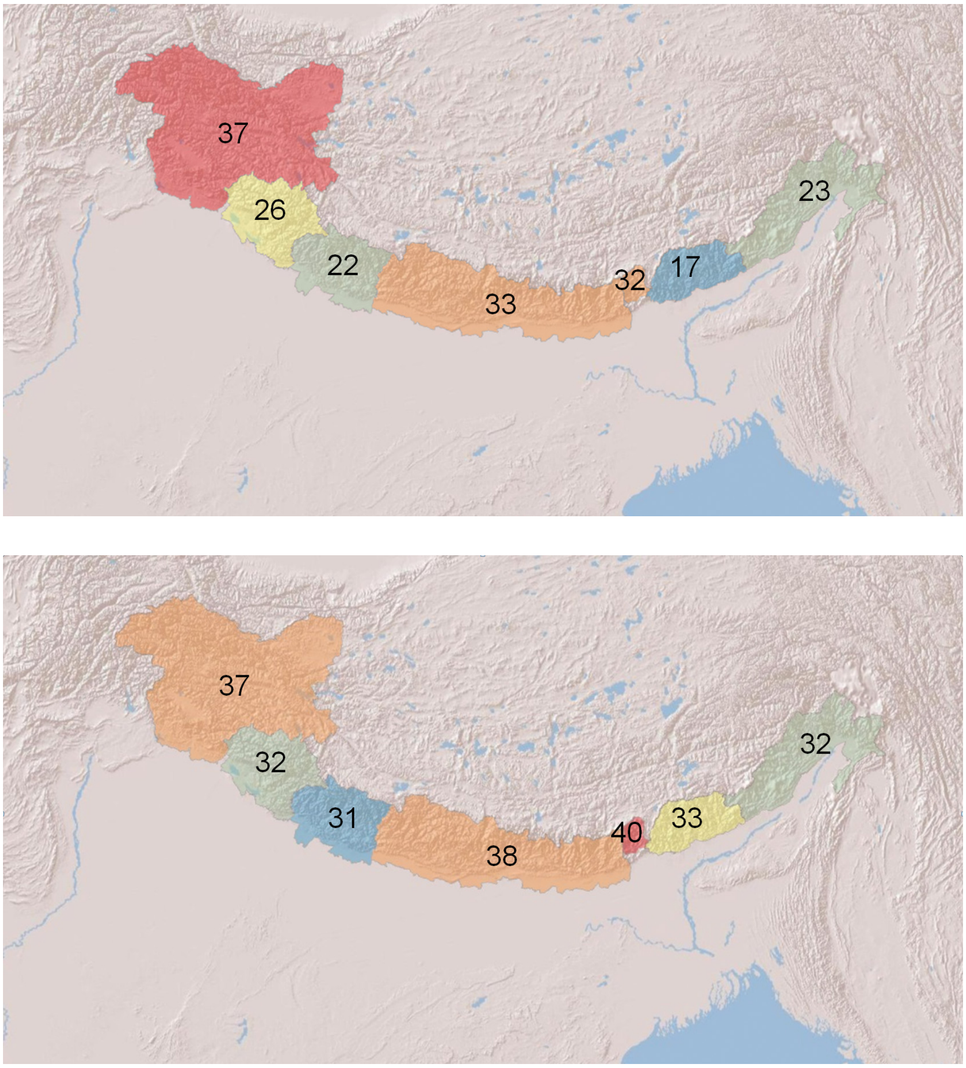
SUBGENUS	SPECIES and synonyms
	Bombus ferganicus (Radoszkowski, 1893) *ochraceus* (Morawitz, 1893) *indicus* (Richards, 1929)
	Bombus morawitzianus (Popov, 1931) *redikorzevi* (Popov, 1931)
	Bombus bohemicus Seidl, 1837 *distinctus* Pérez, 1884
	Bombus skorikovi (Popov, 1927) *gansuensis* (Popov, 1931) *kuani* (Tkalců, 1961)
PYROBOMBUS	***Bombus subtypicus*** (Skorikov,1914) *leucopygus* Morawitz, 1875 (not of Illiger, 1806) *leucurus* Bischoff & Hedicke, 1931 *kohistanensis* (Tkalců, 1989)
	Bombus bryorum Richards, 1930 *fletcheri* Richards, 1934
	Bombus abnormis (Tkalců, 1968)
	Bombus mirus (Tkalců, 1968) *tibetanus* Friese, 1913 (not of Morawitz, 1887)
	Bombus lemniscatus Skorikov, 1912 *peralpinus* Richards, 1930
	Bombus hilaris (Tkalců, 1989) stat. rev.
	Bombus lepidus Skorikov, 1912 *genitalis* Friese, 1913 *tetrachromus* Friese, 1918 (not of Cockerell, 1909) *yuennanicola* Bischoff, 1936
	Bombus infirmus (Tkalců, 1968)
	Bombus pressus (Frison, 1935)
	Bombus parthenius Richards, 1934
	Bombus luteipes Richards, 1934 *signifer* (Tkalců, 1989)
	Bombus biroi Vogt, 1911 *nursei* Friese, 1918 *abbotti* Cockerell, 1922 *anargumentosus* (Skorikov, 1931)
	Bombus kotzschi Reinig, 1940 stat. rev. *agnatus* Skorikov, 1933 (not of Skorikov, 1912)
	Bombus rotundiceps Friese, 1916
	Bombus flavescens Smith, 1852 *alienus* Smith, 1854 *rufocaudatus* Friese, 1905 (not of Friese, 1904) *mearnsi* Ashmead, 1905

SUBGENUS	**SPECIES and synonyms**
BOMBUS s.str.	***Bombus tunicatus*** Smith, 1852 *vallestris* Smith, 1878 *gilgitensis* Cockerell, 1905 *manaliensis* Kumar & Lall, 2004
	Bombus longipennis Friese, 1918 *s.str.*
	Bombus reinigi Tkalců, 1974
	Bombus jacobsoni Skorikov, 1912
	Bombus cryptarum (Fabricius, 1775)
ALPIGENOBOMBUS	***Bombus kashmirensis*** Friese, 1909 *stramineus* Friese, 1909 *tetrachromus* Cockerell, 1909 *pulcherrimus* (Skorikov, 1914) *meinertzhageni* Richards, 1928
	Bombus rainai sp. nov.
	Bombus sikkimi Friese, 1918 stat. rev. *xizangensis* Wang, 1979
	Bombus genalis Friese, 1918
	Bombus breviceps Smith, 1852 *dentatus* Handlirsch, 1888 *simulus* Gribodo, 1892 *orichalceus* Friese, 1916
	Bombus grahami (Frison, 1933) *beresovskii* (Skorikov, 1933) syn. nov.
MELANOBOMBUS	***Bombus eximius*** Smith, 1852
	Bombus festivus Smith, 1861 *atrocinctus* Smith, 1870 *terminalis* Smith, 1870
	Bombus simillimus Smith, 1852 *oculatus* (Frison, 1933) *tonsus* (Skorikov, 1933)
	Bombus miniatus Bingham, 1897 *flavothoracicus* Bingham, 1897 (not of Hoffer, 1889) *stenothorax* Wang, 1982
	Bombus eurythorax Wang, 1982
	Bombus rufofasciatus Smith, 1852 *waterstoni* Richards, 1934

SUBGENUS	SPECIES and synonyms
	Bombus prshewalskyi Morawitz, 1880 *rufocinctus* Morawitz, 1880 (not of Cresson, 1863) *chinensis* Dalla Torre, 1890 (not of Morawitz, 1890)
	Bombus richardsiellus (Tkalců, 1968)
	Bombus tanguticus Morawitz, 1887
	Bombus semenovianus (Skorikov, 1914)
	Bombus ladakhensis Richards, 1928 *phariensis* Richards, 1930 *variopictus* Skorikov, 1933 *reticulatus* Bischoff, 1936
	Bombus tibeticus Williams, 2020
	Bombus keriensis Morawitz, 1887 *trilineatus* Wang, 1982 *karakorumensis* (Tkalců, 1989)
	Bombus separandus Vogt, 1909 *kohli* Vogt, 1909 (not of Cockerell, 1906) *kozlovi* Skorikov, 1910 *tenellus* Friese, 1913 *alpivagus* Richards, 1930 *richardsi* Reinig, 1935 (not of Frison, 1930) *tibetensis* Wang, 1982
SIBIRICOBOMBUS	***Bombus semenovi*** Morawitz, 1887 *xionglaris* Wang, 1982 *duanjiaoris* Wang, 1982 *zhadaensis* Wang, 1982
	Bombus sibiricus (Fabricius, 1781) *flaviventris* Friese, 1905
	Bombus longiceps Smith, 1878 stat. rev. *flavodorsalis* (Skorikov, 1933) *oshanini* (Skorikov, 1933)

12. Distribution maps

Species distribution maps here are intended to show only a broad summary of which countries and provinces have records for a particular species. Consequently the maps (1) do not necessarily imply that the species in question still persist in all or in any of those areas and (2) should certainly not be taken to imply that a species occurs throughout each of the countries or provinces that have records. Countries and provinces shown on these maps in mid grey (level 2) have no known records, but are nevertheless coloured darker because the species is considered likely to occur there, usually because it has been found in similar habitats in areas on either side of the area in question.



Figs 12–13. Numbers of bumblebee species by countries and provinces in the Himalayan region from: (Fig. 12, top) numbers of species recorded from the literature and from specimens examined; and (Fig. 13, bottom) numbers of species expected by interpolating individual species range records (data from Table 3). Maps based on the Himalayan countries and provinces shown in Fig. 2. The colour scale has five classes of equal ranges of scores between red for maximum and blue for minimum for each map separately.

The relative diversity of bumblebees along the Himalaya can be represented by counting the numbers of species actually recorded in countries and provinces (Fig. 12) or the numbers of species expected to occur in countries and provinces (Fig. 13). These estimates are approximate and are likely to be under-estimates because of low sampling effort (sampling can never be complete).

The directly observed richness in species shows that the most species have been seen in Kashmir and Nepal, which are simply the areas that are largest and have been most thoroughly sampled. In contrast, the expected richness is highest in the middle of the Himalaya, in Sikkim. This might also be anticipated, as a result of the method of interpolating within distribution ranges, which would be expected to have the effect of boosting numbers most towards the middle of the region. However, for making these interpolations bumblebee species ranges have been studied throughout Asia, so in this case the centralising effect might be less of an artefact of edge effects from interpolation within a restricted region. Instead, high expected richness in the central Himalaya may be at least partly explained by an overlap in the centre between the rich western bumblebee fauna and the rich eastern bumblebee fauna.

Future studies might explore whether these faunas, where they occur near each other in the central Himalaya, might be segregated between different (*e.g.*) drier and wetter habitats. Most importantly, the differences between the figures on the two maps (Figs 12–13) show how many species are expected to be recorded that have not yet been recorded – a target for new surveys. For details of where searches are most likely to succeed, see the expected areas on the maps for each species.

As yet, modelling of species distributions individually at high resolution is unreliable for Himalayan bumblebees because of: (1) a lack of good, high precision data for both bees and climate; (2) the complexity of local factors, including uncertain factor interactions in high relief habitats and uncertain species interactions; and (3) the problem when applying models of having to assume (unrealistically) that distributions reach equilibrium with governing factors, which is a greater problem when dealing with poorly dispersing species like bumblebees.

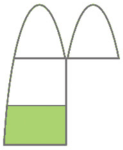
It is hoped that this identification guide will encourage the production of better high-resolution distribution maps for each bumblebee species. This information will be vital for understanding both the evolution of bumblebees world-wide and their ecology and conservation within the Himalaya.

13. Colour-pattern diagrams

The colour-pattern diagrams used here represent the colour of the hair on the dorsal surface of the body (Williams 2007). As diagrams they are simplifications, intended to summarise only the major differences. They have the advantage over photos that it is easier to see precisely which body region or segment has hair of which colour. They are necessarily compromises and as used here do not show subtle variations. For example, relatively few colours are distinguished. Often choices have to be made to show the approximate colour that covers most, or is

HIMALAYAN LOWER FOREST

ca 300–2000 m asl



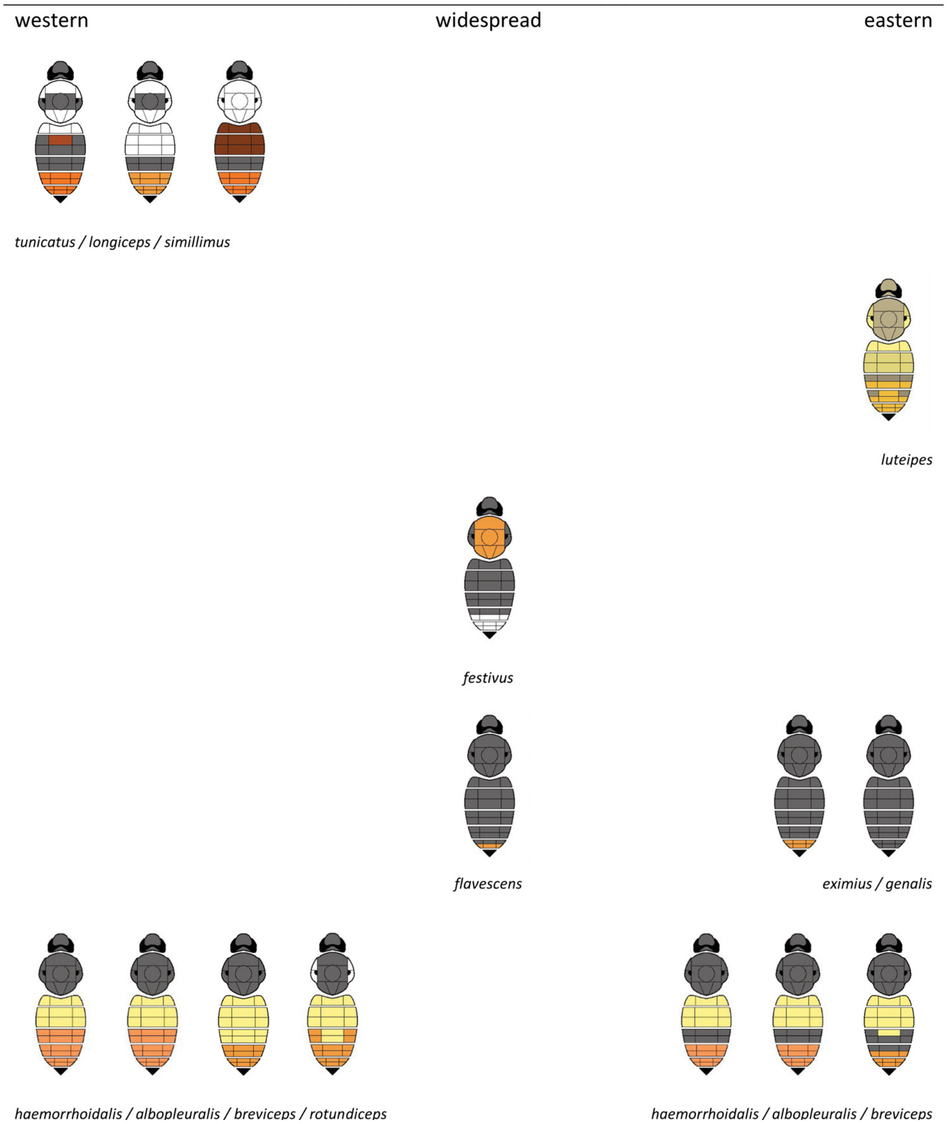


Fig. 14. Example colour patterns for workers of some of the more common or more characteristic species found in the Himalayan lower forest zone (Fig. 4). Western species are shown to the left, widespread species in the middle, and eastern species to the right. Within these regions similar colour patterns are grouped into mimicry groups (Williams 2007). Within each mimicry group, the most abundant species are shown towards the left and the rarer species towards the right.

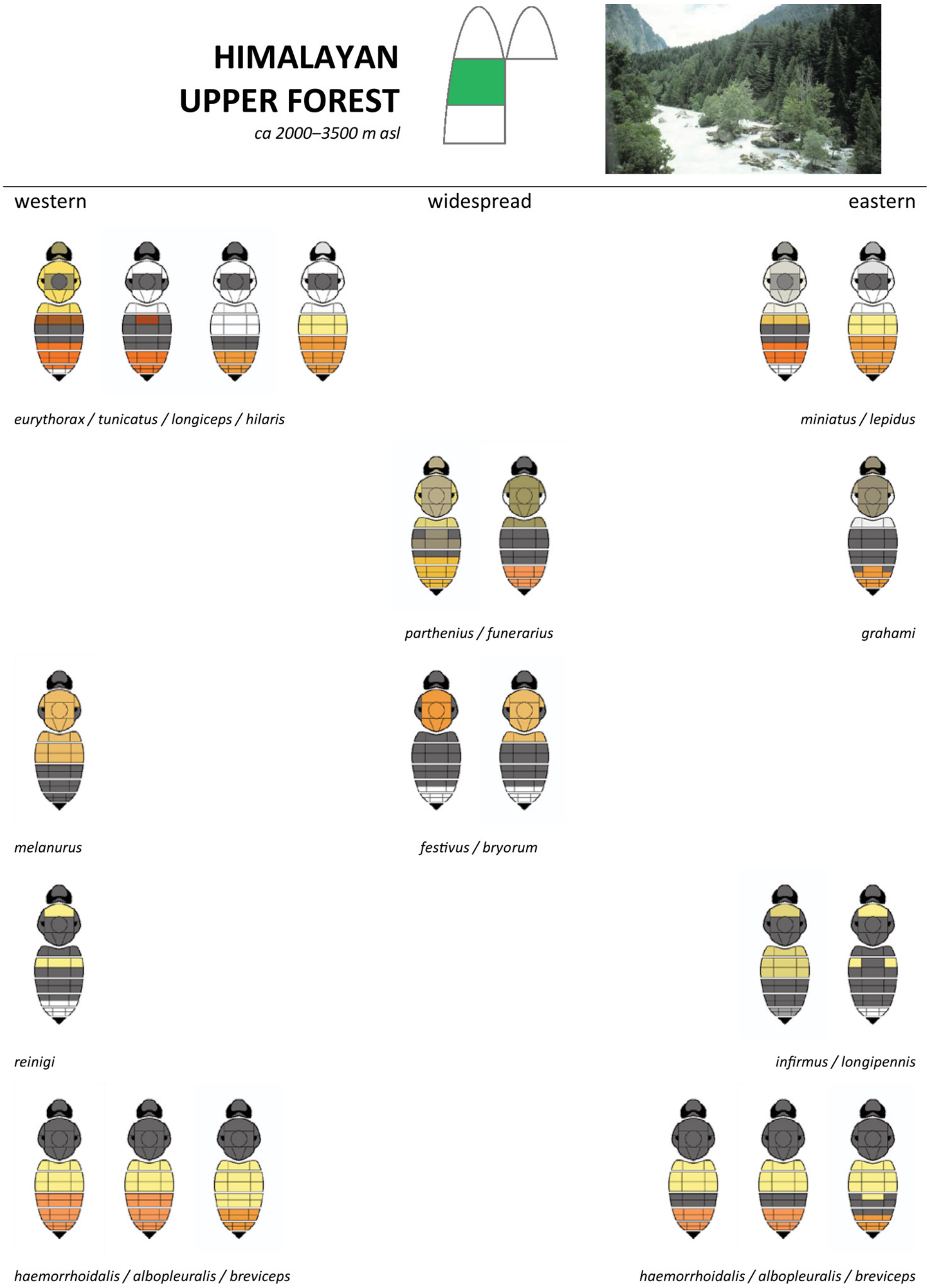


Fig. 15. Example colour patterns for workers of some of the more common or more characteristic species found in the Himalayan upper forest zone (Fig. 4). Western species are shown to the left, widespread species in the middle, and eastern species to the right. Within these regions similar colour patterns are grouped into mimicry groups (Williams 2007). Within each mimicry group, the most abundant species are shown towards the left and the rarer species towards the right.

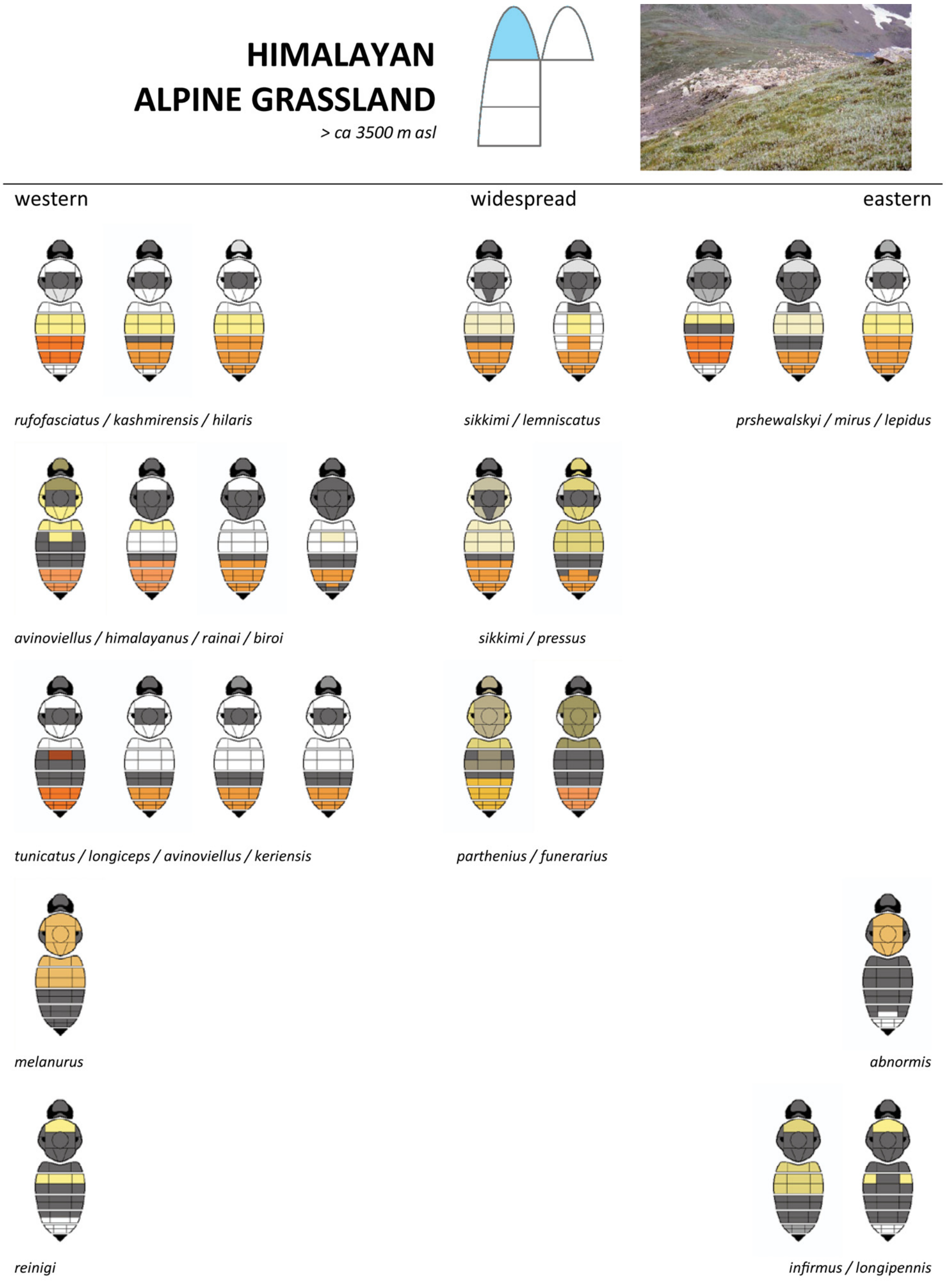


Fig. 16. Example colour patterns for workers of some of the more common or more characteristic species found in the Himalayan alpine/subalpine grassland zone (Fig. 4). Western species are shown to the left, widespread species in the middle, and eastern species to the right. Within these regions similar colour patterns are grouped into mimicry groups (Williams 2007). Within each mimicry group, the most abundant species are shown towards the left and the rarer species towards the right.

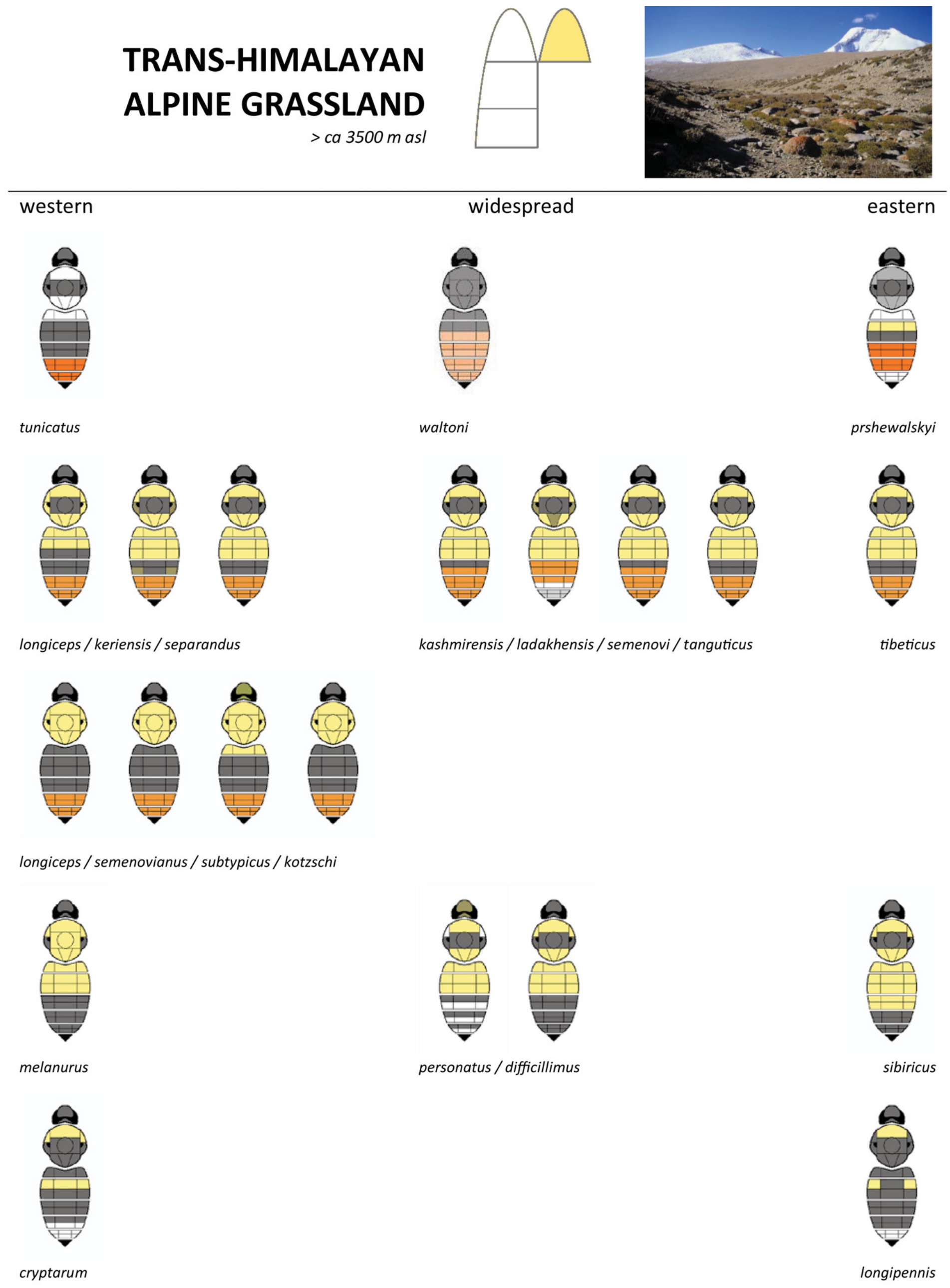


Fig. 17. Example colour patterns for workers of some of the more common or more characteristic species found in the Trans-Himalayan alpine/subalpine grassland zone (Fig. 4). Western species are shown to the left, widespread species in the middle, and eastern species to the right. Within these regions similar colour patterns are grouped into mimicry groups (Williams 2007). Within each mimicry group, the most abundant species are shown towards the left and the rarer species towards the right.

most apparent within, each body region (so that small patches of a different colour will not be represented). A nearly equal mixture of black and yellow hairs is shown as an olive colour and a nearly equal mixture of black and near-white hairs is shown as grey. Each diagram represents a single particular individual examined at the time of writing (others may have been seen previously that are unrecorded) and no doubt others will be found with different colour patterns in the future (although with the extent of previous sampling, these are unlikely to be numerous).

People often look at bumblebee colour patterns when identifying species, but it has been known for more than a century and cannot be stressed enough that colour patterns alone often do not diagnose species (see the section above on what are species?). Colour patterns can be very helpful, but they must be used only in combination with other evidence. In most cases, morphology is used to decide to which subgenus and species-complex an individual bumblebee belongs. At that stage the colour pattern is often helpful in getting closer to identifying the species.

To help provide an overview of the species most likely to be seen in each of the major habitat zones in the Himalaya mountains, Figs 14–17 summarise the worker colour patterns (workers are the sex and caste most often seen in the field and in collections) for the more common or characteristic species within each habitat zone (based on Fig. 4).

Within Figs 14–17, species of the western Himalaya are shown to the left of the figure, widespread species in the middle, and species of the eastern Himalaya to the right. Also within each figure, broadly the more similar colour patterns are grouped together (Williams 2007; Williams *et al.* 2015b). This grouping demonstrates that often different species in the same place can appear closely similar in colour pattern, causing greater problems for identification. Within each similar group, the regionally most widespread and abundant species are shown towards the left whereas the rarer species are shown towards the right. As emphasised above, species can be identified correctly only by morphology, so these figures should not be used on their own to identify species. Not all of the rarer species and not all of the colour patterns for each species are included (none of the parasitic species of the subgenus *Psithyrus* are included because they are generally uncommon).

14. Bumblebee anatomy

The most obvious diagnostic characters of the external morphology of bumblebees are those of the colours of their ‘hair’ (setae or pubescence) (Williams 2007). However, the colour patterns of the hair can be so variable that they may be misleading if used alone for the identification of species (see the section above on what are species?). Fortunately, once subgenera have been recognised from the more reliable differences in shape and sculpturing of the exoskeleton, then variation in some aspects of colour pattern within a region the size of the Himalaya may in many cases still be useful for identifying species. For more detailed descriptions of the external morphology of bumblebees see Gauld and Bolton (1988) and Michener (2007). For the terminology of the principal body parts see Fig. 18.

On the HEAD (Fig. 19), around the mouth the shape and details of the sculpturing of the LABRUM, CLYPEUS and OCULO-MALAR AREA (the 'malar space' of Richards 1968) are frequently used as diagnostic characters. The shape of the malar area can be measured as the ratio of the oculo-malar distance to the proximal breadth of the mandible, which is measured from its anterior corner of the acetabulum to the posterior edge of the condyle (*i.e.*, a measure of the exterior distance between and including the 'hinges' of the mandible, both hinges are visible on the left of the figure). This shape is related to variation in 'tongue' (proboscis) length (Medler 1962a, 1962b), which is in turn related to variation in flower choice, both among and within species. However, within at least some of the species with longer tongues, the shape of the malar area may be subject to allometric effects (changes in shape related to changes in size) among individuals of different sizes within a species (Sakagami 1972). Furthermore, because the boundaries of the malar area require a degree of arbitrary definition, measurements by different authors are not always comparable. Therefore this character is used here for diagnosing species only when the differences in shape are relatively large. The MANDIBLE provides several characters. There is an ANTERIOR TOOTH, variable numbers of SUBSIDIARY TEETH, and often a POSTERIOR TOOTH, which is defined at its base by a notch in the edge of the mandible also known as the INCISURA.

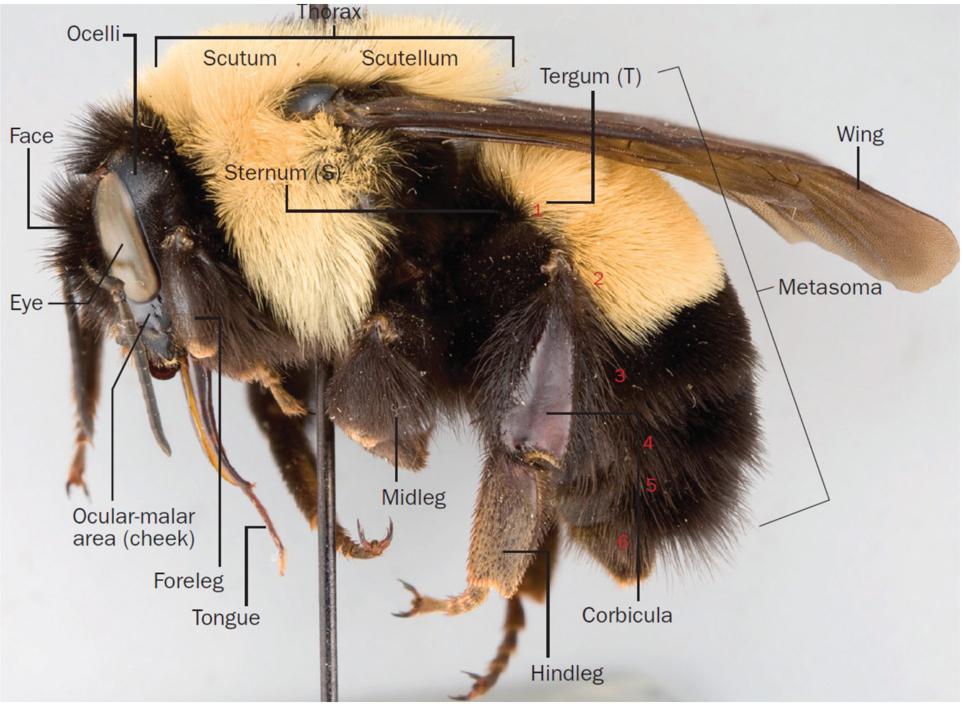


Fig. 18. Adult female bumblebee viewed from the left lateral aspect with external structures important for identification labelled. Diagram from Williams *et al*. (2014) of *Bombus affinis*, a close relative of the Himalayan *B. tunicatus*. Metasomal segments are numbered in red.

These characters vary within species as well as among them and are subject to further apparent variation caused by wear and abrasion. Nonetheless, they can still be useful in some species groups. The shape of the 12 (female) or 13 (male) ANTENNAL 'SEGMENTS' (A1 scape, A2 pedicel, and 10 or 11 flagellomeres), measured as ratios of length to breadth in the orientation shown in Fig. 19, is also used here, but only when the differences in shape are large. On the dorsum of the head, the three OCELLI vary in size and in position relative to the compound eye. One of the most variable characters, both among and within species, is the sculpturing of the OCELLO-OCULAR AREA of the VERTEX, the region between the lateral ocellus and the edge of the compound eye, which usually has many punctures laterally next to the inner margin of the compound eye and no punctures medially next to the lateral ocellus.

On the THORAX, most diagnostic characters are on the legs. The outer surface of the hind TIBIA has large areas without long hair for females of most species, except for females of the subgenera *Psithyrus* and *Mendacibombus*, and for males of some species (Sakagami & Ito 1981). For the females (excluding the subgenus *Psithyrus*), the bare area is surrounded by dense fringes of long, stout hairs or bristles that function as a CORBICULA (basket) for carrying pollen. Within some species groups there is a pronounced development of the distal posterior corner

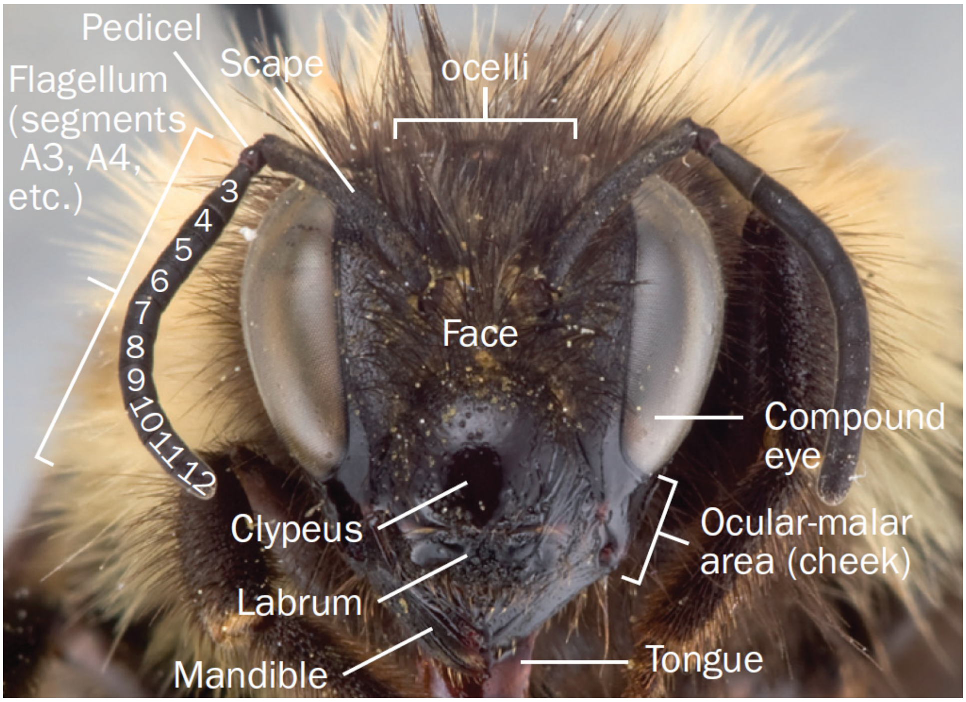


Fig. 19. Adult female bumblebee head viewed from the anterior aspect with external structures important for identification labelled. Diagram from Williams *et al*. (2014). Antennal segments are numbered in white.

of the mid BASITARSUS (first tarsomere). This can form a spinose (spine-like) projection, but differences between closely related species are seldom pronounced.

On the ABDOMEN, the most obvious characters are found in the sculpturing of the posterior sclerites (hard, heavily sclerotized parts). Bumblebees, like other Apocrita, have a waist between the first two abdominal segments, so that the first abdominal segment (propodeum) is associated with the thorax, whereas the subsequent segments form a separate unit, the METASOMA (gaster). In this review, all references to segment numbers for the dorsal TERGA (tergites) and ventral STERNA (sternites) refer to metasomal segments, so metasomal tergum 1 (T1) is the dorsal sclerite of the second abdominal segment.

For the females, variation in sculpturing is often especially clear on metasomal tergum 6 (T6, the epipygium or pygidium) and sternum 6 (S6, hypopygium), which may also show single or double KEELS (callosites or ridges), or a rounded central boss, as well as variation in the shape of the apex. The female genitalia associated with the STING (modified ovipositor) do not always preserve well in dried specimens and may become distorted, so these characters are not used here.

In contrast, the MALE GENITALIA (genital capsule) do preserve well because they are strongly sclerotised. They require no treatment other than a straightforward extraction from the metasoma by hooking them out with a pin (described above, Fig. 7). The male genitalia consist of two opposing pairs of claspers and a central intromittent organ. I follow the homologies of the parts elucidated by Williams (1985, 1991, 1995) and adopted by Michener (2007) (Fig. 20). The larger outer

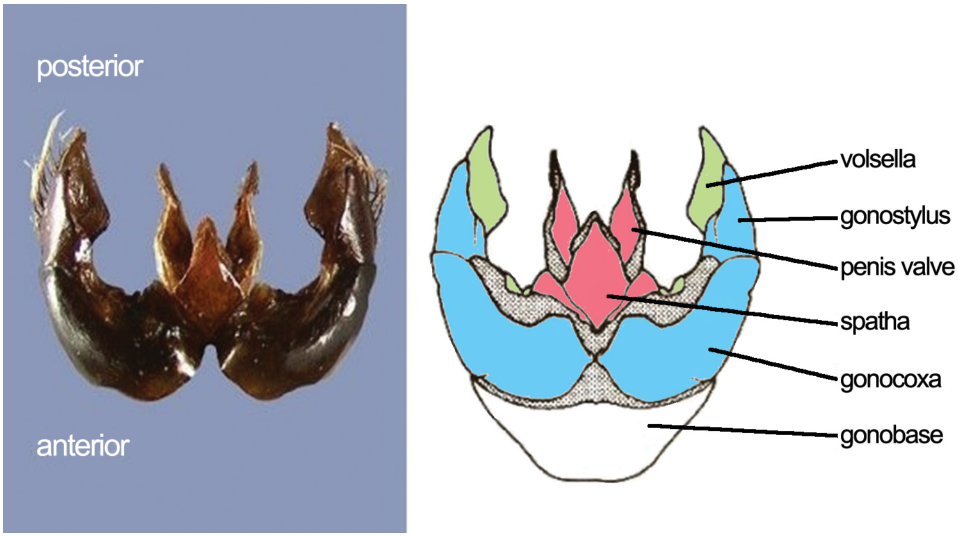


Fig. 20. Male genitalia of *Bombus avinoviellus* viewed from the dorsal view: (left) photo image and (right) diagram with components labelled for homology. In the diagram: red shows the penis structures; green the volsella structures; and blue the gonostylus structures.

claspers consist of a pair of anterior GONOCOXAE (gonocoxites, stipes), their terminal GONOSTYLI (squamae). Between them on their inner and ventral sides are the second pair of claspers, the enlarged VOLSELLAE (laciniae). Both the gonostylus and the volsella often have hook-like processes (extensions) directed inwards towards the midline of the body. Between the claspers are a pair of PENIS VALVES (sagittae) and an inflatable central intromittent organ (penis), which has a median dorsal SPATHA at its base. Many of these male genital structures show complex elaborations that are particularly valuable as taxonomic characters (for discussion of selection mechanisms see Eberhard 1985; Hosken & Stockley 2004).

Several additional informal terms are used here as shorthand, when describing components of colour patterns of the hair that do not correspond precisely with particular sclerites. On the head, 'FACE' is used for the large patch of long hair around the antennal base between the eyes and dorsal to the clypeus and anterior and ventral to the ocelli (frons + supraclypeal area + paraocular area). On the thorax, there is often an 'ANTERIOR BAND' of pale hairs occupying most of the dorsum anterior to the wing base (dorsal pronotum + anterior scutum), and a 'POSTERIOR BAND' of pale hair occupying the dorsum posterior to the wing base (posterior scutum + scutellum). The 'SIDE' of the thorax refers to the long hair covering the lateral parts of the thorax below the level of the wing base, on the lateral pronotum + mesepisternum + metepisternum + lateral propodeum. On the abdomen, the term 'TAIL' is used more flexibly, referring to the region of palest long hair covering all or parts of metasomal T4–6.

15. How to use this guide to identify bumblebee species

Unfortunately using colour pattern alone for bumblebee species identification generally is doomed to fail. The great variety of colour patterns of the hair of bumblebees may give the impression that species should be easy to identify, but colour patterns not only vary within species but are often shared among species (see the secion above on what are species?). Simple keys based on colour patterns may appear easy to use, and may sometimes work well on small local faunas, but they are unreliable for correct identification at the regional scale. This means that even after nearly two centuries of study, some Himalayan bumblebee species remain difficult to identify. This difficulty may be unfortunate, but it does challenge us all to find new and more effective diagnostic characters for identifying the species. Therefore the emphasis here is placed on morphology as the best (tried and tested) compromise.

This guide is arranged around a series of steps to identifying species that is likely to give the most reliable identifications:

(1) distinguishing bumblebees from other insects;
(2) separating bumblebees into females and males;
(3) using separate keys for females and males to identify the subgenera as the larger groups to which species belong;
(4) using separate keys for females and males within each subgenus to identify the species;
(5) checking the diagnostic characters listed for each species to check the species identity.

Some diagnostic characters of morphology may be visible to the unaided eye, but many are clearly visible only with a powerful hand lens or under a (binocular) microscope. For examination with a microscope, specimens will usually need to have been collected and placed on a long pin so they can be handled easily without being damaged. The hair needs to be in an un-matted, un-faded, and un-abraded condition (see the section above on how to catch bumblebees). It is useful to extend the legs and mandibles with forceps, although this may not be easy and is not essential. Male bees must have their genitalia (the small hard capsule in the abdomen) visible for examination if at all possible. The male genitalia of fresh (soft) specimens can be hooked out with a pin and exposed from between the last visible tergum and sternum of the metasoma (see the section above on bumblebee anatomy). It is better to leave the genitalia attached to the specimen, so they do not become separated and lost (Fig. 7), otherwise genitalia can be glued to a small card and placed on the pin with the rest of the specimen to keep them together. Unfortunately, diagnostic morphological characters are not always easy to see or to interpret, and often not as many diagnostic characters are known as we might wish. When technical terms for morphological structures are used (see the section above on bumblebee anatomy), this is only because they are needed in order to label structures with precision.

A quick visual summary of many of the species found by habitat is also provided (Figs 14–17) to give an overview of what might be expected. This should not be relied upon alone for species identification.

15.1. A note on DNA barcodes

Comparing DNA-barcode sequences is widely regarded as one of the most reliable approaches to species identification at present. DNA barcodes, which for bumblebees are a part of the COI gene (ideally amplified with Lep primers or an overlapping primer set), have been used extensively for checking samples for this guide. Indeed in a few cases (especially for a few species of the subgenera *Megabombus*, *Bombus s.str.*, and *Melanobombus*), barcodes may currently be the only really reliable way to identify species. Barcode sequences, like colour patterns and morphology, are not all identical within a species, so that they do still require careful quantitative analysis in order to make identifications (see the section above on what are species?). Unfortunately, barcodes are not accessible to most people. Comparison also requires a reliably identified reference library, which is not yet publicly available for the Himalaya. I do have a reference library of DNA barcodes for the Himalayan bumblebee species, but unfortunately I am prevented by the Nagoya protocol and national data-sharing restrictions from sharing it at this time because some of the sequences (although identified by me) came from specimens collected by others. It will be made publicly available as soon as arrangements can be made.

15.2. Is it a bumblebee?

Bumblebees are large (most are 7–30 mm in length) robust insects with two pairs of wings and long elbowed antennae. Their bodies have a dense covering of variously coloured, long, branched (plumose) hair (pubescence), although hair is sparse or absent on some parts of the ventral surface of the metasoma (S1–6), on parts of the propodeum, on parts of the anterior face of T1, and on parts of the head (see the section above on bumblebee anatomy, Fig. 18). The thicker parts of the exoskeleton (sclerites) are usually black, or lighter brown on the distal parts of the limbs, but they are never marked with bright red, yellow, white, or metallic (interference) colours. The wings may be transparent (hyaline) to strongly darkened (infuscated), but rarely show strongly metallic (interference) reflections. The wings have widely-spaced small hairs (are papillate) throughout and the fore wings have a distinct stigma present proximal to the marginal cell. On the head, bumblebees have the labrum at least twice as broad as long (Fig. 19). The labrum lacks a longitudinal median ridge and the female labrum has a strong transverse basal depression. Next to the labrum, the clypeus has a transverse subapical depression and the apico-lateral corners are curved posteriorly towards the occiput. An oculo-malar area (malar space) separates the compound eye from the base of the mandible, often by a distance greater than the breadth of the mandible at its base. The hind wings lack a jugal (anal) lobe. On the male genitalia, the volsella is greatly enlarged and is produced posteriorly and ventrally beyond the gonostylus (Fig. 20).

15.3. Is it a female or a male?

Female bumblebees have the antenna with 12 'segments' (A1 scape, A2 pedicel, A3–12 flagellomeres), the metasoma has six visible terga (T1–6), and between the externally visible T6 and S6 is the sting (see the section above on bumblebee anatomy, Figs 18–19). Getting stung is a test, but it is not recommended and, if you are allergic, must be avoided.

Male bumblebees have the antenna with 13 'segments' (A1 scape, A2 pedicel, A3–13 flagellomeres), the mtasoma has seven visible terga (T1–7), and between the externally visible T7 and S6 is the genital capsule (Figs 7, 20).

Most bumblebees encountered in the field and in collections are females, usually workers. There may be sex-related colour variation and, especially in the subgenus *Melanobombus*, size-related colour variation, which is then expressed as caste-(queen/worker) related colour variation because queens are larger than workers.

15.4. To which group of species does it belong?

In all of the keys, where possible the most reliable distinguishing characters are placed first within the couplets.

FEMALES: key to SUBGENERA

(these keys are revised and improved from the key by Williams in Williams *et al.* 2008).

1. Hind tibia compared with the mid tibia with the outer surface more broad, almost flat, most of the outer surface in the distal half without moderate to long hairs, but fringed with stout hairs that form a pollen basket (corbicula), the inner distal margin with a comb of stout spines (rastellum); S6 without ventro-lateral keels or ridges………2

– Hind tibia compared with the mid tibia with the outer surface not broadened and similarly uniformly convex and uniformly densely covered with moderate to long stout hairs throughout, the fringing hairs often poorly differentiated and not forming a pollen basket (corbicula), the inner distal margin without a comb of stout spines (rastellum); S6 with ventro-lateral keels or ridges..........................…………………………………***PSITHYRUS***

2. (1) Hind tibia with the outer surface weakly sculptured, smooth and brightly shining, and without long stout hairs in the middle of the proximal half beyond the proximal quarter; labrum with the labral tubercles separated by a deep median longitudinal furrow, often for a quarter of the breadth of the labrum; mandible with the anterior keel reaching and continuous with the distal margin; hind basitarsus with the proximal posteriorly-

directed process usually narrow and pointed, *either* longer than its breadth proximally where it joins the basitarsus *or if* it is shorter than broad *then* the lateral ocellus diameter is equal to half or less than half of the distance separating the lateral ocellus from the inner margin of the eye……3

– Hind tibia with the outer surface coarsely sculptured, matt and not shining, and with very long stout hairs in the middle of the proximal half that are spaced widely by more than the breadth of an antennal segment; labrum with the labral tubercles joined by a ridge that is complete and without a median longitudinal furrow; mandible with the anterior keel not reaching the distal margin and separated from it; hind basitarsus with the proximal posteriorly-directed process broad and blunt, usually shorter than its breadth proximally where it joins the basitarsus; lateral ocellus diameter always nearly three quarters or more of the distance separating the lateral ocellus from the inner margin of the eye……***MENDACIBOMUS***

3. (2) Mandible distally broadly rounded, with two anterior teeth and often a posterior tooth; hind basitarsus with the longest outwardly erect hairs near the anterior margin of the outer surface *either* as long as *or* usually shorter than the narrowest breadth of the basitarsus……………4

– Mandible distally not broadly rounded, but with six evenly-spaced large triangular teeth (which may become worn down); hind basitarsus with the longest outwardly erect hairs near the anterior margin of the outer surface *either* as long as *or* usually longer than the narrowest breadth of the basitarsus (although they may become broken off)..***ALPIGENOBOMBUS***

4. (3) Mid basitarsus with the distal posterior corner extended to form a sharp angle of 45° or less, *either* produced as a narrow tooth *or* spine (it may be less pronounced in some of the smallest individuals) *or* if more rounded *then* the cheek (oculo-malar area) in the centre with a diagonal band of many distinct small widely-spaced punctures; the area between the lateral ocellus and the inner margin of the eye with the unpunctured shining part occupying less than half of the distance between the lateral ocellus and the eye……5

– Mid basitarsus with the distal posterior corner broadly or narrowly rounded, but *either* forming an angle of more than 45° and without a narrow tooth or spine *or if* more narrowly acute *then* the area between the lateral ocellus and the inner margin of the eye with the unpunctured shining part occupying more than three quarters of the distance between the lateral ocellus and the eye; the cheek (oculo-malar area) in the centre with few or no punctures........................……………………………………………7

5. (4) Hind basitarsus with the proximal posteriorly-directed process with the dense plume of moderately long branched hairs on its proximal surface not continuing onto its outer surface, which is shining and often bare, at most the outer surface with widely scattered rather reclining short hairs with broad shining areas visible between them; cheek (oculo-malar area) in the centre smooth and shining at most with a very few very shallow punctures……6

– Hind basitarsus with the proximal posteriorly-directed process with the dense plume of moderately long branched hairs on its proximal surface continuing onto its outer surface as an erect brush of moderately long branched hairs that often obscures the outer surface of the basitarsus between them; cheek (oculo-malar area) in the centre with a diagonal band of small punctures……………………………………***SIBIRICOBOMBUS***

6. (5) Clypeus central area bulbous with at least a few large or medium punctures; antennal segment A4 is shorter than broad……***MEGABOMBUS***

– Clypeus central area flattened and smooth and shining with only micro-punctures, the larger punctures only at the edges; antennal segment A4 is longer than broad…………………………………***SUBTERRANEOBOMBUS***

7. (4) Ocello-ocular area with the unpunctured and shining areas medium or small, more than the outer quarter along the inner eye margin with punctures, the unpunctured area anterior to the three ocelli extending for less than the breadth of an ocellus……………………………………………8

– Ocello-ocular area with the unpunctured and shining areas very large, only the outer quarter along the inner eye margin with punctures, the unpunctured area including most of the area anterior to the three ocelli for a distance of more than the breadth of an ocellus except for narrow bands of punctures between the median and lateral ocelli……***ORIENTALIBOMBUS***

8. (7) Mandible near its distal posterior corner with a notch (incisura) that is nearly as deep as wide and separating a strong posterior tooth (which may become worn down); clypeus in its central area always strongly swollen and bulging, contrasting with deep lateral depressions adjacent and parallel to the labral margin, large punctures dense throughout with few smaller punctures; hind basitarsus posterior margin broadly and evenly strongly curved……………***BOMBUS*** *s.str.*

– Mandible near its distal posterior corner with a notch (incisura) that is less than half as deep as wide, or often completely lacking so that it does not separate a weak posterior tooth; clypeus in its central area usually weakly swollen or nearly flat, with only shallow lateral depressions adjacent and parallel to the ventral labral margin, large punctures at most widely scattered among many more of the smaller punctures; hind basitarsus posterior margin curving much more strongly in its proximal half and nearly straight in its distal half … 9

9. (8) Hind basitarsus in its distal half with short slightly feathered hairs widely spaced so that the surface is clearly visible and shining in between; central area of the clypeus with widely scattered large as well as small punctures, appearing irregular and dull; area between the lateral ocellus and the inner margin of the eye *either* with the band of punctures along the inner margin of the eye dorsally usually for most of its length with very few small punctures, mostly consisting of a few scattered large punctures separated by shining areas broader than the puncture widths, the large unpunctured and shining area adjacent to the ocellus usually large, occupying nearly three quarters of

the distance between the lateral ocellus and the inner margin of the eye, *or* if with many dense small punctures *then* these cover the entire area between the eye and the depression around the lateral ocellus.….***PYROBOMBUS***

– Hind basitarsus in its distal half with dense overlapping short slightly feathered often pale hairs largely obscuring the shining surface; central area of the clypeus *either* with scattered mostly small punctures, appearing smooth and shiny, *or* if with large punctures *then* the labrum with the median longitudinal furrow only 0.2× the labral breadth; area between the lateral ocellus and the inner margin of the eye *either* with the band of punctures along the inner margin of the eye dorsally usually with many small and large punctures intermixed and separated by less than the widths of the large punctures *or* if there are few small punctures then *either* the part of the puncture band with only large punctures is absent *or* occupies only a short part of its length *and* the unpunctured and the shining area adjacent to the ocellus occupies less than half of the distance between the lateral ocellus and the inner margin of the eye.…....***MELANOBOMBUS***

MALES: key to SUBGENERA

1. Hind tibia differing in form strongly from the mid tibia, the outer surface flat with at most only short hairs in the centre and long hairs anteriorly and posteriorly, head in dorsal view unenlarged from anterior to posterior so that the anterior to posterior distance is 0.5× its breath; volsella and gonostylus usually strongly sclerotised and mid or dark brown; gonostylus with the inner proximal process without medium-length branched hairs; volsella often but not always with a process or hooks on its inner margin; penis-valve head *either* straight, *or* curved inwards, *or* curved outwards…2

– Hind tibia similar in form to the mid tibia, the outer surface strongly convex and densely covered with many moderately long hairs, head in dorsal view enlarged from anterior to posterior so that the anterior to posterior distance is 0.66× its breadth; volsella and gonostylus usually weakly sclerotised and pale yellowish; gonostylus with the inner proximal process associated with many medium-length branched hairs; volsella always without a process or hooks on its inner margin; penis-valve head always nearly straight…………***PSITHYRUS***

2. (1) Antenna medium to long, reaching back at least to the anterior margin of the tegula at the wing base; volsella with a process or hook on its inner margin; gonostylus with an inner proximal process; penis-valve head *either* straight, *or* curved inwards, *or* curved outwards; eye *either* enlarged *or* unenlarged relative to the eye of a female bumblebee………3

– Antenna short, not quite reaching back to the anterior margin of the tegula at the wing base; volsella without a process or hook on its inner margin; gonostylus simple and finger-like, without an inner proximal process, at most with a broad low proximal swelling; penis-valve head always straight; eye always strongly enlarged relative to the eye of a female bumblebee...***MENDACIBOMBUS***

3. (2) Penis valve narrow dorso-ventrally, at least in its distal third, which is slightly ventrally curved; antenna *either* of medium length *or* longer, reaching back *either* to *or* beyond the tegula at the wing base……………4

– Penis valve greatly broadened dorso-ventrally so as to form half of a broad irregular tube, the distal end flared outwards as half of a broad funnel; antenna of medium length, not reaching back as far as the posterior margin of the tegula at the wing base…………***BOMBUS*** *s.str.*

4. (3) Penis-valve head from the dorsal view turned inwards distally as a distinct broad hook, *either* dorso-ventrally flattened in the shape of a sickle *or* as a spoon...........................………………………………………6

– Penis-valve head from the dorsal view distally *either* nearly straight *or* turned slightly outwards, at most with only a tiny inwardly directed point…5

5. (4) Gonostylus with a distinct inner proximal process strongly separated from the distal lobe by a deep incision…………………………***MEGABOMBUS***

– Gonostylus without a narrow inner proximal process, at most marked only with a broad weak curve or swelling……………………***ORIENTALIBOMBUS***

6. (4) Gonostylus usually a simple flat triangle, exceptionally reduced to a spine, but without a distinct inner proximal process; gonostylus in cross section with the inner distal margin in part with a narrow submarginal longitudinal groove……………………………………………***PYROBOMBUS***

– Gonostylus with a distinct inner proximal process, although this may be a small rounded stub; gonostylus with the inner distal margin simply flattened and blade-like in cross section without a submarginal longitudinal groove…7

7. (6) Penis-valve shaft with a ventral angle about half way along its length and distinct *either* as a pronounced sharp angle *or* produced as a larger lateral process..………………………………8

– Penis-valve shaft with a ventral angle about half way along its length *either* reduced and very broadly rounded (not sharply marked) *or* absent……9

8. (7) Penis-valve head turned inwards distally as an incurved bowl or spoon shape; penis-valve shaft with the ventral angle about half way along its length produced ventrally and laterally as a broad transverse paddle-like process; mandible distally pointed and with one anterior tooth..........………………………………***SUBTERRANEOBOMBUS***

– Penis-valve head turned inwards distally as a dorso-ventrally flattened sickle shape; penis-valve shaft with the ventral angle about half way along its length produced ventrally as a pronounced angle; mandible distally pointed and with two anterior teeth……………………***ALPIGENOBOMBUS***

9. (7) Mid basitarsus on its outer surface with many medium and long hairs; gonostylus with the distal lobe at least just shorter than broad, sometimes much shorter than broad; antenna *either* medium *or* long, reaching to *or* beyond the tegula at the wing base……………………….***MELANOBOMBUS***

– Mid basitarsus on its outer surface with sparse short hairs and very few or no moderate and long hairs; gonostylus with the distal lobe always longer than broad; antenna very long, reaching far beyond the wing base...........................……………………………***SIBIRICOBOMBUS***

16. Systematic account

16.1. Subgenus *MENDACIBOMBUS*

These bumblebees are specialists in high alpine grasslands. Medium tongue-length bumblebees visiting medium-depth flowers. Nest underground, among rocks. Larvae are reared in separate cells throughout their development, as non-pocket makers, and food reserves are held in hexagonal cells outside the brood-nest envelope (Haas 1976). Males have enlarged compound eyes relative to the females. The six species studied globally race after potential mates and may be truly territorial (Williams 1991).

FEMALES: key to SPECIES

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

– Hair of the thoracic dorsum and T1 with broad pale bands of yellow or white hairs ……………………………………………………………………2

2 (1) Hair of the thoracic dorsum almost entirely yellow, at most with an obscure small spot with a few black hairs centrally between the wing bases……3

– Hair of the thoracic dorsum yellow and/or white, but *either* usually with a black band *or* sometimes an obvious large spot of black hairs between the wing bases…………………………………………………………………4

3. (2) Wings nearly clear; labrum with a broad convex transverse ridge, the ridge broader than the basal depression (adjacent to the clypeus), 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, the ridge narrower than the basal depression (adjacent to the clypeus), clypeus in its central half with few large punctures relative to the number of small punctures……… ***B. avinoviellus*** (part)

4. (2) Wings lightly clouded with brown; labrum with a narrow high transverse ridge, in the middle the ridge narrower than the basal depression (adjacent to the clypeus), the transverse ridge often 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…… ***B. avinoviellus*** (part)

– Wings nearly clear; labrum with a broad low transverse ridge, in the middle the 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…………………… ***B. himalayanus***

MALES: key to SPECIES

1. Volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point with a raised curved ridge with small teeth just inside the inner margin, running for 0.3–0.5× the remaining distal length of the volsella……………………………………………………***B. waltoni***

– Volsella at its broadest near the midpoint of its length, the dorsal surface just distal to this point without a raised curved toothed ridge just inside the inner margin......................…………………………………………………2

2. (1) Penis valve proximal to the outer shoulder more than 2× as broad as the penis-valve head (defined by an outer toothed flange), gonostylus distally strongly dorso-ventrally flattened and plate-like, thickness less than 0.25× its own breadth; wings light brown…………***B. avinoviellus***

– Penis valve proximal to the outer shoulder less than 2× as broad as the penis-valve head (defined by an outer toothed flange), gonostylus distally thick, thickness more than 0.25× its own breadth; wings nearly clear…3

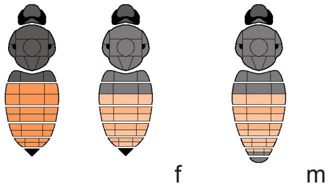
3. (2) Gonostylus from the dorsal view rectangular, with a distinct outer distal corner; hair of the thoracic dorsum between the wing bases *either* usually extensively black (Himalaya) *or* rarely (Trans Himalaya) yellow with many black hairs intermixed across the breadth………***B. himalayanus***

– Gonostylus from the dorsal view almost triangular, without a distinct outer distal corner but broadly rounded; hair of the thoracic dorsum between the wing bases entirely yellow except in a central spot that sometimes has a few black hairs………***B. marussinus***

16.1.1. *Bombus* (*Mendacibombus*) *waltoni* Cockerell, 1910

Bombus waltoni Cockerell 1910 (September): 239. Holotype queen by monotypy NHMUK, examined.

[*Bombus* (*Psithyrus*) *novus* (Frison); Saini *et al.* 2015: 103 (in part), misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2016).

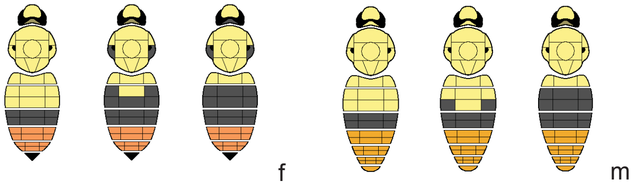
Identification. Small body (queen length 14–16 mm; worker 10–12 mm; male 13–16 mm) and medium length tongue. Similar to some *B.* (*Pr.*) *flavescens* or *B.* (*Ml.*) *eximius* (which occur at much lower elevation). Females can be distinguished: (cf. *B. flavescens*, *B. eximius*) by the long hairs of the mid tibia in its proximal half black, by the labrum which lacks a median groove and lamella, and by the hind tibia having a few long hairs on the outer surface. Male genitalia are uniquely diagnostic: by the volsella dorsal surface having a curved finely toothed ridge near its distal medial (inner) margin and with the apex curled dorsally.

Habitat. Rare in high alpine flower-rich grassland.

Distribution. Trans-Himalaya and QTP, especially in the east (global distribution mapped by Williams *et al.* 2016).

16.1.2. ***Bombus*** **(*Mendacibombus*)** ***marussinus*** **Skorikov, 1910**

Bombus mendax subsp. *marussinus* Skorikov 1910a: 330. Lectotype queen by designation of Williams *et al.* (2016) ZIN, examined.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2016).

Identification. Small body (queen length 15–17 mm; worker 11–13 mm; male 15–17 mm) and medium length tongue. Most similar to some *B.* (*Md.*) *avinoviellus* (see also *B.* (*Sb.*) *longiceps*, *B.* (*Ml.*) *semenovianus*, *B.* (*Pr.*) *subtypicus* and *B.* (*Pr.*) *kotzschi*). Females can be distinguished: (cf. *B. avinoviellus*) by the clear wings, by the labrum having the transverse ridge broader than the basal depression; and (cf. species of other subgenera) by the female labrum lacking a median groove and lamella, and the hind tibia having a few long hairs near the middle on the outer surface. Male genitalia are uniquely diagnostic: (cf. *B. avinoviellus*, *B. longiceps*, *B. semenovianus*, *B. subtypicus*, *B. kotzschi*) by having the penis valve nearly straight and the gonostylus strongly thickened, with the thoracic dorsum entirely yellow.

Habitat. Uncommon in alpine and subalpine flower-rich semi-desert grassland.

Distribution. Trans-Himalayan northern border with the Hindu Kush and Central Asia (global distribution mapped by Williams *et al.* 2016).

16.1.3. *Bombus* (*Mendacibombus*) *avinoviellus* (Skorikov, 1914)

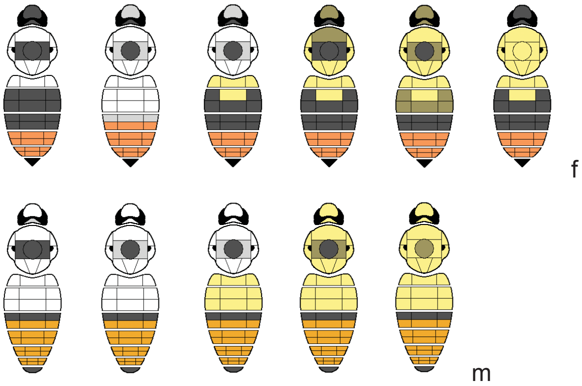
Mendacibombus avinoviellus Skorikov 1914a: 126. Lectotype queen by designation of Williams *et al.* (2016) ZIN, examined.

Bombus niveatus subsp. *callophenax* Cockerell 1917: 122. Holotype queen by monotypy USNM, examined.

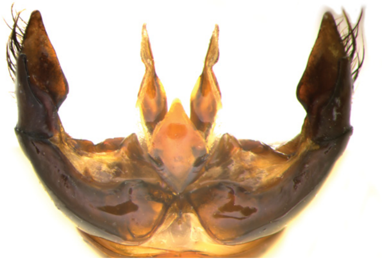
[*Mendacibombus afghanus* (Reinig); Tkalců 1969a: 193, misidentification].

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

[*Bombus* (*Bombus*) *tunicatus* Smith; Saini *et al.* 2015: 219, fig. 273 (in part), misidentification; Jaffar *et al.* 2019: 983 fig. 2 (in part), misidentification].



Colour patterns of the hair of females (*above*) *and males* (*below*), *variation shown* (*approximately*) *from west to east.*



Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest, alpine, and Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2016). The species includes both white-banded (western) and yellow-banded (eastern) colour patterns, and with an unbanded yellow thorax in the Karakoram.

Identification. Small body (queen length 15–17 mm; worker 11–13 mm; male 13–15 mm) and medium length tongue. Most similar to *B.* (*Md.*) *himalayanus* and

B. (*Md.*) *marussinus* (see also many other species with similar pale-banded colour patterns). Females can be distinguished: (cf. *B. himalayanus*, *B. marussinus*) by the weakly clouded wings, labrum having the transverse ridge narrower than the basal depression; and (cf. species of other subgenera) by the labrum lacking a median groove or lamella, and the hind tibia having a few long hairs near the middle on the outer surface. Male genitalia are diagnostic: by the penis valve being strongly laterally compressed and not turned outwards or inwards distally as a hook.

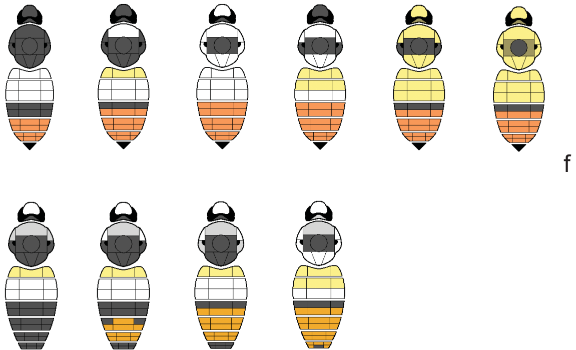
Habitat. Alpine and subalpine flower-rich grassland and open areas in the upper forest.

Distribution. Endemic to the western Himalaya (common) and Karakoram (rare) (global distribution mapped by Williams *et al.* 2016).

16.1.4. *Bombus* (*Mendacibombus*) *himalayanus* (Skorikov, 1914)

Mendacibombus varius Skorikov 1914a: 125 (not of Lepeletier de Saint-Fargeau 1832: 381, = *B.campestris* (Panzer)). Lectotype queen by designation of Williams *et al.* (2016) ZIN, examined.

Mendacibombus mendax subsp. *himalayanus* Skorikov 1914a: 127. Holotype queen by monotypy ZIN, examined.



Colour patterns of the hair of females (*above*) *and males* (*below*), *variation shown* (*approximately*) *from west to east.*

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (*left: cf. Fig. 4*) *alpine and Trans-Himalayan alpine, recorded by province* (*right: cf. Fig. 3*) *from specimens* (*dark*), *likely interpolation* (*mid*), *or no records* (*light*).

Taxonomy and variation. Williams *et al.* (2016). The species includes both white-banded (outer humid zone of the Great Himalaya) and yellow-banded (semi-arid Trans Himalaya) colour patterns.

Identification. Small body (queen length 15–17 mm; worker 10–12 mm; male 13–16 mm) and medium length tongue. Yellow-banded individuals without white (Ladakh and Zanskar) are most similar to *B.* (*Md.*) *avinoviellus* (see also many species with yellow-banded or white-banded colour patterns). Females can be distinguished: (cf. *B. avinoviellus*) by the clear wings and the labrum having the transverse ridge broader than the basal depression; (cf. species of other subgenera) by the labrum lacking a median groove or lamella, and the hind tibia having a few long hairs near the middle on the outer surface. Male genitalia are uniquely diagnostic: by the gonostylus being strongly thickened, and by the apex of the penis valve being broad and narrowing abruptly without being turned inwards or outwards.

Habitat. High alpine flower-rich grassland.

Distribution. Endemic to the western Himalaya (uncommon) including Zanskar and Ladakh (extremely rare) (global distribution mapped by Williams *et al.* 2016).

16.2. Subgenus *SUBTERRANEOBOMBUS*

These bumblebees are associated with open grasslands, from semi-deserts to the high alpine zone. Long tongue-length bumblebees visiting deep flowers. Nest underground or sometimes on the surface. Larvae are reared together in wax pockets throughout their development. Males have been recorded congregating at the entrances of nests to pursue emerging queens.

FEMALES: key to SPECIES

1. Clypeus with very few micropunctures, which are separated by more than 2× their own breadths; hair of T3–5 entirely black…………………2

– Clypeus with many micropunctures, which are separated by 2× their own breadths; hair of T3–5 black with posterior fringes of white……***B. personatus***

2. (1) Wings light to dark brown; thoracic dorsum with the pale hair *either* lemon yellow *or* straw yellow *or* brown, but usually only cream yellow if faded by the sun, the thoracic dorsum *either* entirely yellow, *or if* a black is present between the wing bases, *then* it is as a spot or band less than 0.8× the breadth of the anterior yellow band………………***B. melanurus***

– Wings nearly clear; thoracic dorsum with the pale hair cream yellow, with a well defined black band between the wing bases, which is 0.75–1.0× the breadth of the anterior yellow band……………………………***B. difficillimus***

MALES: key to SPECIES

1. T3–6 black, posteriorly with a fringe of pale hair; penis-valve head with a strong long spine basally on the outer side directed anteriorly; gonocoxa with a sharp dorsal ridge reaching all the way to the distal (posterior) edge, on its inner side distally with a dorsally flat or concave triangular inwardly directed process adjacent to the gonostylus……***B. personatus***

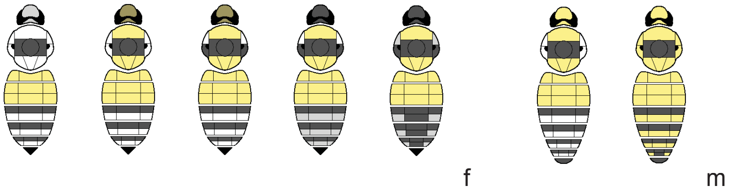
– T3–6 black, posteriorly without a fringe of pale hair; penis-valve head without a long spine basally on the outer side directed anteriorly; gonocoxa with the sharp dorsal ridge subsiding into the convex dorsal surface before the distal edge, so that the distal portion is rounded and finger-like……2

2. (1) Hair of the face *either* (usually) yellow, *or if* black *then* there is no band of black hair between the wing bases; gonostylus with the inner proximal process breadth at its narrowest 0.25× the length (measured in parallel) of the gonostylus; hair short and even……***B. melanurus***

– Hair of the face *either* (usually) black, *or if* with many pale hairs *then* there are few or no pale hairs just above the wing base in the black band between the wing bases; gonostylus with the inner proximal process at its narrowest as broad as nearly 0.5× the length of the gonostylus; hair long and uneven……………………………***B. difficillimus***

16.2.1. *Bombus* (*Subterraneobombus*) *personatus* Smith, 1879

Bombus personatus Smith 1879: 132. Lectotype queen by designation of Richards (Richards 1930) NHMUK, examined.
Bombus Roborowskyi Morawitz 1887: 197. Syntype queen ZIN, examined.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2011). Small workers tend to be darker in colour than large queens.

Identification. Medium size body (queen length 19–20 mm; worker 14–16 mm; male 16–17 mm) and long tongue. Most similar to *B.* (*St.*) *difficillimus* and *B.* (*St.*) *melanurus*. Females can be distinguished: (cf. *B. difficillimus*, *B. melanurus*) by scattered small punctures on the clypeus and by the white posterior fringes on T3-5. Male genitalia are uniquely diagnostic: by the penis-valve head on the outer side basally having a long stout spine directed anteriorly.

Habitat. Uncommon in alpine flower-rich grasslands.

Distribution. Trans-Himalaya and QTP (global distribution mapped by Williams *et al.* 2011).

16.2.2. *Bombus* (*Subterraneobombus*) *melanurus* Lepeletier, 1835

Bombus melanurus Lepeletier de Saint-Fargeau [1835]: 469. Lectotype queen by designation of Tkalců (1969a) OUMNH, examined.

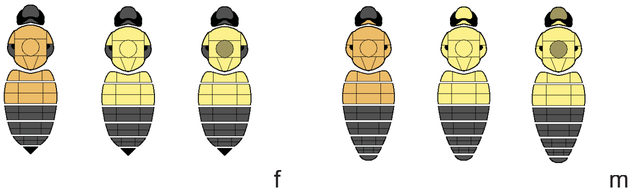
Bombus altaicus Eversmann 1846: 436. Lectotype queen by monotypy (Skorikov 1910b) not seen.

Bombus Tschitscherini Radoszkowski 1862: 591 by indication of Radoszkowski 1860: 485. Lectotype queen by designation of Williams *et al.* (2011) ISEAK, examined.

Bombus melanurus subsp. *subdistinctus* Richards 1928b: 333. Holotype queen by original designation NHMUK, examined.

[*Megabombus* (*Subterraneobombus*) *difficillimus* (Skorikov); Tkalců, 1974: 345, misidentification].

[*Bombus* (*Psithyrus*) *skorikovi* (Popov); Saini *et al.* 2015: 239, figs 396, 411, 412 (in part), misidentification].



Colour patterns of the hair of females (*left*) *and males* (*right*), *variation shown* (*approximately*) *from west to east.*

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest, subalpine, and Trans-Himalayan subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2011). Analyses of COI barcodes continue to support this as a single species, to include not only the individuals from Nepal with a weak spot or band of black between the wing bases, but also others from the eastern QTP with a distinct black band between the wing bases. The species also includes both brown (outer humid zone of the Great Himalaya) and yellow (semi-arid Trans Himalaya) colour patterns.

Identification. Large body (queen length 21–25 mm worker 13–19 mm male 15–19 mm) and long tongue. Most similar to *B.* (*St.*) *personatus* and *B.* (*St.*) *difficillimus*. Females can be distinguished: (cf. *B. personatus*, *B. difficillimus*) by the short hair and dark wings, and usually by the lack of a black band between the wing bases. Male genitalia can be distinguished: (cf. *B. personatus*, *B. difficillimus*) by the gonostylus having the inner proximal process breadth at its narrowest 0.25× the adjacent greatest (parallel) length of the gonostylus.

Habitat. Common in subalpine flower-rich grasslands, forest edges, to low-elevation desert-edge flower-rich grasslands.

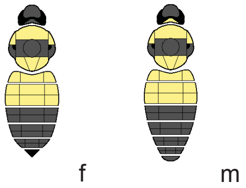
Distribution. Western Himalaya, Trans-Himalaya, and QTP, as well as Turkey to Mongolia and northern China (global distribution mapped by Williams *et al.* 2011).

16.2.3. *Bombus* (*Subterraneobombus*) *difficillimus* Skorikov, 1912

Bombus difficillimus Skorikov 1912b: 609. Lectotype queen by designation of Williams *et al.* (2011) ZIN, examined.

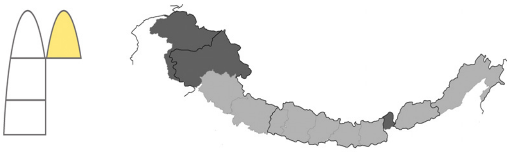
Bombus (*Subterraneobombus*) *melanurus* subsp. *griseofasciatus* Reinig 1930: 83. Lectotype queen by designation of Williams *et al.* (2011) RMNH, examined.

[*Bombus* (*Subterraneobombus*) *melanurus* Lepeletier; Williams, 1991: 61 (in part), misidentification; Saini *et al.* 2015: 92 (in part), misidentification].



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.



Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2011).

Identification. Large body (queen length 19–23 mm; worker 15–20 mm; male 18–20 mm) and long tongue. Most similar to *B.* (*St.*) *melanurus* and *B.* (*St.*) *personatus* (see also *B.* (*Sb.*) *sibiricus* and *B.* (*Sb.*) *longiceps*). Females can be distinguished: (cf. *B. melanurus*, *B. personatus*) by the combination of long hair, distinct black band between the wing bases, and pale wings; and (cf. *B. sibiricus*, *B. longiceps*) by the lack of punctures in the oculo-malar area and in the centre of the clypeus. Male genitalia can be distinguished: (cf. *B. melanurus*, *B. personatus*) by the gonostylus having the inner proximal process at its narrowest as broad as nearly 0.5× the adjacent greatest (parallel) length of the gonostylus; and (cf. *B. sibiricus*, *B. longiceps*) by the penis-valve head being spoon-shaped.

Habitat. Uncommon in alpine flower-rich grasslands.

Distribution. Trans-Himalaya, QTP, and southern Central Asia (global distribution mapped by Williams *et al.* 2011).

16.3. Subgenus *MEGABOMBUS*

These bumblebees are associated with grasslands, forest edges, or sometimes with forb vegetation along streams. Long tongue-length bumblebees visiting deep flowers, including the longest-tongued bumblebees world-wide, often specialising in a narrow range of bilaterally symmetrical flowers. Nests are usually underground. Larvae are reared together in wax pockets throughout their development. Males patrol circuits of scent-marked places that attract young queens.

FEMALES: key to SPECIES

1. Clypeus in the anterior (lower) third with many large scattered punctures, spaced by about 1–3 large puncture diameters and interspersed with small punctures, in the median anterior area with large punctures; queen with the oculo-ocellar area along the inner eye margin, anterior to the posterior field of dense small punctures, with an area matt with shallow transverse micro ridges………………………… ***B. albopleuralis***

– Clypeus in the anterior (lower) third with few medium to large punctures, spaced by 3–4 large puncture diameters and interspersed with small punctures, in the median anterior area with almost no punctures; queen with the oculo-ocellar area along the inner eye margin, anterior to the posterior field of dense small punctures, with an area smooth and shiny without clear micro ridges………………………… ***B. montivagus***

MALES: key to SPECIES

1. Gonostylus from the posterior aspect with the inner basal projection divided into two long narrow spines, dorsal and ventral, of nearly equal length……………………………… ***B. albopleuralis***

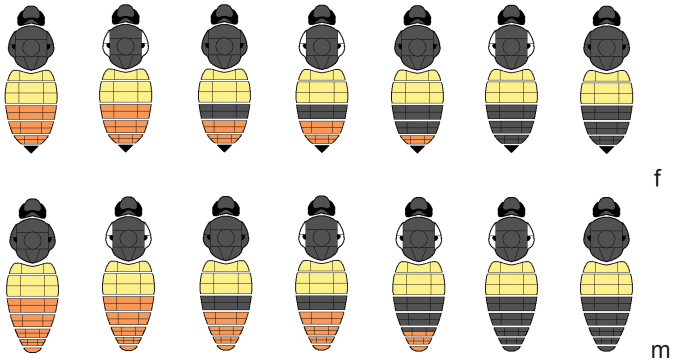
– Gonostylus from the posterior aspect with the inner basal projection divided into two long narrow spines, dorsal and ventral, the ventral spine nearly 2× as long as the dorsal spine…………………… ***B. montivagus***

16.3.1. *Bombus* (*Megabombus*) *albopleuralis* Friese, 1916

Bombus haemorrhoidalis var. [subsp.] *albopleuralis* Friese 1916: 108. Lectotype queen by designation of Tkalců (1974) ZMHB, examined.

Bombus mimeticus Richards 1931: 529. Holotype queen by original designation NHMUK, examined.

[*Bombus* (*Diversobombus*) *trifasciatus* Smith; Williams, 1991: 52 (in part), misidentification; Burger *et al.* 2009: 461, misidentification; Williams *et al.* 2010: 125, misidentification; Saini *et al.* 2015: 144, misidentification]



Colour patterns of the hair of females (above) and males (below), variation shown (approximately) from west to east.

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Morphology in this species-complex was reviewed by Williams *et al.* (2009); *B.* (*Mg.*) *montivagus* was split from *B.* (*Mg.*) *trifasciatus* from DNA evidence by Hines & Williams (2012); and *B.* (*Mg.*) *albopleuralis* was split from *B. montivagus* from DNA evidence by Huang *et al.* (2015). Continuing species-coalescent (PTP) analyses of MrBayes phylogenetic trees from COI barcodes support *B. albopleuralis* as a species separate from *B. trifasciatus* and *B. montivagus*, with the latter also occurring in the Himalaya (see comments on

B. montivagus). However, their diagnosis is difficult and unreliable from the information currently available. It is likely that understanding of the two species in the Himalaya will change substantially when more data become available. The extent of the black hair on T3–5 shows a progressive increase from west to east.

Identification. Medium size body (queen length 16–19 mm; worker 11–16 mm; male 15–16 mm) and long tongue. Most similar to *B.* (*Mg.*) *montivagus* and difficult to distinguish reliably without COI barcodes (see also *B.* (*Or.*) *haemorrhoidalis*, *B.* (*Ag.*) *breviceps*, and *B.* (*Pr.*) *rotundiceps*). Females can be distinguished: (cf. *B. montivagus*) by the clypeus being densely and coarsely punctured, especially anteriorly (in its lower part); (cf. *B. haemorrhoidalis*, *B. montivagus*) by T3 anteriorly in the middle with a few yellow hairs; and (cf. *B. haemorrhoidalis*, *B. breviceps*, *B. rotundiceps*) by the midleg basitarsus having the distal posterior corner extended to form a sharp angle of less than 45° and produced as a narrow spine. Male genitalia can be distinguished: (cf. *B. montivagus*, *B. haemorrhoidalis*, *B. breviceps*, *B. rotundiceps*) by the gonostylus from the posterior view having the inner basal projection divided into two long narrow spines, dorsal and ventral, of nearly equal length.

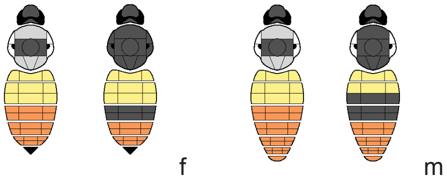
Habitat. Appears to be common around low and mid-elevation forests, but the species identity needs to be confirmed (Williams 1991; Williams *et al.* 2010).

Distribution. Widespread in the Himalaya and extending into northern Burma.

16.3.2. *Bombus* (*Megabombus*) *montivagus* Smith, 1878

Bombus montivagus Smith 1878a: 168 (re-proposal in error Smith 1879: 131). Lectotype queen by designation of Tkalců (1968) NHMUK, examined.

[*Bombus* (*Diversobombus*) *trifasciatus* Smith; Williams, 1991: 52 (in part), misidentification; Williams *et al.* 2010: 125, misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009), Hines & Williams (2012), and Huang *et al.* (2015) (see comments on *B.* (*Mg.*) *albopleuralis*). Continuing species-coalescent (PTP) analyses of Mr Bayes phylogenetic trees from COI barcodes not only support *B.* (*Mg.*) *trifasciatus*, *B.* (*Mg.*) *albopleuralis*, *and B.* (*Mg.*) *montivagus* as three separate species, but also support *B. montivagus* as occurring in the Himalaya (for the first time), where its diagnosis is currently difficult and unreliable. It is likely that understanding of the two species in the Himalaya will change with more data. The extent of the black hair on T3–5 is expected to increase from west to east as in *B. albopleuralis*.

Identification. Medium size body (queen length 17–20 mm; worker 12–15 mm; male 15–16 mm) and long tongue. Most closely similar to *B.* (*Mg.*) *albopleuralis* and difficult to distinguish reliably without COI barcodes (see also *B.* (*Or.*) *haemorrhoidalis*, *B.* (*Ag.*) *breviceps*, and *B.* (*Pr.*) *rotundiceps*). Females can be distinguished: (cf. *B. albopleuralis*) by the clypeus being sparsely and finely punctured, especially anteriorly (in its lower part); (cf. *B. haemorrhoidalis*, *B. albopleuralis*) by T3 anteriorly in the middle with no yellow hairs; and (cf. *B. haemorrhoidalis*, *B. breviceps*, *B. rotundiceps*) by the midleg basitarsus having the distal posterior corner extended to form a sharp angle of less than 45° and produced as a narrow spine. Male genitalia can be distinguished: (cf. *B. albopleuralis*, *B. haemorrhoidalis*, *B. breviceps*, *B. rotundiceps*) by the gonostylus from the posterior view having the inner basal projection divided into two long narrow spines, dorsal and ventral, the ventral spine nearly twice as long as the dorsal spine.

Habitat. Information on this species in the Himalaya is very uncertain – larger samples are needed to clarify its characteristics and distribution. Presumed to be widespread at some low to medium elevations in forest edges, but data are insufficient (Williams *et al.* 2009; Williams *et al.* 2010). Entrance to an underground nest seen in an earth bank in Southeast Asia.

Distribution. Himalaya to southern China and Southeast Asia.

16.4. Subgenus *ORIENTALIBOMBUS*

These bumblebees are associated with forest edges, and are especially common at relatively low elevations. Long tongue-length bumblebees visiting deep flowers. Nests are underground. Larvae are likely to be reared together in wax pockets throughout their development and males are likely to patrol circuits of scent-marked places that attract young queens, although this has not been recorded.

FEMALES: key to SPECIES

1. Hair of the thoracic dorsum *either* black *or* rarely with light grey, not paler along the median line, T1 yellow……………………… ***B. haemorrhoidalis***

– Hair of the thoracic dorsum dark olive-grey but paler along the median line, T1 from light olive-grey to nearly white…… ***B. funerarius***

MALES: key to SPECIES

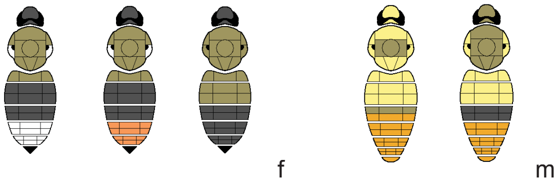
1. Hair of the thoracic dorsum black or with some grey hair intermixed in anterior and posterior bands but not paler along the median line; gonostylus nearly square (as long as broad); the volsella apex only slightly narrowed and strongly curled dorsally…… ***B. haemorrhoidalis***

– Hair of the thoracic dorsum yellow or with some black hair intermixed, paler along the median line; gonostylus much shorter than broad; the volsella apex strongly narrowed and nearly straight……… ***B. funerarius***

16.4.1. *Bombus* (*Orientalibombus*) *funerarius* Smith, 1852

Bombus funerarius Smith 1852a: 47. Holotype queen by original designation NHMUK, examined.

Bremus priscus Frison 1935: 349. Holotype male by monotypy ZSC, examined.



Colour patterns of the hair of females (left) and males (right), variation shown (approximately) from west to east.

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest and subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009). The tail colour is usually red for workers, but white for some queens and black on the Burmese border.

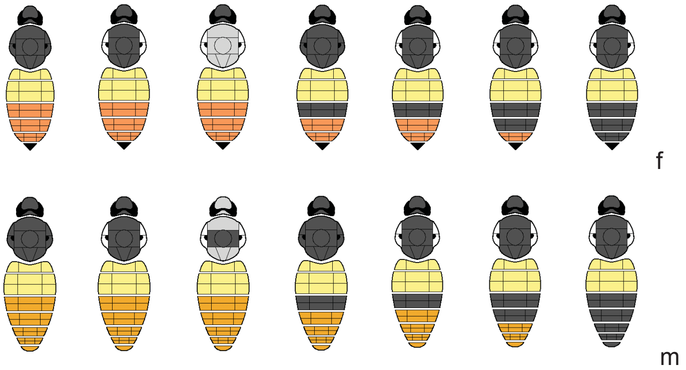
Identification. Medium size body (queen length 19–20 mm; worker 11–14 mm; male 13–14 mm) and long tongue. Similar to *B.* (*Ag.*) *grahami* and *B.* (*Pr.*) *parthenius*. Females can be distinguished: (cf. *B. grahami*, *B. parthenius*) by the oculo-malar distance being much longer than the basal breadth of the mandible, and by the female area between the lateral ocellus and the eye being almost unpunctured. Male genitalia are uniquely diagnostic: (cf. *B. grahami*, *B. parthenius*) by the penis-valve head being straight and not curved inwards in the shape of a sickle, by the gonostylus being much shorter than broad, and by the volsella apex being nearly straight.

Habitat. Common in the mid-elevation and upper forest and subalpine grassland (Williams *et al.* 2009).

Distribution. Eastern Himalaya and south-western China.

16.4.2. ***Bombus* (*Orientalibombus*) *haemorrhoidalis* Smith, 1852**

Bombus hæmorrhoidalis [= *haemorrhoidalis*] Smith 1852b: 43. Type presumed lost by Williams (1991), identity not in doubt.
Bombus orientalis Smith 1854: 402. Lectotype queen by designation of Richards (Richards 1929b) NHMUK, examined.
Bombus assamensis Bingham 1897: 550. Lectotype male by designation of Richards (Richards 1929b) NHMUK, examined.
[*Bombus* (*Megabombus*) *trifascatus* Smith; Burger *et al.* 2009: 461 (in part), misidentification].



Colour patterns of the hair of females (above) and males (below), variation shown (approximately) from west to east.

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no

Taxonomy and variation. Williams *et al.* (2009), Hines & Williams (2012). There is a progressive increase in the extent of the black hair on T3–5 from west to east.

Identification. Large body (queen length 23–25 mm; worker 13–17 mm; male 15–19 mm) and long tongue. Similar to *B.* (*Mg.*) *albopleuralis*, *B.* (*Mg.*) *montivagus*, *B.* (*Ag.*) *breviceps*, and *B.* (*Pr.*) *rotundiceps*. Females can be distinguished: (cf. *B. albopleuralis*, *B. montivagus*, *B. breviceps*, *B. rotundiceps*) by the area between the lateral ocellus and the eye being almost unpunctured, and by T2–5 with the hair nearly decumbent. Male genitalia are uniquely diagnostic: (cf. *B. albopleuralis*, *B. montivagus*, *B. breviceps*, *B. rotundiceps*) by the gonostylus being nearly square (as long as broad), and by the volsella apex being strongly curled dorsally.

Habitat. One of the most abundant species at low elevations in the foothills in forest-edge habitats (Williams 1991). Entrance to an underground nest seen in an earth bank.

Distribution. Widespread in the Himalaya, south-western China, and Southeast Asia.

16.5. Subgenus *PSITHYRUS*

These bumblebees are associated with grasslands and forests. Short to medium tongue-length bumblebees visiting shallow to medium depth flowers. There is no worker caste and all species are obligate social parasites in colonies of the other social *Bombus* species (Alford 1975; Fisher 1987; Goulson 2010). The degree of host specificity and resemblance to the host species in colour pattern varies among species (Williams 2008). Males patrol circuits of scent-marked places that attract young queens.

FEMALES: key to SPECIES

1. T6 very strongly curved under the metasoma so that the apex points anteriorly almost parallel to S2, S6 strongly projecting distally (at the tip posteriorly) beyond T6 as a shiny curved spine, S6 lateral keels small as just short curved bumps…………………………………………***B. skorikovi***

– T6 at most weakly curved under the metasoma so that the apex points ventrally at 90° to S2, S6 scarcely projecting distally (at the tip posteriorly) beyond T6, S6 lateral keels long and strongly projecting as pronounced ridges……………………………………………………2

2. (1) Hair of the thoracic dorsum extensively yellow at least anteriorly………3

– Hair of the thoracic dorsum predominantly black with only a few pale hairs intermixed or a very narrow broken band anteriorly………***B. turneri***

3. (2) Tail *either* white *or* yellow *or* brown…………………………………………4

– Tail *either* red *or* orange *or* pink *or* black……………………………………7

4. (3) Hair of the thorax predominantly brown, *either* with a few black hairs scattered between the wing bases *or* a small black spot, hair short……… ………………………………………………………………***B. ferganicus***

– Hair of the thoracic dorsum yellow with a broad black band between the wing bases, hair length medium………………………………………………5

5. (4) Hair of the thoracic dorsum posteriorly black, T6 strongly shining with only very shallow micropunctures…………………………………***B. bohemicus***

– Hair of the thoracic dorsum posteriorly yellow, T6 with many medium-sized punctures……………………………………………………………………6

6. (5) Hair of T4-5 medially white, T6 with many deep medium-sized punctures spaced by less than their own breadth………………………***B. novus*** (part)

– Hair of T4-5 medially black, T6 with many shallow medium-sized punctures spaced by more than their own breadth………………***B. morawitzianus***

7. (3) Labral lamella weakly projecting medially in a semi-circle………………8

– Labral lamella strongly projecting medially in a narrow triangle…***B. cornutus***

8. (7) Hair of T2 predominantly black, sometimes with posterior yellow fringes laterally……………………………………………………………***B. branickii***

– Hair of T2 yellow…………………………………………………***B. novus*** (part)

MALES: key to SPECIES

1. Volsella in its posterior distal half beyond the inner corner greatly narrowed, almost parallel sided, and finger shaped (nearly as thick as broad); gonostylus with only a few long hairs………***B. skorikovi***

– Volsella distally *either* a broad nearly triangular plate, *or if* the distal part is narrowed (much broader than thick) *then* the inner corner is very strongly produced; gonostylus usually with many long hairs around the inner proximal process……………………………………2

2. (1) Penis valve half way along its length with the ventral lateral angle reduced to a small notch and not visible from the dorsal view…………………………………………………………………………………***B. bohemicus***

– Penis valve half way along its length with the ventral lateral angle strongly and broadly produced ventrally and outwardly so that it is visible from the dorsal view…………………………………………………3

3. (2) Hair of T5 orange-red……………………………………………………5

– Hair of T5 *either* yellow-brown *or* white ……………………………………4

4. (3) Hair of the thoracic dorsum brown, between the wing bases without a black band, T5 laterally yellow-brown……………………………***B. ferganicus***

– Hair of the thoracic dorsum light yellow, between the wing bases with a black band, T5 entirely white………………………………***B. morawitzianus***

5. (3) Volsella in its distal posterior half very pale yellow, with the inner corner strongly produced in towards the mid-line to almost twice the breadth of the volsella halfway along its distal half…………………………7

– Volsella in its distal posterior half brownish, with the inner corner scarcely produced in towards the mid-line…………………………………6

6. (5) Gonocoxa from the inner aspect distally broadened and truncate, with a doubly pointed end, gonostylus broader near the inner (medial) side and narrowing towards the outer side; hair of the thoracic dorsum with broad anterior and posterior yellow bands with many black hairs intermixed, hair of the head predominantly yellow……………***B. cornutus***

– Gonocoxa from the inner aspect distally narrowed to a singly pointed end, gonostylus narrower near the inner (medial) side and broadening towards the outer side; hair of the thoracic dorsum and head predominantly black……………………………………………………………………***B. turneri***

7. (5) Hair of the thoracic dorsum and T1 white, between the wing bases with a distinct black band; volsella in its distal posterior half beyond

the inner corner forming a broad, almost equilateral triangle, with the inner margin only weakly incurved or almost straight when viewed perpendicularly to its dorsal surface……………………………………***B. novus***

– Hair of the thoracic dorsum and T1 yellow, between the wing bases without a distinct black band and only a few black hairs intermixed; volsella in its distal posterior half beyond the inner corner distinctly longer than broad, with the inner margin strongly incurved when viewed perpendicularly to its dorsal surface…………………………………………………***B. branickii***

16.5.1. ***Bombus* (*Psithyrus*) *cornutus*** **(Frison, 1933)**

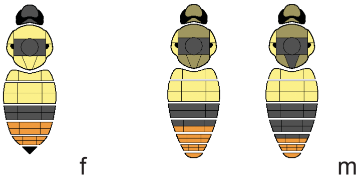
Psithyrus (*Psithyrus*) *cornutus* Frison 1933: 338. Holotype female by original designation ZSC, examined.

Psithyrus (*Psithyrus*) *pyramideus* Maa 1948: 19. Paratype male ZIB, examined.

Psithyrus (*Psithyrus*) *acutisqameus* Maa 1948: 21. Holotype male by original designation ZIB, examined.

Psithyrus (*Ceratopsithyrus*) *klapperichi* Pittioni 1949: 273 (not of Pittioni, 1949: 266 = *B. picipes* Richards). Paratype female NHMUK, examined.

Psithyrus (*Eopsithyrus*) *cornutus* subsp. *canus* Tkalců 1989: 42 (not of Schmiedeknecht 1883 = *B. pomorum* (Panzer)). Paratype female ZMHB, examined.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009).

Identification. Medium size body (female length 14–19 mm; male 13–14 mm) and medium length tongue. Most similar to *B.* (*Ps.*) *novus*, (see also *B.* (*Ml.*) *miniatus*, *B.* (*Ml.*) *eurythorax*, *B.* (*Ag.*) *sikkimi*, and *B.* (*Ml.*) *keriensis*). Females can be distinguished: (cf. *B. novus*) by the labrum having an acute median projection; and (cf. *B. miniatus*, *B. eurythorax*, *B. sikkimi*, *B. keriensis*) by the hind tibia having the outer surface convex and hairy. Male genitalia are closely similar to *B. turneri* but can be distinguished: by the gonocoxa from the inner midline view being distally broadened and truncate with a double-pointed end, and by the gonostylus being broader near the inner (medial) side and narrowing towards the outer side.

Habitat. Uncommon around the upper forest.

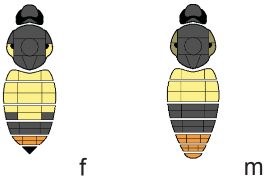
Distribution. Central and eastern Himalaya, central and southern China. A record from Ladakh (Saini *et al.* 2015) needs to be confirmed.

16.5.2. *Bombus* (*Psithyrus*) *turneri* (Richards, 1929)

Psithyrus turneri Richards 1929a: 141. Holotype male by original designation NHMUK, examined.

Psithyrus (*Psithyrus*) *decoomani* Maa 1948: 26. Holotype male by original designation ZIB, examined.

Psithyrus (*Eopsithyrus*) *martensi* Tkalců 1974: 314. Holotype female by original designation NMS, examined.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009).

Identification. Medium size body (female length 16 mm; male 12–14 mm) and medium length tongue. Similar to *B.* (*Or.*) *haemorrhoidalis*, *B.* (*Mg.*) *albopleuralis*, *B.* (*Ag.*) *breviceps*, and *B.* (*Pr.*) *rotundiceps*. Females can be distinguished: (cf. *B. haemorrhoidalis*, *B. albopleuralis*, *B. breviceps*, *B. rotundiceps*) by the hind tibia having the outer surface convex and hairy. Male genitalia are closely similar to *B. cornutus* but can be distinguished: by the gonocoxa from the inner midline view being distally narrowed to a single-pointed end, and by the gonostylus being narrower near the inner side and broadening towards the outer side.

Habitat. Rare around the lower forest.

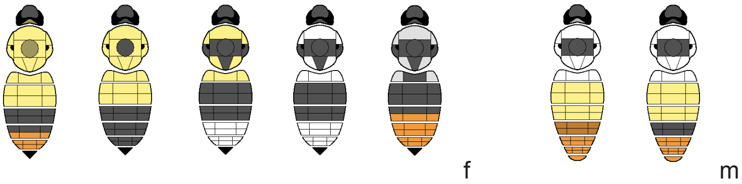
Distribution. Eastern Himalaya, eastern QTP, and southern China.

16.5.3. *Bombus* (*Psithyrus*) *novus* (Frison, 1933)

Psithyrus (*Psithyrus*) *novus* Frison 1933: 340. Holotype female by original designation ZSC, examined.

Psithyrus (*Psithyrus*) *novus* subsp. *nepalensis* Tkalců 1974: 318. Holotype female by original designation ZSM, examined.

[*Bombus* (*Mendacibombus*) *waltoni* Cockerell; Saini *et al.* 2015: 155 (in part), misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. This species-complex appears to include both yellow-banded and white-banded individuals (Williams *et al.* 2010). It is uncertain whether females with T2 yellow (and the tail red or black) and those with T2 black (and the tail white) are conspecific (Williams 1991) so that a revision including COI-barcode variation is needed to assess their status when fresh material becomes available.

Identification. Medium size body (female length 18–20 mm; male 13–14 mm) and medium length tongue. Most similar to *B.* (*Ps.*) *cornutus*, *B.* (*Ps.*) *branickii* (see also *B.* (*Ml.*) *miniatus*, *B.* (*Ml.*) *eurythorax*, *B.* (*Ag.*) *sikkimi*, and *B.* (*Ml.*) *keriensis*). Females can be distinguished: (cf. *B. cornutus*, *B. branickii*) by the labrum being without an acute median projection; (cf. *B. branickii*) by S6 lateral keels not projecting beyond T6 in dorsal view; and (cf. *B. miniatus*, *B. eurythorax*, *B. sikkimi*, *B. keriensis*) by the hind tibia with the outer surface convex and hairy. Male genitalia are closely similar to *B. branickii* but can be distinguished: by the volsella in its distal posterior half beyond the inner corner forming a broad, almost equilateral triangle, with the inner margin only weakly incurved or almost straight when viewed from perpendicular to the dorsal surface.

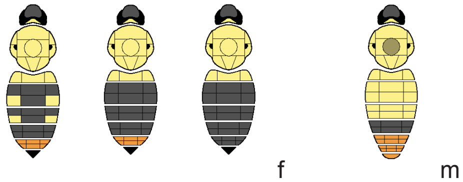
Habitat. Uncommon in mesic subalpine flower-rich grassland.

Distribution. Widespread Himalayan endemic.

16.5.4. *Bombus* (*Psithyrus*) *branickii* (Radoszkowski, 1893)

Psithyrus Branickii Radoszkowski 1893: 241. Lectotype female by designation of Tkalců (1969a) ZMHB, examined.

Apathus chloronotus Morawitz 1893: 6. Holotype female by monotypy ZIN, examined.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image (left volsella, shown right, damaged).

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009).

Identification. Medium size body (female length 18–20 mm; male 13–14 mm) and medium length tongue. Most similar to some *B.* (*Ps.*) *novus*, (see also some *B.* (*Sb.*) *longiceps*, *B.* (*Ml.*) *semenovianus*, *B.* (*Pr.*) *kotzschi*, and *B.* (*Md.*) *marussinus*). Females can be distinguished: (cf. *B. novus*) by S6 lateral keels projecting beyond T6 in dorsal view; and (cf. *B. longiceps*, *B. semenovianus*, *B. kotzschi*, *B. marussinus*) by the hind tibia with the outer surface convex and hairy. Male genitalia are closely similar to *B. novus* but can be distinguished: by the volsella in its distal posterior half beyond the inner corner being distinctly longer than broad, and with the inner margin strongly incurved when viewed from perpendicular to the dorsal surface.

Habitat. Common in subalpine flower-rich grassland.

Distribution. Western Himalaya, QTP, extending into Afghanistan and Central Asia, northern China, and Mongolia.

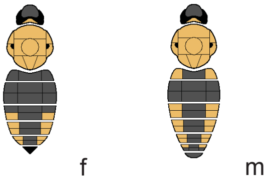
16.5.5. *Bombus* (*Psithyrus*) *ferganicus* (Radoszkowski, 1893)

Psithyrus ferganicus Radoszkowski 1893: 241. Lectotype female by designation of Tkalců (1969) ZMHB, examined.

Apathus ochraceus Morawitz 1893: 5. Holotype female by monotypy, not seen but identity not in doubt.

Psithyrus indicus Richards 1929a: 139. Holotype male by original designation NHMUK, examined.

[*Bombus* (*Pyrobombus*) *parthenius* Richards; Saini *et al.* 2015: 232. Fig. 356 (in part), misidentification].



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1991).

Identification*.* Medium size body (female length 16–21 mm; male 15–17 mm) and medium length tongue. Most similar to *B.* (*Ps.*) *morawitzianus*, (see also *B.* (*St.*) *melanurus*, *B.* (*Pr.*) *hypnorum*, and some *B.* (*Ml.*) *festivus*). Females can be distinguished: (cf. *B. morawitzianus*) by the thoracic dorsum being without black hair; and (cf. *B. melanurus*, *B. hypnorum*, *B. festivus* workers) by the hind tibia having the outer surface convex and hairy. Male genitalia are similar to *B. morawitzianus* but can be distinguished: by the volsella in its broad distal part being as long as 1.5× its maximum breadth, and with the gonostylus being broadly triangular.

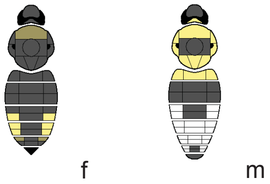
Habitat. Common around the upper forest.

Distribution. Western Himalaya extending into Afghanistan and Central Asia.

16.5.6. *Bombus* (*Psithyrus*) *morawitzianus* (Popov, 1931)

Psithyrus (*Metapsithyrus*) *morawitzianus* Popov 1931: 148, 183. Syntype female ZIN, examined.

Psithyrus (*Metapsithyrus*) *redikorzevi* Popov 1931: 160, 181. Syntype males, not seen but identity not in doubt.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest and subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1991).

Identification. Medium size body (female length 17 mm; male 13–16 mm) and medium length tongue. Most similar to *B.* (*Ps.*) *ferganicus*, *B.* (*Ps.*) *bohemicus*, *B.* (*Ps.*) *skorikovi*. Females can be distinguished: (cf. *B. ferganicus*) by the thoracic dorsum being predominantly black; and (cf. *B. bohemicus*, *B. skorikovi*) by T3-4 both having black hair in the middle. Male genitalia are similar to *B. ferganicus* but can be distinguished: by the volsella in its broad distal part being only just longer than its maximum breadth, and by the gonostylus being reduced to a narrow transverse band.

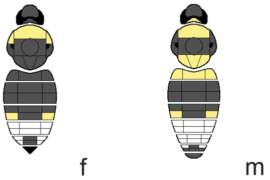
Habitat. Rare around the upper forest and subalpine flower-rich grassland.

Distribution. Western Himalaya extending into Afghanistan and Central Asia.

16.5.7. *Bombus* (*Psithyrus*) *bohemicus* Seidl, 1837

Bombus bohemicus Seidl 1837: 73. Type not found by Tkalců (1969b), but identity not in doubt.

Psithyrus distinctus Pérez 1884: 268. Type not seen, but identity not in doubt.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest and subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al*. (2009).

Identification. Medium size body (female length 17–19 mm; male 14–16 mm) and medium length tongue. Most similar to *B.* (*Ps.*) *morawitzianus*, *B.* (*Ps.*) *skorikovi*. Females can be distinguished: (cf. *B. skorikovi*) by the thoracic dorsum being posteriorly black; and (cf. *B. morawitzianus*) by T4 having white hair in the middle. Male genitalia are uniquely diagnostic: by the combination of the penis valve having the outer ventral angle much reduced and not visible from from the dorsal view, and by the gonostylus having long branched hairs along its inner margin.

Habitat. Rare around the upper forest and subalpine flower-rich grassland.

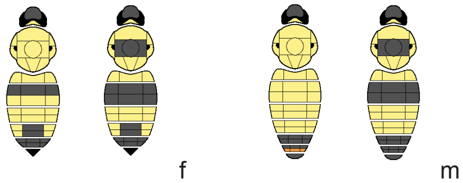
Distribution. Western Himalaya extending into Afghanistan, Central Asia, Mongolia, the northern Palaearctic and Nearctic regions.

16.5.8. *Bombus* (*Psithyrus*) *skorikovi* (Popov, 1927)

Psithyrus skorikovi Popov 1927: 267. Holotype female by original designation ZIN, examined.

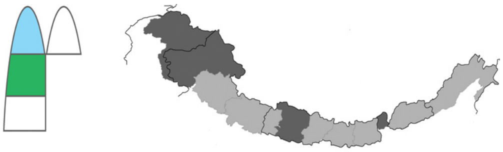
Psithyrus (*Fernaldaepsithyrus*) *gansuensis* Popov 1931: 202. Holotype male by monotypy ZIN, examined.

Psithyrus (*Fernaldaepsithyrus*) *kuani* Tkalců 1961: 362. Holotype female by original designation. OLML, examined.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.



Core habitat (left: cf. Fig. 4) upper forest and subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009).

Identification. Medium size body (female length 16–18 mm; male 14–15 mm) and medium length tongue. Most similar to *B.* (*Ps.*) *bohemicus*, *B.* (*Ps.*) *morawitzianus*. Females can be distinguished: (cf. *B. bohemicus*) by the thoracic dorsum being posteriorly yellow; and (cf. *B. morawitzianus*) by the thoracic dorsum posteriorly being yellow and T3 having yellow hair in the middle. Male genitalia are uniquely diagnostic by the combination of: the volsella being much narrowed and finger-like, and the gonostylus having long branched hairs along its inner margin.

Habitat. Rare around the upper forest and subalpine flower-rich grassland.

Distribution. Widespread in the Himalaya and eastern QTP.

16.6. Subgenus *PYROBOMBUS*

These bumblebees are associated with mountain grasslands, forests, or semi-desert. Short tongue-length bumblebees visiting shallow flowers. Workers often have particularly small body sizes and are more likely to visit small flowers where they have to hang upside down. Nests are underground, on the surface, or in cavities above ground, but colonies often remain small and complete their development in the earlier part of the summer. Older larvae are reared separately, as non-pocket makers. Males patrol circuits of scent-marked places that attract young queens.

FEMALES: key to SPECIES

1. Oculo-ocellar area for at least a quarter of the distance from the depression around the lateral ocellus to the inner eye margin without punctures and smooth and shiny……………………………………………3
– Oculo-ocellar area with the area outside the depression around the lateral ocellus for the entire distance to the inner eye margin covered very densely with small punctures…………………………………………2

2. (1) Hair of the thoracic dorsum with white bands, tail orange………***B. mirus***
– Hair of the thoracic dorsum orange-brown, tail white or black…***B. abnormis***

3. (1) Hair of the thoracic dorsum entirely bright lemon yellow, at most with a few black hairs in the centre between the wing bases, hair of the legs black, T3 black……………………………………………4
– Hair of the thoracic dorsum *either* black, white *or* brown, *but if* yellow *then either* with a band of back hair between the wing bases *or* with black hairs broadly intermixed, hair of the legs and T3 *either* black *or* pale……5

4. (3) Oculo-ocellar area along the inner margin of the eye with a narrow band of dense fine and medium punctures; hair of T1–2 usually predominantly yellow but may be black, hair of T4–5 *either* orange *or* white…………***B. subtypicus***
– Oculo-ocellar area along the inner margin of the eye with a broad band of very widely-spaced medium punctures; hair of T1–2 black or with a few pale hairs, hair of T4–5 orange…………………***B. kotzschi***

5. (3) Hair of T5 *either* orange-red *or* yellow…………………………………………7
– Hair of T5 *either* black *or* white…………………………………………………6

6. (5) Hair of the thoracic dorsum uniformly brown……………………***B. bryorum***
– Hair of the thoracic dorsum black with an anterior yellow band…***B. infirmus***

7. (5) Hair of the thoracic dorsum *either* with white *or* yellow bands anteriorly and posteriorly *or* with yellow hairs intermixed throughout……………10
– Hair of the thoracic dorsum black……………………………………………8

8. (7) Hair of T2 black, hair of mid and hind tibiae bright orange; wings yellow with veins orange………………………………………………………***B. flavescens***

– Hair of T2 yellow or white, hair of mid and hind tibiae black; wings *either* clear *or* dark brown with veins dark brown……………………………………9

9. (8) Wings clear; hair of T2–4 laterally narrowly white, on T3–4 contrasting with the medial orange-red……………………………………***B. biroi*** (part)

– Wings dark brown; hair of T2–4 laterally similar in colour to the medial area……………………………………………………………***B. rotundiceps***

10. (7) Hair of the thoracic dorsum entirely pale with black hairs intermixed broadly including between the wing bases……………11

– Hair of the thoracic dorsum with pale anterior and posterior bands with a discrete black band between the wing bases…………………12

11. (10) S2–5 exoskeleton posteriorly with the narrow hairless margins yellow; mid tibia with the exoskeleton on the outer surface light orange-brown, hind tibia exoskeleton on the outer surface orange-brown and the with long hair proximally only orange or at most with only a few short hairs near the joint with the femur dark brown……………***B. luteipes***

– S2–5 exoskeleton posteriorly with the narrow hairless margins orange-brown or dark brown; mid tibia exoskeleton on the outer surface dark brown, hind tibia with the exoskeleton on the outer surface proximally dark brown and usually with many long and short hairs near the joint with the femur dark brown…………***B. parthenius***

12. (10) Hair of the head entirely black………………………………………………13

– Hair of the head with at least some short pale hair………………………14

13. (12) Ocello-ocular area along the inner margin of the eye posteriorly with many close fine punctures between the larger punctures, the punctures uniformly spaced and dense; T6 posteriorly with the apex broad and straight (truncated)……………………***B. lemniscatus***

– Ocello-ocular area along the inner margin of the eye posteriorly with very few fine punctures between the larger punctures, the punctures becoming more dense posteriorly; T6 posteriorly with the apex pointed (convex)……………………………………………***B. biroi*** (part)

14. (12) Hair long, the longest hairs perpendicular to the surface of the hind basitarsus longer than the narrowest distal part of the basitarsus; T6 posteriorly with the apex deeply divided (more apparent for larger individuals)…***B. pressus***

– Hair short, the longest hairs perpendicular to the surface of the hind basitarsus shorter than the narrowest distal part of the basitarsus; T6 posteriorly with the apex convex or straight (truncated)………………15

15. (14) Hair of the corbicular fringes of the hind tibia predominantly orange, T2 posteriorly and T3 anteriorly usually with bands of black hair…***B. lepidus***

– Hair of the corbicular fringes of the hind tibia predominantly black, T2 posteriorly yellow and T3 anteriorly orange with very few or no black hairs..**B. hilaris**

MALES: key to SPECIES

1. Oculo-ocellar area for at least a quarter of the distance from the depression around the lateral ocellus to the inner eye margin without punctures and smooth and shiny……………………3

– Oculo-ocellar area with the area outside the depression around the lateral ocellus for the entire distance to the inner eye margin covered very densely with small punctures……………………………2

2. (1) Hair of the thoracic dorsum with white bands, tail orange………**B. mirus**

– Hair of the thoracic dorsum orange-brown, tail white or black…**B. abnormis**

3. (1) Gonostylus broad and often nearly triangular and distally rounded, penis-valve head distally turned inwards in a dorso-ventrally flattened sickle-shape with a single point………………………………4

– Gonostylus narrowed as a long acute spine, penis-valve head distally with an outer flange turned outwards and ventrally so that distally the penis-valve head is dorso-ventrally broad and strongly bifid…**B. pressus**

4. (3) Penis-vale head in its curved part in dorsal view *either* no broader than the adjacent penis-valve shaft *or* no longer than the breadth of the adjacent penis-valve shaft…………………………………………6

– Penis-vale head in its curved part in dorsal view nearly twice as broad as the adjacent penis-valve shaft………………………………5

5. (4) Hair of the thoracic dorsum between the wing bases with a black band…… ………………………………………………………………………**B. biroi**

– Hair of the thoracic dorsum between the wing bases yellow without a black band…………………………………………………………**B. kotzschi**

6. (4) Gonocoxa distally with its inner corner *either* broadly rounded *or* at most just acute..……………………………………………………………7

– Gonocoxa distally with its inner corner produced as a narrowly acute sharp spine………………………………………………………**B. luteipes**

7. (6) Hair of the tail in part orange-red……………………………………………9

– Hair of the tail in part white....……………………………………………………8

8. (7) Penis-valve head with the recurved hook about twice as long as broad, gonostylus at its inner proximal corner separated from the inner corner of the gonocoxa by a deep cleft as broad as the breadth of the penis-valve head………………………………………………………………**B. bryorum**

– Penis-valve head with the recurved hook shorter than broad, gonostylus at its inner proximal corner coincident with the inner corner of the gonocoxa……………………………………………………………***B. infirmus***

9. (7) Pale hair of the thoracic dorsum yellow……………………………………10
– Pale hair of the thoracic dorsum white……………………***B. lemniscatus***

10. (9) Mid and hind tibiae dark brown with long *either* yellow *or* pale orange hair, wings nearly clear with wing veins and stigma dark brown……11
– Mid and hind tibiae orange with long bright orange hair, wings yellow with wing veins and stigma orange………………………***B. flavescens***

11. (10) Hair of the thoracic dorsum predominantly yellow, sometimes with a band of black between the wing bases…………………………12
– Hair of the thoracic dorsum predominantly black………***B. rotundiceps***

12. (11) Penis-valve head with the recurved apex evenly rounded, the penis-valve shaft with the ventro-lateral angle closer to the penis-valve head than to the base of the penis valve………………………13
– Penis-valve head with the sides of the recurved apex converging and sharply pointed, the penis-valve shaft with the ventro-lateral angle closer to the base of the penis valve than to the penis-valve head…***B. subtypicus***

13. (12) Hair of the thoracic dorsum predominantly yellow without a distinct black band between the wing bases……………………………………14
– Hair of the thoracic dorsum yellow with a distinct black band between the wing bases..........……………………………………………………***B. lepidus***

14. (13) Hair of T3 with many black hairs, thoracic dorsum with yellow and black hair intermixed throughout……………………………………***B. parthenius***
– Hair of T3 without black hairs, thoracic dorsum yellow with black hair only between the wing bases………………………………………***B. hilaris***

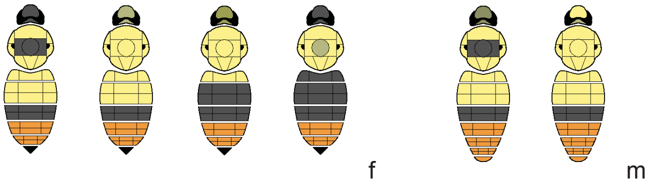
16.6.1. *Bombus* (*Pyrobombus*) *subtypicus* (Skorikov, 1914)

Bombus leucopygus Morawitz 1875: 3 (not of Illiger 1806 = *B. hypnorum* (Linnaeus)). Lectotype female by designation of Skorikov (1914b) ZIN, not seen but identity not in doubt.

Pratobombus leucopygos var. [subsp.] *subtypicus* Skorikov 1914b: 294. Syntype queen ZIN, examined.

Bombus leucurus Bischoff & Hedicke 1931: 391. Unnecessary replacement name for *B. leucopygus* Morawitz.

Pyrobombus (*Pyrobombus*) *kohistanensis* Tkalců 1989: 49. Holotype queen by original designation ZSM, examined.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1991). It is unknown whether COI barcode sequences support the females with T2 yellow and those with T2 black as being conspecific (Williams 1991), so that a revision including COI barcode variation is needed to assess their status when fresh material becomes available.

Identification. Small body (queen length 14–15 mm; worker 9–10 mm; male 11–12 mm) and short tongue. Similar to *B.* (*Pr.*) *kotzschi* (see also *B.* (*Ml.*) *semenovianus*, and some *B.* (*Sb.*) *longiceps*, *B.* (*Md.*) *avinoviellus*). Females can be distinguished: (cf. *B. kotzschi*) by the ocello-ocular area immediately along the inner margin of the eye having few large punctures and only a very narrow band of dense fine and medium punctures; and (cf. *B. semenovianus*, *B. longiceps*, *B. avinoviellus*) by the oculo-malar area being just shorter than broad, and the ocello-ocular area with the inner eye margin having few large punctures and only a very narrow band of dense fine and medium punctures. Male genitalia are uniquely diagnostic by the combination of: the gonostylus being without an inner proximal process, and the penis valve having the recurved head narrowly acutely pointed.

Habitat. Common in subalpine flower-rich semi-desert grassland. Entrance to an above-ground nest seen in a hut roof.

Distribution. Trans Himalaya and Central Asia.

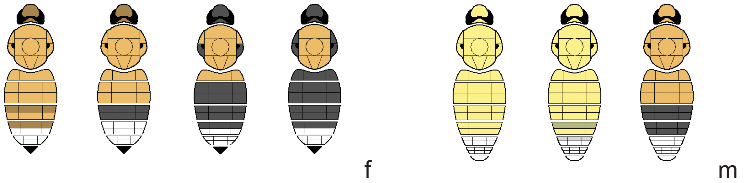
16.6.2. ***Bombus* (*Pyrobombus*) *bryorum* Richards, 1930** stat. rev.

Bombus hypnorum var. [subsp.] *bryorum* Richards 1930: 650. Holotype queen by original designation NHMUK, examined.

Bombus fletcheri Richards 1934: 90. Holotype queen by original designation NHMUK, examined.

[*Bombus* (*Pyrobombus*) *hypnorum* (Linnaeus); Williams 1991: 70, misidentification; Burger *et al.* 2009: 458, misidentification; Williams *et al.* 2010: 125, misidentification; Saini *et al.* 2015: 65, misidentification; Streinzer *et al.* 2019: table 1, misidentification].

[*Bombus* (*Pyrobombus*) *parthenius* Richards; Burger *et al.* 2009: 460 (in part), misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Tkalců (1974), and most recently by Williams *et al.* (2009), although species-coalescent (PTP) analysis of a MrBayes phylogenetic tree for COI barcodes and morphology with the females having especially sparse punctures in the oculo-ocellar areas now support this as a species separate from the other species in the *hypnorum*-complex. The west Himalayan individuals of *B. bryorum* have much more extensive pale hair than those in the east (which resemble a similar dark but unnamed Tibetan and Hengduan species with distinct COI barcodes and morphology).

Identification. Medium size body (queen length 16–18 mm; worker 11–13 mm; male 12–13 mm) and short tongue. Similar to *B.* (*Pr.*) *abnormis* (see also workers and males of *B.* (*Ml.*) *festivus*). Females can be distinguished: (cf. *B. abnormis*) by the ocello-ocular area having large smooth unpunctured areas; and (cf. *B. festivus*) by having clear wings. Male genitalia can be distinguished: (cf. *B. abnormis*, *B. festivus*) by the gonostylus proximally having the inner corner separated from the inner margin by a broad notch.

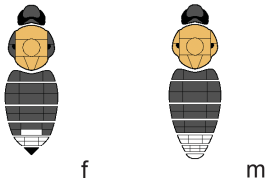
Habitat. Uncommon around and inside the upper forest.

Distribution. Widespread in the Himalaya.

16.6.3. *Bombus* (*Pyrobombus*) *abnormis* (Tkalců, 1968)

Pyrobombus (*Pyrobombus*) *abnormis* Tkalců 1968a: 33. Holotype queen by original designation NHMUK, examined.

[*Bombus* (*Pyrobombus*) *festivus* Smith; Burger *et al.* 2009: 457 (in part), misidentification].



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2010). The status of this species as separate from *B. bryorum* has been confirmed from COI barcodes.

Identification. Small body (queen length 17 mm; worker 11–12 mm; male 15 mm) and short tongue. Similar to *B.* (*Pr.*) *bryorum* (see also workers and males of *B.* (*Ml.*) *festivus*). The female and male can be distinguished: (cf. *B. bryorum*, *B. festivus*) by the ocello-ocular area for almost the entire distance from the ocellar depression to the inner eye margin being very densely covered with small punctures. Male genitalia can be distinguished: (cf. *B. bryorum*, *B. festivus*) by the volsella having the distal posterior outer corner strongly produced.

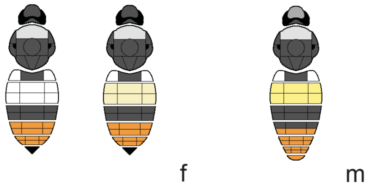
Habitat. Rare in subalpine flower-rich grassland.

Distribution. East Himalayan endemic.

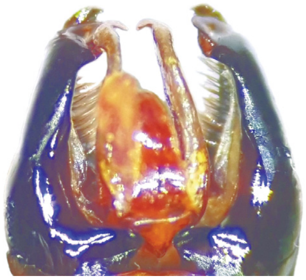
16.6.4. *Bombus* (*Pyrobombus*) *mirus* (Tkalců, 1968)

Bombus pratorum var. [subsp.] *tibetanus* Friese 1913: 86 (not of Morawitz 1887 = *B. tibetanus* (Morawitz)). Holotype male by monotypy ZMHB, examined.

Pyrobombus (*Pyrobombus*) *mirus* Tkalců 1968a: 37. Holotype queen by original designation ZMHB, examined.



Colour patterns of the hair of females (left) and males (right).



Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2010). The status of this species as separate from *B.* (*Pr.*) *lemniscatus* has been confirmed from COI barcodes.

Identification. Small body (queen length 16–18 mm; worker 10–11 mm; male 12–13 mm) and short tongue. Similar to *B.* (*Pr.*) *lemniscatus* and *B.* (*Pr.*) *lepidus*, (see also *B.* (*Ag.*) *sikkimi*). The female and male can be distinguished: (cf. *B. lemniscatus*, *B. lepidus*, *B. sikkimi*) by the ocello-ocular area for almost the entire distance from the ocellar depression to the inner eye margin being very densely covered with small punctures; and (cf. *B. sikkimi*) by the mandibles having just two (male) or three (female) anterior teeth.

Habitat. Rarer towards the west but common locally in the east (Arunachal Pradesh) in alpine flower-rich grassland.

Distribution. East Himalayan endemic.

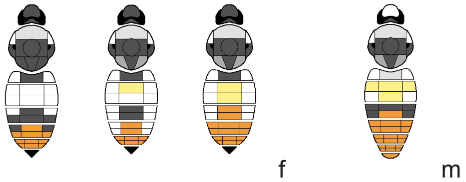
16.6.5. *Bombus* (*Pyrobombus*) *lemniscatus* Skorikov, 1912

Bombus lemniscatus Skorikov 1912b: 607. Holotype queen by monotypy ZIN, examined.

Bombus nursei var. [subsp.] *flavopilosus* Friese 1918: 84. Lectotype queen by designation of Williams (1991) ZMHB, examined.

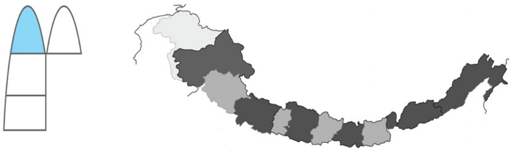
Bombus (*Lapidariobombus*) *peralpinus* Richards 1930: 646. Holotype queen by original designation NHMUK, examined.

[*Bombus* (*Pyrobombus*) *rufofasciatus* Smith; Burger *et al.* 2009: 461 (in part), misidentification].



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.



Core habitat (left: cf. Fig. 4) alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009). The status of this species as separate from *B.* (*Pr.*) *mirus* has been confirmed from COI barcodes.

Identification. Small body (queen length 16–18 mm; worker 10–12 mm; male 10–12 mm) and short tongue. Similar to *B.* (*Pr.*) *mirus*, *B.* (*Pr.*) *lepidus*, *B.* (*Pr.*) *hilaris*, and *B.* (*Pr.*) *biroi* (see also *B.* (*Ag.*) *sikkimi*). Females can be distinguished: (cf. *B. mirus*, *B. lepidus*, *B. hilaris*, *B. sikkimi*) by the combination of the black head hair and pronounced white hair on T3–4 laterally; (cf. *B. biroi*) by the ocello-ocular area of the head having the band of punctures along the inner eye margin with many close small punctures among the large punctures; and (cf. *B. sikkimi*) by the mandibles having just two anterior teeth. Males can be distinguished: (cf. *B. mirus*) by the ocello-ocular area being unpunctured in part; (cf. *B. lepidus*, *B. hilaris*) by the thorax having the pale hair white; and (cf. *B. sikkimi*) by the mandibles having just two anterior teeth.

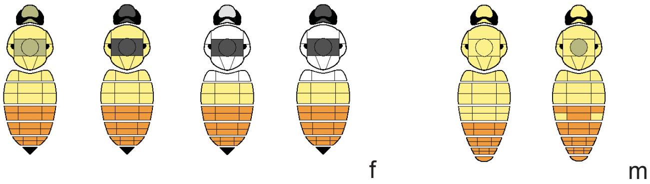
Habitat. Uncommon in alpine flower-rich grassland.

Distribution. Widespread in the Himalaya and eastern QTP.

16.6.6. ***Bombus* (*Pyrobombus*) *hilaris* (Tkalců, 1989)** stat. rev.

Pyrobombus (*Pyrobombus*) *lepidus* subsp*. hilaris* Tkalců 1989: 48. Holotype queen by original designation ZSM, examined.

[*Bombus* (*Pyrobombus*) *lepidus* Skorikov; Williams 1991: 75 (in part), misidentification; Williams *et al.* 2010: 125, misidentification; Saini *et al.* 2015: 83, misidentification].



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest and subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams *et al.* (2009), although recent species-coalescent (PTP) analysis of a Mr Bayes phylogenetic tree for COI barcodes and morphological differences including the female ocello-ocular area with fewer punctures along the inner margin of the eye now support this as a species separate from its sister species *B.* (*Pr.*) *lepidus*. Much more thorough sampling and analysis of COI-barcode variation in the Himalaya is needed to confirm its status, to clarify its diagnostic characters, and to clarify the extent of its distribution.

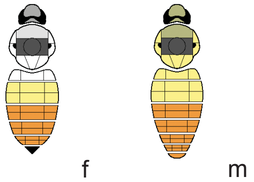
Identification. Small body (queen length 14–15 mm; worker 8–11 mm; male 10–12 mm) and short tongue. Similar to *B.* (*Pr.*) *lepidus*, *B.* (*Pr.*) *lemniscatus* and *B.* (*Pr.*) *biroi* (see also *B.* (*Ag.*) *sikkimi*). Females can be distinguished: (cf. *B. lepidus*) by the corbicular fringes being predominantly black, T2 posteriorly yellow and T3 anteriorly orange with few or no black hairs, and by the hair around the clypeus being often predominantly black; (cf. *B. lemniscatus*, *B. biroi*, *B. sikkimi*) by the combination of the many pale hairs on the head and the few white hairs on T3–4 laterally; and (cf. *B. sikkimi*) by the mandibles having just two anterior teeth. Males can be distinguished: (cf. *B. lepidus*) by the pale thoracic anterior band and T3 being without black hairs; (cf. *B. mirus*, *B. lemniscatus*) by the thorax having the pale hair yellow; and (cf. *B. sikkimi*) by the mandibles having just two anterior teeth.

Habitat. Uncommon in upper forest and subalpine flower-rich grassland.

Distribution. West Himalayan endemic.

16.6.7. ***Bombus* (*Pyrobombus*) *lepidus* Skorikov, 1912**

Bombus lepidus Skorikov 1912b: 606. Syntype queen ZIN, examined.
Bombus genitalis Friese 1913: 85. Holotype male by monotypy ZMHB, examined.
Bombus nursei var. [subsp.] *tetrachromus* Friese 1918: 85 (not of Cockerell (1909) = *B. kashmirensis* Friese). Lectotype queen by designation of Williams (1991) ZMHB, examined.
Bombus (*Pratobombus*) *yuennanicola* Bischoff 1936: 7. Holotype queen by original designation ZMHB, examined.
Bombus (*Pyrobombus*) *yunnanicola* Bischoff; S.-F. Wang 1982: 435. Unjustified emendation.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest and subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009). See the comments on *B.* (*Pr.*) *hilaris*.

Identification. Small body (queen length 13–15 mm; worker 8–11 mm; male 9–12 mm) and short tongue. Similar to *B.* (*Pr.*) *hilaris*, *B.* (*Pr.*) *mirus* and *B.* (*Pr.*) *lemniscatus* (see also *B.* (*Ag.*) *sikkimi*). Females can be distinguished: (cf. *B. hilaris*) by the corbicular fringes at least in the distal posterior corner of the tibia being orange, T2 posteriorly and T3 anteriorly usually having bands of black hair, and by the hair around the clypeus being often predominantly orange; (cf. *B. mirus*, *B. lemniscatus*, *B. sikkimi*) by the combination of the many pale hairs on the head and the few white hairs on T3–4 laterally; and (cf. *B. sikkimi*) by the mandibles having just two anterior teeth. Males can be distinguished: (cf. *B. hilaris*) by the pale thoracic anterior band and T3 having black hairs;

(cf. *B. mirus*, *B. lemniscatus*) by the thorax having the pale hair yellow; and (cf. *B. sikkimi*) by the mandibles having just two anterior teeth.

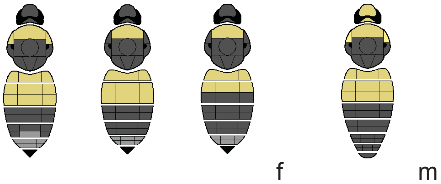
Habitat. Uncommon in upper forest and subalpine flower-rich grassland.

Distribution. Central and eastern Himalaya and eastern QTP.

16.6.8. ***Bombus* (*Pyrobombus*) *infirmus* (Tkalců, 1968)**

Pyrobombus (*Pyrobombus*) *infirmus* Tkalců 1968a: 24. Holotype male by original designation NHMUK, examined.

Pyrobombus (*Pyrobombus*) *infirmus* subsp. *clarior* Tkalců 1968a: 28. Holotype worker by original designation NHMUK, examined.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (*left: cf. Fig. 4*) *upper forest and subalpine*, *recorded by province* (*right: cf. Fig. 3*) *from specimens* (*dark*), *likely interpolation* (*mid*), *or no records* (*light*).

Taxonomy and variation. Williams *et al.* (2009).

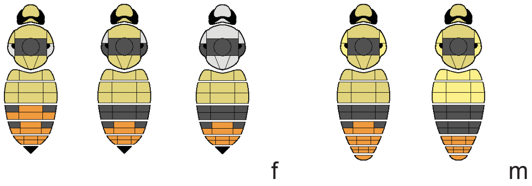
Identification. Small body (queen length 15–16 mm; worker 10–12 mm; male 10–13 mm) and short tongue. Similar to *B.* (*Bo.*) *reinigi* and *B.* (*Bo.*) *longipennis*. Females can be distinguished: (cf. *B. reinigi*, *B. longipennis*) by the hind basitarsus having an only weakly curved posterior edge, ocello-ocular area and clypeus both having widely scattered large punctures with wider smooth areas between them. Males can be distinguished: (cf. *B. reinigi*, *B. longipennis*) by the penis-valve head having a simple dorso-ventrally flattened incurved sickle shape.

Habitat. Uncommon in upper forest and subalpine flower-rich grassland.

Distribution. Eastern Himalaya and eastern QTP.

16.6.9. ***Bombus* (*Pyrobombus*) *pressus*** (Frison, 1935)

Bremus (*Pressibombus*) *pressus* Frison 1935: 342. Holotype male by original designation ZSC, examined.



*Colour patterns of the hair of females (*left*) and males (*right*).*

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2010).

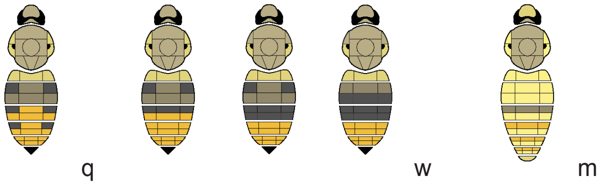
Identification. Small body (queen length 18–19 mm; worker 10–11 mm; male 12–15 mm) and short tongue. Similar to *B.* (*Pr.*) *parthenius*, *B.* (*Pr.*) *luteipes*, *B.* (*Pr.*) *lemniscatus*, and *B.* (*Pr.*) *mirus* (see also *B.* (*Ag.*) *sikkimi*, *B.* (*Md.*) *avinoviellus*). Females can be distinguished: (cf. *B. parthenius*, *B. luteipes*, *B. lemniscatus*) by T6 posteriorly having the apex deeply divided (more apparent for large individuals); (cf. *B. lemniscatus*) by T2 having the pale hair densely and uniformly mixed with black; (cf. *B. parthenius*, *B. luteipes*) by a distinct band of black hair between the wing bases; (cf. *B. sikkimi*) by the mandibles having just two anterior teeth and a broadly rounded distal margin; and (cf. *B. avinoviellus*) by the labrum having a median longitudinal groove. Male genitalia can be distinguished: (cf. *B. parthenius*, *B. luteipes*, *B. lemniscatus*, *B. mirus*, *B. sikkimi*, *B. avinoviellus*) by the penis-valve head having an outer flange turned outwards and ventrally in a point so that in lateral view the penis-valve head is dorso-ventrally broad and distally strongly bifid.

Habitat. Uncommon in subalpine flower-rich grassland.

Distribution. Central and eastern Himalaya and eastern QTP.

16.6.10. *Bombus* (*Pyrobombus*) *parthenius* Richards, 1934

Bombus (*Pratobombus*) *parthenius* Richards 1934: 89. Holotype queen by original designation NHMUK, examined.



Colour patterns of the hair of females (queens left, workers centre) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest and subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams *et al.* (2010), although species-coalescent (PTP) analysis of a MrBayes phylogenetic tree for COI barcodes and morphology now support *B. parthenius* as separate from the other closely related species: *B.* (*Pr.*) *avanus* (Skorikov) (China, Burma); *B.* (*Pr.*) *sonani* (Frison) (Taiwan); *B.* (*Pr.*) *luteipes* (Himalaya); and *B.* (*Pr.*) *infrequens* (Tkalců) (China).

Identification. Small body (queen length 13–14 mm; worker 9–12 mm; male 10–12 mm) and short tongue. Similar to *B.* (*Pr.*) *luteipes* (see also *B.* (*Or.*) *funerarius*, *B.* (*Ag.*) *grahami*). Females can be distinguished: (cf. *B. luteipes*) by the hind tibia on the outer surface proximally having the exoskeleton dark brown and usually with many long and short hairs near the joint with the femur dark brown; (cf. *B. funerarius*) by the ocello-oculo area having a broad band of punctures along the inner margin of the eye; and (cf. *B. grahami*) by the mandibles having just two anterior teeth and a broadly rounded distal margin. Male genitalia can be distinguished: (cf. *B. luteipes*) by the gonocoxa having the inner distal corner rounded at ca 90°; (cf. *B. funerarius*) by the penis-valve head curved inwards as a sickle shape; and (cf. *B. grahami*) by the gonostylus having the inner basal corner not strongly projecting.

Habitat. Common in upper forest and subalpine flower-rich grassland.

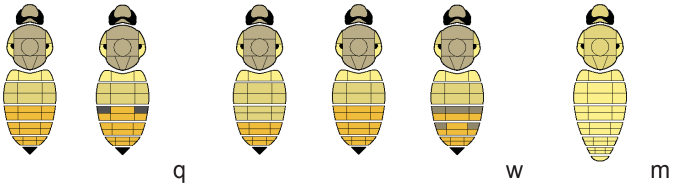
Distribution. Central and east Himalayan endemic. A record from Kashmir (Saini *et al.* 2015) needs to be confirmed.

16.6.11. *Bombus* (*Pyrobombus*) *luteipes* Richards, 1934

Bombus (*Pratobombus*) *parthenius* var. [subsp.] *luteipes* Richards 1934: 89. Holotype worker by original designation NHMUK, examined.

Bombus (*Pyrobombus*) *signifier* Tkalců 1989: 52. Paratype worker NHMUK, examined.

[*Bombus* (*Pyrobombus*) *flavescens* Smith; Saini *et al.* 2015: 195, fig. 80 (in part), misidentification].



Colour patterns of the hair of females (queens left, workers centre) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams *et al.* (2010), although species-coalescent (PTP) analysis of a MrBayes phylogenetic tree for COI barcodes and morphology now support *B. luteipes* as separate from the other closely related species: *B.* (*Pr.*) *avanus* (Skorikov) (China, Burma); *B.* (*Pr.*) *sonani* (Frison) (Taiwan); *B.* (*Pr.*) *parthenius* (Himalaya); and *B.* (*Pr.*) *infrequens* (Tkalců) (China). Until barcodes were examined, the queens had not been identified.

Identification. Small body (queen length 14–15 mm; worker 10–13 mm; male 11–13 mm) and short tongue. Similar to *B.* (*Pr.*) *parthenius* (see also *B.* (*Or.*) *funerarius*, *B.* (*Ag.*) *grahami*). Females can be distinguished: (cf. *B. parthenius*) by the hind tibia exoskeleton on the outer surface being orange-brown and the with long hair proximally only orange or at most with only a few short hairs near the joint with the femur dark brown; (cf. *B. funerarius*) by the ocello-ocular area having a broad band of punctures along the inner margin of the eye; and (cf. *B. grahami*) by the mandibles having just two anterior teeth and a broadly rounded distal margin. Male genitalia are uniquely diagnostic: by the gonocoxa distally having its inner corner produced as a narrowly acute sharp spine.

Habitat. Common in the lower and upper forest.

Distribution. East Himalayan endemic.

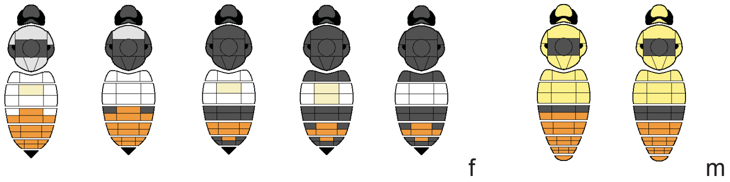
16.6.12. *Bombus* (*Pyrobombus*) *biroi* Vogt, 1911

Bombus (*Pratobombus*) *biroï* Vogt 1911: 51. Lectotype queen by designation of Tkalců (1969a) TM, examined.

Bombus nursei Friese 1918: 84. Holotype queen by monotypy ZMHB, examined.

Bombus abbotti Cockerell 1922: 2. Holotype queen by original designation USNM, examined.

Lapidariobombus anargumentosus Skorikov 1931: 22, 237. Syntype queens ZIN, examined.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams (1991), although species-coalescent (PTP) analysis of a Mr Bayes phylogenetic tree for COI barcodes and morphology, including the slightly narrower and narrowing recurved head of the penis valve, now support this as a species separate from its sister species *B.* (*Pr.*) *kotzschi.* Much more thorough sampling and analysis of COI barcode variation is needed to confirm its status and the extent of its distribution (it may prove to be a West Himalayan endemic, *B.* (*Pr.*) *nursei*).

Identification. Small body (queen length 14–17 mm; worker 10–12 mm; male 10–12 mm) and short tongue. Similar to *B.* (*Pr.*) *lemniscatus* and *B.* (*Pr.*) *hilaris* (see also *B.* (*Ag.*) *rainai*, *B.* (*Ag.*) *sikkimi*). Females can be distinguished: (cf. *B. lemniscatus*, *B. hilaris*) by the ocello-ocular area along the inner margin of the eye being smooth and shining with a band of very widely-spaced large punctures with very few small punctures between them; and (cf. *B. rainai*, *B. sikkimi*) by the mandibles having just two anterior teeth and a broadly rounded distal margin. Males can be distinguished: by the combination of the thorax being yellow banded with the genitalia having the penis valve with the recurved head broadened at the tip like a spatula.

Habitat. Uncommon in alpine flower-rich grassland.

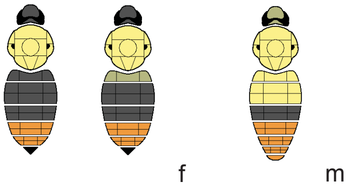
Distribution. Western Himalaya and Central Asia.

16.6.13. *Bombus* (*Pyrobombus*) *kotzschi* Reinig, 1940 stat. rev.

Bombus agnatus Skorikov 1933a: 248 (not of Skorikov (1912a) after Tkalců 1969a = *B. lapponicus* (Fabricius)). Syntype queen ZIN, examined.

Bombus (*Pratobombus*) *kotzschi* Reinig 1940: 227. Holotype male by monotypy presumed lost (Williams 1991), not seen but identity not in doubt.

[*Bombus* (*Pyrobombus*) *biroi* Vogt; Williams 1991: 77 (in part), misidentification; Saini *et al.* 2015: 29 (in part), misidentification].



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams (1991), although species-coalescent (PTP) analysis of a Mr Bayes phylogenetic tree for COI barcodes and morphology, including the slightly broader and broadening recurved head of the penis valve, now support this as a species separate from its sister species *B.* (*Pr.*) *biroi.* Much more thorough sampling and analysis of COI barcode variation is needed to confirm its status and the extent of its distribution.

Identification. Small body (queen length 16 mm; worker 10–12 mm; male 10–11 mm) and short tongue. Similar to *B.* (*Pr.*) *subtypicus* (see also *B.* (*Ml.*) *semenovianus*, and some *B.* (*Sb.*) *longiceps*, *B.* (*Md.*) *avinoviellus*). Females can be distinguished: (cf. all of these species) by the ocello-ocular area along the inner margin of the eye being smooth and shining with a band of very widely-spaced large punctures with very few small punctures between them. Males can be distinguished: by the combination of the thorax being yellow and unbanded with the genitalia having the penis valve with the recurved head broadened at the tip like a spatula.

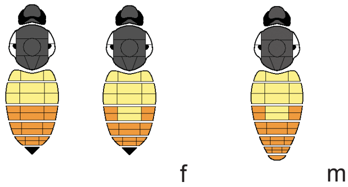
Habitat. Rare in subalpine flower-rich semi-desert grassland.

Distribution. Trans Himalaya, Afghanistan and Central Asia.

16.6.14. *Bombus* (*Pyrobombus*) *rotundiceps* Friese, 1916

Bombus rotundiceps Friese 1916: 108. Lectotype male by designation of Tkalců (1974) ZMHB, examined.

Pyrobombus (*Pyrobombus*) *rotundiceps* subsp. *shillongensis* Tkalců 1974: 334. Holotype queen by original designation NHMUK, examined.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2010). Revision of this complex in the Himalaya and China with COI barcodes is needed. The extent of the black hair on T3–5 is expected to increase progressively from west to east.

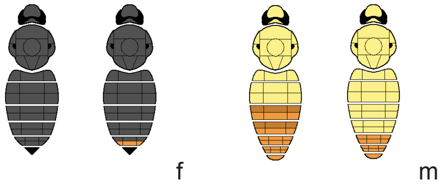
Identification. Small body (queen length 14–15 mm; worker 10–13 mm; male 12 mm) and short tongue. Similar to *B.* (*Mg.*) *albopleuralis*, *B.* (*Mg.*) *montivagus*, *B.* (*Or.*) *haemorrhoidalis* and *B.* (*Ag.*) *breviceps.* Females can be distinguished: (cf. *B. albopleuralis*, *B. montivagus*) by the oculo-malar area being no longer than broad, and the mid basitarsus having the distal posterior corner broadly rounded; (cf. *B. haemorrhoidalis*) by the ocello-oculo area having a broad band of punctures along the inner margin of the eye; and (cf. *B. breviceps*) by the mandibles having just two anterior teeth and a broadly rounded distal margin. Males can be distinguished: (cf. *B. albopleuralis*, *B. montivagus*, *B. haemorrhoidalis*, *B. breviceps*) by the penis-valve head recurved part being more than 3× longer than broad.

Habitat. Rare in the lower forest.

Distribution. Central and eastern Himalaya, south-western China, and Southeast Asia.

16.6.15. *Bombus* (*Pyrobombus*) *flavescens* Smith, 1852

Bombus flavescens Smith 1852a: 45. Holotype male by monotypy NHMUK, examined.
Bombus alienus Smith 1854: 402. Holotype worker by monotypy NHMUK, examined.
Bombus rufocaudatus Friese 1905: 510 (not of Friese (1904) = *B. tucumanus* Vachal). Syntype queens ZMHB, not seen but identity not in doubt.
Bombus mearnsi Ashmead 1905: 959. Holotype worker by monotypy USNM, not seen but identity not in doubt.
[*Bombus* (*Pyrobombus*) *eximius* Smith; Burger *et al.* 2009: 457 (in part), misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009).

Identification. Small body (queen length 17–18 mm; worker 11–15 mm; male 12–15 mm) and short tongue. Similar to *B.* (*Ml.*) *eximius* and *B.* (*Ag.*) *genalis* with bright orange legs. Females can be distinguished: (*cf. B. eximius*) by the labrum having the lamella in the middle narrow and semi-circular; and (*cf. B. genalis*) by the mandible having two anterior teeth and a broadly rounded distal margin. Males can be distinguished: (cf. *B. eximius*, *B. genalis*) by the penis-valve head having the recurved part more than 3× longer than broad and by the hair of the thorax being extensively yellow.

Habitat. Common in the lower and upper forest.

Distribution. Central and eastern Himalaya, central and southern China, Southeast Asia.

16.7. Subgenus *BOMBUS* (in the strict sense)

These bumblebees are associated with mountain grasslands and forest edges. Short tongue-length bumblebees visiting shallow flowers, although females frequently bite holes in corollas and rob deeper flowers. Nests are underground and colonies and may be large. Older larvae are reared separately, as non-pocket makers. Males patrol circuits of scent-marked places that attract young queens.

Aside from the distinctive *B. tunicatus*, the species of this subgenus are very difficult to identify to species reliably without using COI barcodes. In the Himalaya, it may be possible to use the region they come from as a first guide.

FEMALES: key to SPECIES

1. Hair of T4–5 red……………………………………………………***B. tunicatus***
– Hair of T4–5 nearly white…………………………………………………………2

2. (1) Hair medium to long and fine, the yellow pale or grey; *if* the yellow is darker *then* the oculo-ocellar area *either* without an isolated anterior patch of small punctures *or* the punctures are very few…………………3
– Hair short and thick, the yellow golden; oculo-ocellar unpunctured area with an isolated anterior lateral round patch of dense small punctures occupying at least a quarter of the distance between the large punctures along the inner eye margin and the lateral ocellus (species not yet recorded from the Himalaya, but likely to be introduced)…………***B. terrestris***

3. (2) Hair of the thoracic dorsum anteriorly and T2 lemon yellow *either* without black hair intermixed extensively *or if* present *then* the bands are narrow, T2 *either* with a broad posterior fringe of black hair *or* the scutellum with yellow hair……………………………4
– Hair of the thoracic dorsum anteriorly and T2 cream-white or very pale yellow with scattered black hair intermixed extensively, T2 predominantly pale with only a very narrow fringe of black hair *and* the scutellum without pale hair………………***B. jacobsoni***

4. (3) Dorsum of the head (vertex), side of the thorax, and thoracic dorsum posteriorly (scutellum) with thickly feathery sometimes slightly greyish hair intermixed, hair of the scutellum and T1 predominantly black……………5
– Dorsum of the head (vertex), side of the thorax, and thoracic dorsum posteriorly (scutellum) with few thickly feathery slightly greyish hair intermixed, hair of the scutellum and T1 often extensively yellow……………***B. cryptarum***

5. (4) Hair of the thoracic dorsum anteriorly with a narrow yellow band that does not extend laterally below the base of the wings, T2 with a narrow anterior yellow band, interrupted medially by black hair……………***B. longipennis***
– Hair of the thoracic dorsum anteriorly with a broad yellow band that extends laterally below the base of the wings to nearly half of

the distance to the leg base, T2 with a broad anterior yellow band, uninterrupted medially and continuous…………………………***B. reinigi***

MALES: key to SPECIES

1. Hair of T5–6 red………………………………………………***B. tunicatus***

– Hair of T5–6 white……………………………………………………………2

2. (1) Hair medium to long and fine, the yellow pale; hair of the face predominantly bright yellow…………………………………………………3

– Hair short and thick, the yellow golden; hair of the face *either* black *or* at most with dull brownish yellow (species not yet recorded from the Himalaya, but likely to be introduced)………………………***B. terrestris***

3. (2) Hair the thoracic dorsum between the wing bases and T3 predominantly black……………………………………………………………4

– Hair the thoracic dorsum between the wing bases and T3 predominantly yellow……………………………………………***B. reinigi***

4. (3) Hair of the thoracic dorsum posteriorly (scutellum) yellow and without thickly feathery slightly greyish hair intermixed………………5

– Hair of the thoracic dorsum posteriorly (scutellum) black and with thickly feathery slightly greyish hair intermixed……………………***B. longipennis***

5. (4) Hair of the thoracic dorsum anteriorly and T2 lemon yellow without black hair intermixed extensively, the black band between the wing bases with very few yellow hairs intermixed………………***B. cryptarum***

– Hair of the thoracic dorsum anteriorly and T2 cream-white or very pale yellow often with a few scattered black hairs intermixed, the black band between the wing bases sometimes with many yellow hairs intermixed……***B. jacobsoni***

16.7.1. ***Bombus* (*Bombus*) *tunicatus* Smith, 1852**

Bombus tunicatus Smith 1852b: 43. Lectotype queen by designation of Tkalců (1974) NHMUK, examined.

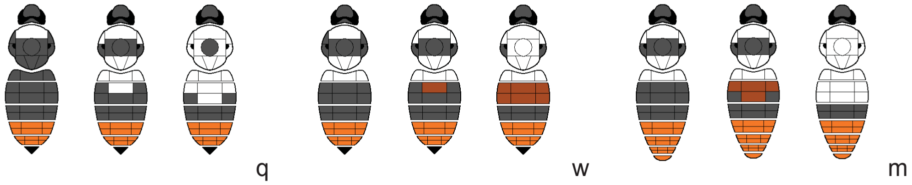
Bombus vallestris Smith 1878b: 8. Holotype worker by monotypy NHMUK, examined.

Bombus gilgitensis Cockerell 1905: 223. Holotype queen by monotypy NHMUK, examined.

Bombus terrestris var. [subsp.] *simlaënsis* Friese 1909: 674. Lectotype queen by designation of Tkalců (1974) ZMHB, examined.

Bombus terrestris var. [subsp.] *fulvocinctus* Friese 1909: 674. Type worker not found by Tkalců (1974), not seen but identity not in doubt.

Bombus (*Bombus*) *manaliensis* Avdhesh Kumar & Lall 2004: 236. Holotype male by original designation [? Kumar coll.], not seen but identity not in doubt.



Colour patterns of the hair of females (*queens left*, *workers centre*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, subalpine and Trans-Himalayan subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1991), Williams *et al.* (2012), and Williams (2021). Size/caste-related colour variation in females involving white (queens) or brown (workers) hair on T2, although males may have either. Queens from the far northwest of the range have T1–2 entirely black.

Identification. Medium size body (queen length 17–19 mm; worker 13–15 mm; male 13–17 mm) and short tongue. Workers most similar in colour pattern to *B.* (*Ml.*) *simillimus*, but also to white-banded *B.* (*Sb.*) *longiceps* and *B.* (*Md.*) *avinoviellus*. Females can be distinguished: (cf. *B. simillimus*) by having T1 white, the hind basitarsus having the posterior margin strongly arched; and (cf. *B. longiceps*, *B. avinoviellus*) by having the wings dark and T2 often with brown, the hind basitarsus having the posterior margin strongly arched. Male genitalia can be distinguished: (cf. *B. simillimus*, *B. longiceps*, *B. avinoviellus*) by the penis-valve head being flared outwards to form half of a funnel.

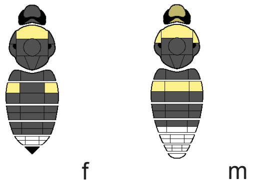
Habitat. One of the most abundant species in open areas in the lower and upper forest zones. Entrance to an underground nest seen in an earth bank.

Distribution. Western and central Himalaya and the Trans Himalaya in western Ladakh, extending into Afghanistan.

16.7.2. ***Bombus* (*Bombus*) *longipennis* Friese, 1918** *s.str.*

Bombus pratorum var. [subsp.] *longipennis* Friese 1918: 83. Lectotype worker by designation of Williams (1991) ZMHB, examined. Not infrasubspecific after Tkalců (1974).

[*Bombus* (*Bombus*) *lucorum* (Linnaeus); Williams 1991: 81 (in part), misidentification; Saini *et al.* 2015: 87 (in part), misidentification].



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine and Trans-Himalayan subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1991), Williams *et al.* (2012), and Williams (2021), the most recent analysis supports *B.* (*Bo.*) *longipennis* as a species separate from the other species: *B.* (*Bo.*) *reinigi* (western Himalaya, below) and *B.* (*Bo.*) *minshanicola* Bischoff (eastern QTP).

Identification. Medium size body (queen length 16–18 mm; worker 12–14 mm; male 12–14 mm) and short tongue. Female closely similar to *B.* (*Bo.*) *reinigi*, *B.* (*Bo.*) *jacobsoni* and *B.* (*Bo.*) *cryptarum* and often difficult to distinguish reliably without COI barcodes (see also *B. infirmus*). Females can be distinguished: (cf. *B. reinigi*, *B. jacobsoni*, *B. cryptarum*) by the thoracic dorsum anteriorly having a narrow yellow band that does not extend laterally below the base of the wings, T2 yellow usually being medially interrupted by black; (cf. *B. jacobsoni*, *B. cryptarum*) by the area above the antenna base having dense thickly feathery hair; (cf. *B. jacobsoni*) by the yellow bands being dull brownish yellow rather than light grey-yellow; (cf. *B. infirmus*) by T1 being black, and the hind basitarsus having the posterior margin strongly arched. Males can be distinguished: (cf. *B. reinigi*, *B. jacobsoni*, *B. cryptarum*) by the hair of the scutellum being black intermixed with short greyish feathered hairs; and (cf. *B. infirmus*) by the penis-valve head being flared outwards to form half of a funnel.

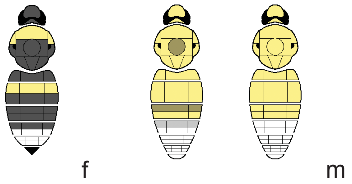
Habitat. Uncommon in flower-rich subalpine grassland.

Distribution. Eastern Himalaya, extending into the neighbouring QTP.

16.7.3. ***Bombus*** **(*Bombus*)** ***reinigi*** **Tkalců, 1974**

Bombus reinigi Tkalců 1974: 322. Holotype queen NMS, examined.

[*Bombus* (*Bombus*) *lucorum* (Linnaeus); Williams 1991: 81 (in part), misidentification; Williams *et al.* 2010: 125, misidentification; Saini *et al.* 2015: 87 (in part), misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest and subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1991), Williams *et al.* (2012), and Williams (2021), the most recent analysis supports *B.* (*Bo.*) *reinigi* as a species separate from the other species: *B.* (*Bo.*) *longipennis* (eastern Himalaya, above) and *B.* (*Bo.*) *minshanicola* Bischoff (eastern QTP).

Identification. Medium size body (queen length 16–18 mm; worker 12–15 mm; male 12–15 mm) and short tongue. Female closely similar to *B.* (*Bo.*) *longipennis*, *B.* (*Bo.*) *jacobsoni* and *B.* (*Bo.*) *cryptarum* and difficult to distinguish reliably without COI barcodes. Females can be distinguished: (cf. *B. longipennis*) by the yellow hair of the thoracic dorsum anteriorly extending down the side of the thorax to half of the distance to the leg base, T2 having a continuous yellow band; (cf. *B. jacobsoni*) by the yellow bands being lemon yellow rather than grey-yellow without black hairs intermixed extensively; (cf. *B. cryptarum*) by the hair of the scutellum and T1 being black, the head (vertex), side of the thorax, and scutellum having thickly feathery slightly greyish hair intermixed.

Males can be distinguished: (cf. *B. longipennis*, *B. jacobsoni*, *B. cryptarum*) by the thoracic dorsum and T3 having yellow hair intermixed extensively.

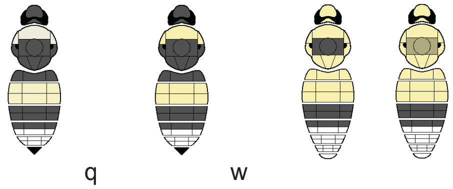
Habitat. Uncommon in the upper forest and flower-rich subalpine grassland.

Distribution. Endemic to the western Himalaya, extending into the neighbouring QTP.

16.7.4. ***Bombus*** **(*Bombus*)** ***jacobsoni*** **Skorikov, 1912**

Bombus lucorum subsp. *jacobsoni* Skorikov 1912b: 610. Syntype queens ZIN NHMUK, examined.

[*Bombus* (*Bombus*) *lucorum* (Linnaeus); Williams 1991: 81 (in part), misidentification; Saini *et al.* 2015: 87 (in part), misidentification].



Colour patterns of the hair of females (queens left, workers centre) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine and Trans-Himalayan subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1991), Williams *et al.* (2012), and Williams (2021).

Identification. Medium size body (queen length 17–19 mm; worker 14 mm; male 12–14 mm) and short tongue. Female closely similar to *B.* (*Bo.*) *longipennis*, *B.* (*Bo.*) *reinigi* and *B.* (*Bo.*) *cryptarum* and difficult to distinguish reliably without COI barcodes. Females can be distinguished: (cf. *B. longipennis*, *B. reinigi*, *B. cryptarum*) by the thoracic dorsum having the anterior pale band grey or very pale yellow rather than lemon yellow and with black hairs intermixed extensively; (cf. *B. longipennis*) by the pale hair of the thoracic dorsum anteriorly extending down the side of the thorax to half of the distance to the leg base, T2 having a continuous yellow band; (cf. *B. cryptarum*) by the hair of the scutellum and T1 being black. Males can be distinguished: (cf. *B. longipennis*, *B. reinigi*, *B. cryptarum*) by the yellow bands being very pale yellow rather than lemon yellow (unreliable for faded individuals); (cf *B. longipennis*) by the hair of the scutellum being yellow; (cf. *B. reinigi*) by the hair of T3 being predominantly black.

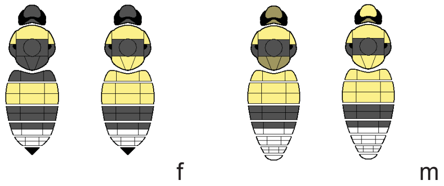
Habitat. Rare in flower-rich subalpine grassland.

Distribution. Endemic to Kashmir.

16.7.5. *Bombus* (*Bombus*) *cryptarum* (Fabricius, 1775)

Apis cryptarum Fabricius 1775: 379. Lectotype queen by designation of Løken (1966) KU, not seen but identity not in doubt.

[*Bombus* (*Bombus*) *lucorum* (Linnaeus); Williams 1991: 81 (in part), misidentification; Saini *et al.* 2015: 87 (in part), misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1991), Williams *et al.* (2012), and Williams (2021).

Identification. Medium size body (queen length 18–20 mm; worker 10–16 mm; male 14–15 mm) and short tongue. Female closely similar to *B.* (*Bo.*) *longipennis*, *B.* (*Bo.*) *reinigi*, and *B.* (*Bo.*) *jacobsoni* and difficult to distinguish reliably without COI barcodes. Females can be distinguished: (cf. *B. longipennis*, *B. reinigi*, *B. jacobsoni*) by the scutellum and T1 often having yellow hair; (cf. *B. longipennis*) by the head having only weakly plumose hair above the base of the antenna, T2 having a continuous yellow band; (cf. *B. jacobsoni*) by the yellow bands being lemon yellow rather than grey-yellow and without black hairs intermixed extensively. Males can be distinguished: (cf. *B. reinigi*) by T3 being entirely black; (cf. *B. longipennis*) by the hair of the scutellum being yellow; (cf. *B. jacosoni*) by the yellow bands being lemon yellow rather than very pale yellow (unreliable for faded individuals).

Habitat. Common in flower-rich subalpine grassland.

Distribution. Northern Pakistan, Afghanistan, Central Asia, Mongolia, and the northern Palaearctic and Nearctic regions.

16.8. Subgenus *ALPIGENOBOMBUS*

These bumblebees are associated with alpine grasslands and forest edges in mountains. Short to medium tongue-length bumblebees visiting shallow to medium flowers, although females (with six large teeth on the mandibles) very frequently bite holes in corollas and rob deeper flowers. Nests are underground. Older larvae are usually reared separately, as non-pocket makers. Males of some species patrol circuits of scent-marked places that attract young queens, although for *B. kashmirensis* at least they have slightly enlarged eyes and hover and race after potential mates without being territorial (Williams 1991).

FEMALES: key to SPECIES

1. Oculo-malar distance as long as or shorter than the breadth of the mandible proximally between the outer ends of its articulations…………2

– Oculo-malar distance longer than the breadth of the mandible proximally between the outer ends of its articulations………***B. sikkimi***

2. (1) Hair of T1–3 *either* with some white *or* yellow *or* orange……………………3

– Hair of T1–3 black………………………………………………………***B. genalis***

3. (2) Hair of the thoracic dorsum with pale anterior and posterior bands………4

– Hair of the thoracic dorsum *either* entirely black *or* with varying amounts of dark olive-grey, sometimes with paler hairs along the midline………6

4. (3) Hair of the thoracic dorsum black; the hair short, wings dark brown…… ……………………………………………………………***B. breviceps*** (part)

– Hair of the thoracic dorsum with the pale bands *either* white *or* yellow; the hair long, wings clear.........……………………………………………………5

5. (4) Oculo-ocellar area in almost its outer half with large and medium punctures; hair of T5 orange with white tips, T2 *either* white *or* yellow, scutellum predominantly *either* white *or* yellow, side of the thorax in at least its upper half *either* white *or* yellow……………***B. kashmirensis***

– Oculo-ocellar area in its outer half with only a few small shallow punctures, any larger punctures confined to the eye margin; hair of T5 entirely orange with barely any paler tips, T2 white, scutellum usually predominantly black, side of the thorax only in its upper third white, lower two thirds black …………………………***B. rainai*** sp. nov.

6. (3) Hair of T1 bright yellow……………………………………***B. breviceps*** (part)

– Hair of T1 *either* white *or* grey *or* extensively black……………***B. grahami***

MALES: key to SPECIES

1. Hair of the thoracic dorsum with a black band between the wing bases without many pale hairs intermixed and between broad anterior and posterior pale bands……………………………………4

– Hair of the thoracic dorsum *either* predominantly black *or* olive-grey with yellow and black hair intermixed, any pale bands narrow and intermixed with black...........................……………………………………2

2. (1) Wings *either* clear *or* yellow…………………………………………………3

– Wings dark brown...……………………………………………***B. breviceps***

3. (2) Wings clear with wing veins dark brown, hair of the thoracic dorsum and T1–2 predominantly *either* yellow *or* olive grey……………***B. grahami***

– Wings yellow with wing veins orange-brown, hair of the thoracic dorsum and T1–2 predominantly black……………………………………***B. genalis***

4. (1) Hair of the face black, oculo-malar distance shorter than the breadth of the mandible proximally between the outer ends of its articulations………5

– Hair of the face *either* yellow *or* white, oculo-malar distance longer than the breadth of the mandible proximally between the outer ends of its articulations………………………………………***B. sikkimi***

5. (4) Hair of the side of T5–6 orange at the base but white-tipped, T3 usually predominantly black; the side of the thorax *either* yellow *or* white, the pale hair reaching to the midleg bases; genitalia with penis valve recurved head broad, the recurved section narrowing only just before the apex…………………………***B. kashmirensis***

– Hair of the side of T5–6 orange, T3 usually predominantly orange; the side of the thorax with black and white intermixed, but predominantly black in its lower half; genitalia with penis valve recurved head narrow, the recurved section tapering gradually to the apex…………………***B. rainai*** sp. nov.

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

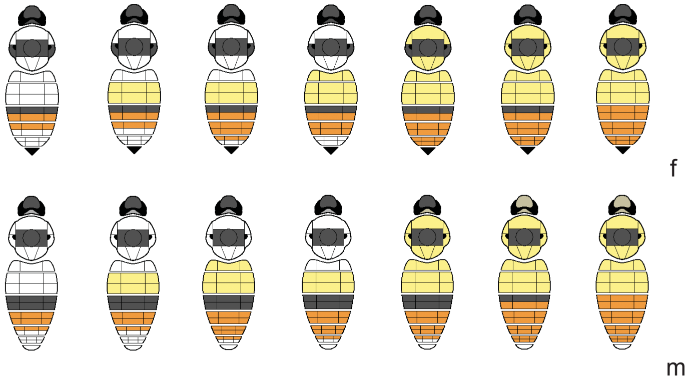
Bombus mastrucatus var. [subsp.] *kashmirensis* Friese 1909 [September: Tkalců 1974]: 673. Lectotype queen by designation of Tkalců (1974) ZMHB, examined.

Bombus mastrucatus var. [subsp.] *stramineus* Friese 1909 [September: Tkalců 1974]: 673. Type not found (Tkalců 1974) but identity not in doubt.

Bombus tetrachromus Cockerell 1909 [November: Tkalců 1974]: 397. Holotype queen by original designation NHMUK, examined.

Alpigenobombus pulcherrimus Skorikov 1914a: 128. Holotype queen by monotypy ZIN, not seen but identity not in doubt.

Bombus (*Mastrucatobombus*) *mastrucatus* subsp. *meinertzhageni* Richards 1928b: 335. Holotype queen by monotypy NHMUK, examined.



Colour patterns of the hair of females (*above*) *and males* (*below*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine, alpine and Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams (1991), although analyses of COI barcodes now support this species as separate from *B.* (*Ag.*) *rainai* sp. nov., see below. This species includes both white-banded (outer humid alpine Great Himalaya) and yellow-banded colour patterns (semi-arid Trans Himalaya).

Identification. Medium size body (queen length 17–20 mm; worker 10–15 mm; male 14–16 mm) and short tongue. Most similar to *B.* (*Ag.*) *rainai*, *B.* (*Ag.*) *sikkimi* (see also *B.* (*Ml.*) *ladakhensis*, *B.* (*Ml.*) *rufofasciatus*, *B.* (*Ml.*) *prshewalskyi*). Females can be distinguished: (cf. *B. rainai*) by the ocello-ocular area along the inner eye margin having large and medium punctures, the thoracic dorsum posteriorly and on the side having extensively pale hair, T-5 having hair that is frequently red at the base and white at the tip; (cf. *B. sikkimi*) by the oculo-malar distance being less than the breadth of the mandible at its base; (cf. *B. ladakhensis*, *B. rufofasciatus*, *B. prshewalskyi*) by the mandible distally having six large pointed teeth; (cf. *B. rufofasciatus*, *B. prshewalskyi*) by T-5 having hair that is frequently red at the base and white at the tip. Males can be distinguished: (cf. *B. rainai*) by the side of the thorax being without black hair intermixed, T-5 having hair that is frequently red at the base and white at the tip; (cf. *B. sikkimi*) by the oculo-malar distance being less than the breadth of the mandible at its base; (cf. *B. ladakhensis*, *B. rufofasciatus*, *B. prshewalskyi*) by the mandible distally having three large pointed teeth; and (cf. *B. rufofasciatus*, *B. prshewalskyi*) by the eye being only weakly enlarged relative to female bumblebees.

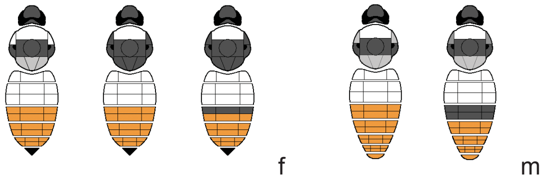
Habitat. Common in subalpine and alpine flower-rich grassland. Entrance to an underground nest seen among rocks.

Distribution. Western and central Himalaya (common), Trans Himalaya (uncommon), extending into the QTP (global distribution mapped by Williams 1991).

16.8.2. *Bombus* (*Alpigenobombus*) *rainai* sp. nov.

[*Bombus* (*Alpigenobombus*) *kashmirensis* Friese; Williams 1991: 66 (in part), misidentification; Saini *et al.* 2015: 200, figs 116–117 (in part), misidentification; Jaffar *et al.* 2019: 983, figs 7–8 (in part), misidentification].

Bombus (*Alpigenobombus*) *rainai* sp. nov. Holotype queen by present designation ZSC, examined.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine and alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. This taxon was discussed as divergent from *B. kashmirensis* by Williams (1991: pages 68–69, figs 308–310) although it was not then named as a separate species. Recent species-coalescent (PTP) analysis of a MrBayes phylogenetic tree for COI barcodes and morphology now support it as a species separate from *B. kashmirensis.*

Identification. Medium size body (queen length 17–19 mm; worker 12–13 mm; male 14–17 mm) and short tongue. Most similar to *B.* (*Ag.*) *kashmirensis*, *B.* (*Ag.*) *sikkimi* (see also *B.* (*Pr.*) *biroi*, *B.* (*Md.*) *himalayanus*, *B.* (*Ml.*) *ladakhensis*, *B.* (*Ml.*) *rufofasciatus*, *B.* (*Ml.*). *prshewalskyi*). Females can be distinguished: (cf. *B. kashmirensis*) by the ocello-ocular having the area along the inner eye margin with only small shallow punctures, the thoracic dorsum posteriorly (scutellum) and on the side (below wing bases) having extensive black hair, T4-5 hair being entirely orange-red; (cf. *B. sikkimi*) by the oculo-malar distance being less than the breadth of the mandible at its base; (cf. *B. biroi*, *B. himalayanus*, *B. ladakhensis*, *B. rufofasciatus*, *B. prshewalskyi*) by the mandible distally having six large pointed teeth. Males can be distinguished: (cf. *B. kashmirensis*) by side of the thorax having black hair intermixed, T4-5 hair being entirely orange-red; (cf. *B. sikkimi*) by the oculo-malar distance being less than the breadth of the mandible at its base; (cf. *B. biroi*, *B. himalayanus*, *B. ladakhensis*, *B. rufofasciatus*, *B. prshewalskyi*) by the mandible distally having three large pointed teeth; and (cf. *B. rufofasciatus*, *B. prshewalskyi*) by the eye being only weakly enlarged relative to female bumblebees.

Habitat. Uncommon in subalpine and alpine flower-rich grassland.

Distribution. Endemic to the western Himalaya (global distribution mapped by Williams 1991).

Etymology. Named after Dr Rifat Raina, specialist in Kashmir bumblebees.

Description. Female with hair (pubescence) moderately short and even, wings clear. Mandibles with six large triangular pointed teeth. Oculo-malar area ('cheek' sensu Williams *et al.* 2014; not the gena) short, the length, measured between the ventral edge of the compound eye and the edge of the malar area at the articulation of the mandible midway between the mandibular condyles, less than the breadth of the mandible between and including the mandibular condyles. Clypeus strongly swollen, its raised area weakly domed, the central area with scattered small punctures, the punctures anteriorally, adjacent to the labrum, larger. The area between the inner edge of the compound eye and the outer edge of the lateral ocellus occupied in its outer half by a band with very few very large punctures, most spaced by more than their own widths, the smaller punctures between the larger punctures near the eye margin very few. Mid basitarsus with the distal posterior corner broadly less than a right angle; hind tibia outer surface with a corbicula, the surface sculpturing weakly reticulate so that the surface appears shining; hind basitarsus in the distal three quarters densely covered with short branched decumbent dark brown hairs; T6 posteriorly truncate and with longitudinal median groove. Colour pattern of the hair of the body predominantly black. Head entirely black except for orange hairs anteriorly on the labrum. Thoracic dorsum with a broad anterior grey-white band with a few scattered black hairs intermixed, posteriorly with small patches laterally with some white hair; side of the thorax (mesepisternum) predominantly black, in its dorsal third with some white hairs intermixed. T1–2 white; T3–6 almost entirely orange-red.

Holotype. ♀ (queen, habitus left lateral aspect below in Fig. 21) pinned (deposited in the ZSC collection) with three labels: (1) hand written 'Sp. N. / Loc. Affarwatt / Date. 21-08-09 / Alt. 4000 m'; (2) white printed in black '*Bombus* / (*Alpigenobombus*) / *kashmirensis* / det. PH Williams 2010'; (3) red printed in black '**HOLOTYPE** ♀ (q) / *Bombus* / ***rainai*** / Williams, 2021 / det. PH Williams 2020'. Right mid leg missing [removed for barcoding].

Paratype. One ♀ (queen) pinned (deposited in the NHMUK collection) with three labels: (1) white printed in black 'Cachem.et Jam. / Chittakatha Sar / 19-24-VIII-1953 / F. Schmid'; (2) white printed in black 'F.Schmid Coll. / B.M.1962-457.'; (3) yellow printed in black '**PARATYPE** ♀ (q) / *Bombus* / ***rainai*** / Williams, 2021 / det. PH Williams 2020'.

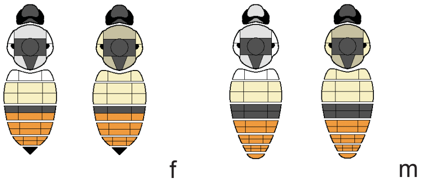
Fig. 21. Image of the holotype queen of *Bombus rainai* sp. nov. from Mt Apharwat at 4000 m a.s.l. in the Pir Panjal Range, Kashmir, viewed from the left lateral aspect (body length 18 mm).

16.8.3. ***Bombus* (*Alpigenobombus*) *sikkimi* Friese, 1918** stat. rev.

Bombus sikkimi Friese 1918: 82. Syntype queen ZMHB, examined.

Bombus (*Nobilibombus*) *xizangensis* S.-F. Wang 1979: 188. Holotype queen by original designation IOZ, examined.

[*Bombus* (*Alpigenobombus*) *nobilis* Friese; Burger *et al.* 2009: 460, misidentification; Williams *et al.* 2010: 130 (in part), misidentification; Saini *et al.* 2015: 100, misidentification; Streinzer *et al.* 2019: table 1, misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine and alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. The status of this taxon was discussed by Williams *et al.* (2007), although recent species-coalescent (PTP) analysis of a Mr Bayes phylogenetic tree for COI barcodes and morphological differences including the female ocello-ocular area with a consistently much more dense broad band of fine punctures along the inner eye margin now support this as a species separate from the closely similar but golden-yellow-banded *B.* (*Ag.*) *nobilis* Friese (eastern QTP). *Bombus sikkimi* includes both white-banded and pale yellow-banded colour patterns.

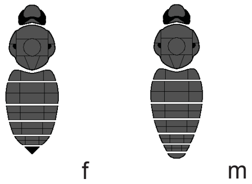
Identification. Large body (queen length 21–23 mm; worker 12–14 mm; male 15–16 mm) and medium length tongue. Most similar to *B.* (*Ag.*) *kashmirensis*, *B.* (*Ag.*) *rainai* (see also *B.* (*Ml.*) *ladakhensis*, *B.* (*Ml.*) *rufofasciatus*, *B.* (*Ml.*) *prshewalskyi*, *B.* (*Pr.*) *lemniscatus*, *B.* (*Pr.*) *lepidus*, *B.* (*Pr.*) *pressus*). Females can be distinguished: (cf. *B. kashmirensis*, *B. rainai*) by the oculo-malar distance being longer than the breadth of the mandible at its base; (cf. *B. ladakhensis*, *B. rufofasciatus*, *B. prshewalskyi*, *B. lemniscatus*, *B. lepidus*, *B. pressus*) by the mandible distally having six large pointed teeth. Males can be distinguished: (cf. *B. kashmirensis*, *B. rainai*) by the oculo-malar distance being more than the breadth of the mandible at its base; (cf. *B. ladakhensis*, *B. rufofasciatus*, *B. prshewalskyi*, *B. lemniscatus*, *B. lepidus*, *B. pressus*) by the mandible distally having three large pointed teeth; and (cf. *B. rufofasciatus*, *B. prshewalskyi*) by the eye being unenlarged relative to female bumblebees.

Habitat. Uncommon in subalpine and alpine flower-rich grassland.

Distribution. Central and eastern Himalaya extending into the QTP (distribution mapped by Williams *et al.* 2010).

16.8.4. ***Bombus* (*Alpigenobombus*) *genalis*** **Friese, 1918**

Bombus genalis Friese 1918: 84. Syntype queen and worker ZMHB, examined.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (1998).

Identification. Medium size body (queen length 21–22 mm; worker 12–13 mm; male 15 mm) and short tongue. Similar to *B.* (*Pr.*) *flavescens* and *B.* (*Ml.*) *eximius* with bright orange legs. Females can be distinguished: (cf. *B. flavescens*, *B. eximius*) by the mandible distally having six large pointed teeth. Males can be distinguished: (cf. *B. flavescens*, *B. eximius*) by the mandible distally having three large pointed teeth. (The male genitalia are similar to *B. breviceps*.)

Habitat. Rare in the lower forest.

Distribution. Eastern Himalaya and south-western China.

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

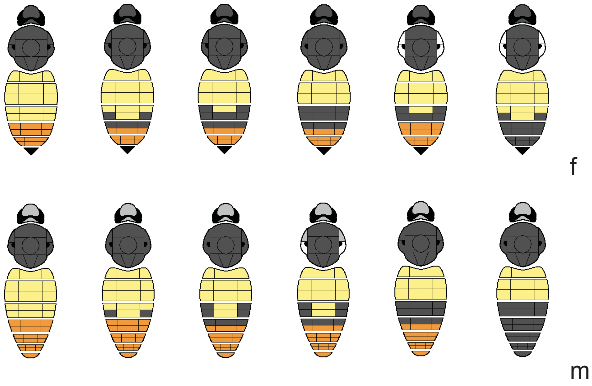
Bombus nasutus Smith 1852b: 44. Lectotype queen by designation of Tkalců (1968) NHMUK, examined.

Bombus breviceps Smith 1852b: 44. Holotype worker by monotypy NHMUK, examined. Precedence by action of first reviser Tkalců (1968b).

Bombus dentatus Handlirsch 1888: 227. Holotype worker by monotypy NHMW, not seen but identity not in doubt.

Bombus simulus Gribodo 1892: 114. Holotype worker by monotypy MCSN, examined.

Bombus orichalceus Friese 1916: 107. Holotype queen by monotypy ZMHB, examined.



Colour patterns of the hair of females (above) and males (below), variation shown (approximately) from west to east.

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009). The extent of the black hair on T3–5 increases progressively from west to east.

Identification. Medium size body (queen length 18–21 mm; worker 10–16 mm; male 13–15 mm) and short tongue. Similar to *B.* (*Mg.*) *albopleuralis*, *B.* (*Mg.*) *montivagus*, *B.* (*Or.*) *haemorrhoidalis* and *B.* (*Pr.*) *rotundiceps.* Females can be distinguished: (cf. *B. albopleuralis*, *B. montivagus*, *B. haemorrhoidalis*, *B. rotundiceps*) by the mandible distally having six large pointed teeth; (cf. *B. haemorrhoidalis*, *B. albopleuralis*, *B. montivagus*) by the oculo-malar area being shorter than broad; (cf. *B. albopleuralis*, *B. montivagus*) by the mid basitarsus having the distal posterior corner rounded; (cf. *B. haemorrhoidalis*) by the ocello-oculo area having a broad band of punctures along the inner margin of the eye. Males can be distinguished: (cf. *B. albopleuralis*, *B. montivagus*, *B. haemorrhoidalis*, *B. rotundiceps*) by the mandible distally having three large pointed teeth; (cf. *B. haemorrhoidalis*, *B. albopleuralis*, *B. montivagus*) by the oculo-malar area being shorter than broad; (cf. *B. albopleuralis*, *B. montivagus*, *B. haemorrhoidalis*) by the penis-valve head being turned inwards in a sickle shape.

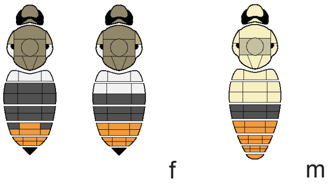
Habitat. Common in the lower and mid-elevation forest.

Distribution. Central and eastern Himalaya, southern China, and Southeast Asia.

16.8.6. *Bombus* (*Alpigenobombus*) *grahami* (Frison, 1933)

Bremus (*Alpigenobombus*) *grahami* Frison 1933 [30] September]: 334. Holotype worker by original designation USNM, examined.

Alpigenobombus beresovskii Skorikov 1933a [30 September: Pesenko & Astafurova 2003]: 248. Syntype (unpublished Podbolotskaya lectotype) queen ZIN, examined. Syn. nov.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2009). The names *beresovskii* and *berezovskii* were published by Skorikov (1923, 1931) without description and are unavailable. The name *B. beresovskii* (Skorikov, 1933) is available and is recognized here as a new synonym of *B. grahami*, technically published on the same date (ICZN, 1999: Article 21.3.1). Use of the name *B. grahami* is continued for the sake of stability because the name *B. beresovskii* has not been used for this species since its first available publication.

Identification. Medium size body (queen length 18–22 mm; worker 12–14 mm; male 13–15 mm) and short tongue. Similar to *B.* (*Or.*) *funerarius* and *B.* (*Pr.*) *parthenius.* Females can be distinguished: (cf. *B. funerarius*, *B. parthenius*) by the mandible distally having six large pointed teeth. Males can be distinguished: (cf. *B. funerarius*, *B. parthenius*) by the mandible distally having three large pointed teeth.

Habitat. Uncommon in the mid and upper forest and subalpine grassland (Williams *et al.* 2009).

Distribution. Eastern Himalaya and south-western China.

16.9. Subgenus *MELANOBOMBUS*

These bumblebees are associated with high alpine grasslands, open areas in forest, and semi-desert. Short or medium tongue-length bumblebees visiting shallow or medium flowers. Nests are underground and colonies and may be large. Older larvae are reared separately, as non-pocket makers. Males of most species patrol circuits of scent-marked places that attract young queens. In a few species with males with enlarged eyes relative to the females, the males hover or perch before racing after potential mates. Some of these species are truly territorial (*e.g.*, *B. rufofasciatus*: Williams 1991).

FEMALES: key to SPECIES

1. Hair of the thoracic dorsum entirely black……………………………………2
– Hair of the thoracic dorsum with some pale hair that is *either* white *or* yellow *or* brown…………………………………………………………3

2. (1) Wings bright yellow with wing veins orange……………………***B. eximius***
– Wings nearly black with wing veins black ....***B. simillimus*** (part)

3. (1) Hair of the thoracic dorsum between the wing bases in the centre *either* white *or* yellow *or* brown……………………………………………4
– Hair of the thoracic dorsum between the wing bases in the centre black, sometimes with some pale hair intermixed, with paler anterior and often posterior bands of pale hair that is *either* white *or* yellow………………6

4. (3) Hair of T5 white…………………………………………………***B. festivus***
– Hair of T5 red…………………………………………………………………5

5. (4) Hair of the thoracic dorsum yellow………………………***B. semenovianus***
– Hair of the thoracic dorsum white………………………***B. simillimus*** (part)

6. (3) Long hair of the face at the antennal base with an obvious patch dominated by long *either* pale grey *or* pale yellow hair, which in its centre often has few or no black hairs intermixed…………………***B. keriensis*** (part)
– Long hair of the face mostly black, sometimes with just a few long *either* yellow *or* grey hairs intermixed…………………………………7

7. (6) Hair of the tail entirely orange-red, although sometimes pale, especially in posterior fringes……………………………………………8
– Hair of the tail with at least some bright white hair posteriorly on T5…13

8. (7) Hindleg basitarsus broad, length 3× greatest breadth, with the distal posterior corner broadly angled at nearly 90°, outer surface with the short hairs golden, hair of the scutellum with few or no black hairs intermixed…9
– Hindleg basitarsus narrow, length 4× greatest breadth, with the distal posterior corner sharply angled at nearly 45°, outer surface with

the short hairs predominantly black, hair of the scutellum often with many black hairs intermixed………………………………***B. tanguticus***

9. (8) [NB couplets 9–12 may be reliable only for queens and not for workers] Hair of the pale bands *either* white *or* grey *or* cream……………………10

– Hair of the pale bands light yellow………………………………………11

10. (9) Hair of the face entirely black, T3 more often with a few pale hairs usually only laterally, leg bases more often with many black hairs, T4–5 uniformly orange-red……………………………………***B. separandus*** (part)

– Face with at least a very few long pale hairs and/or some short branched pale hairs at the base of the antenna, T3 more often with pale hairs laterally and often posteriorly, leg bases more often predominantly pale with *either* few *or* no black hairs, T4–5 *either* uniformly orange-red *or* posteriorly with distinctly paler fringes……………………***B. keriensis*** (part)

11. (9) Clypeus in its ventral half with many scattered medium-sized punctures; side of the thorax with yellow hair reaching scarcely more than half of the distance ventrally to the leg bases and the more ventral part entirely black, leg bases entirely black, face entirely black, T3 entirely black……***B. tibeticus***

– Clypeus in its ventral half (excluding the depressions adjacent to the labrum) with only scattered small punctures; side of the thorax with yellow hair reaching ventrally nearly to the leg bases at least as a very few scattered yellow hairs, leg bases with or without yellow hairs, face *either* black *or* with a few yellow hairs, T3 *either* with *or* without scattered yellow hairs laterally and sometimes posteriorly…………12

12. (11) Hair of the face often with at least a very few long pale hairs and/or some short branched pale hairs at the base of the antenna, leg bases (mid and hind coxae) with at least a few pale hairs, T3 more often with pale hairs laterally and sometimes posteriorly, thoracic dorsum pale bands sometimes with a few black hairs intermixed, T4–5 *either* uniformly orange-red *or* posteriorly with distinctly paler fringes……………***B. keriensis*** (part)

– Hair of the face entirely black, leg bases (mid and hind coxae) *either* with only one or two yellow hairs *or* without pale hairs, T3 often without pale hairs, thoracic dorsum pale bands without black hairs intermixed, T4–5 uniformly orange-red…………………………***B. separandus*** (part)

13. (7) Hair on the side of the thorax *either* black, *or if* white in part *then* the hair on the metasoma is short *and* T2 is black or anteriorly yellow *and* the thoracic dorsum has the pale posterior band broad and bright with few black hairs………………………………………14

– Hair on the side of the thorax predominantly *either* yellow *or* cream, *or if* black *or* white in part *then* the hair on the metasoma is long *and* T2 is usually with some white or cream (rarely yellow) *and* the thoracic dorsum has the pale posterior band often obscured by many black hairs………………16

14.(13) Hair of T3 posteriorly red……………………………………………………15
– Hair of T3 entirely black……………………………………***B. richardsiellus***

15.(14) *Either* large individuals (body length more than 18 mm: queens) with the hair on T2 usually with at least a few scattered yellow hairs intermixed in the anterior lateral corners, *or* small individuals (body length less than 18 mm: workers) with T2 predominantly yellow with only a very narrow posterior black fringe, thoracic dorsum with anterior and posterior pale bands bright grey with a minority of black hairs intermixed (western Himalaya eastwards to Nepal)…………………………………………***B. rufofasciatus***
– *Either* large individuals (body length more than 18 mm: queens) with the hair of T2 entirely black, at most with some grey hairs intermixed near the anterior median edge, *or* small individuals (body length less than 18 mm: workers) with T2 in the anterior half yellow and in much of the posterior half black, thoracic dorsum with anterior and posterior pale bands dull grey, especially posteriorly often obscure with many black hairs intermixed (eastern Himalaya westwards to Sikkim)……………………***B. prshewalskyi***

16.(13) Hair of the thoracic dorsum with the black band between the wing bases without any pale hair intermixed next to the wing bases, the hair of the face black……………………………………***B. ladakhensis***
– Hair of the thoracic dorsum with the black band between the wing bases with pale hair intermixed next to the wing bases, the hair of the face with black and pale hair intermixed………………………………………………17

17.(16) Hair of the thoracic dorsum with the dark band between the wing bases predominantly black with few pale hairs intermixed, the pale bands of the thorax and T1 *either* brownish-yellow, golden-yellow, *or* pale greenish-yellow (western Himalaya eastwards to Nepal)…………………***B. eurythorax***
– Hair of the thoracic dorsum with the dark band between the wing bases with nearly equal numbers of black and pale hairs intermixed, the pale bands of the thorax and T1 *either* cream *or* grey-white (eastern Himalaya westwards to Sikkim)……………………………***B. miniatus***

MALES: key to SPECIES

1. Hair of the thoracic dorsum uniformly *either* black *or* orange-brown *or* black with short grey hairs intermixed; genitalia with the penis-valve head with the recurved inner hook nearly as broad as long…………2
– Hair of the thoracic dorsum in part *either* yellow *or* white, often with a band of black between the wing bases; genitalia with the penis-valve head with the recurved inner hook *either* much longer than broad *or* the recurved part fused to the shaft (*B. ladakhensis*)…………3

2. (1) Hair of the thoracic dorsum uniformly orange-brown; genitalia with penis-valve head with the outer distal outer flange narrower than the length of the recurved inner hook……………***B. festivus***

– Hair of the thoracic dorsum *either* uniformly black *or* black with short grey hairs intermixed; genitalia with the penis-valve head with the outer distal outer flange broader than the length of the recurved inner hook...***B. eximius***

3. (1) Genitalia with the gonostylus posteriorly reduced and transverse, less than 0.5× as long as broad, the volsella projecting beyond the gonostylus by more than 2× the length of the gonostylus..............4

– Genitalia with the gonostylus rounded and disc-like, nearly 1× as long as broad, the volsella projecting beyond the gonostylus by less than 1× the length of the gonostylus.................9

4. (3) Hair of the thoracic dorsum in part white, not yellow.................................5

– Hair of the thoracic dorsum in part yellow, not white..............................7

5. (4) Hair of the thoracic dorsum entirely white........................***B. simillimus***

– Hair of the thoracic dorsum with a band of black at least intermixed between the wing bases...6

6. (5) Hair of T2 bright yellow without black hairs intermixed and with only a narrow band with few black hairs along the posterior margin...***B. rufofasciatus***

– Hair of T2 dull yellow with *either* at least a few black hairs intermixed *or* often with many black hairs intermixed and with a broad black band in the posterior quarter that often extends medially towards the anterior..***B. prshewalskyi***

7. (4) Gonostylus inner basal process narrow with the distal angle less than 45°; hair of T3 sometimes partly black but with at least the posterior margin fringed with yellow..........................8

– Gonostylus inner basal process broad with the distal angle nearly 90°; hair of T3 predominantly black................................***B. richardsiellus***

8. (7) Hair of T3–5 orange-red with at least a narrow band of yellow along the posterior margin, sometimes entirely yellow....................***B. eurythorax***

– Hair of T3–5 orange-red sometimes with a few black hairs along the posterior margin...***B. miniatus***

9. (3) Genitalia with the penis-valve head with the recurved inner hook extensively fused for 0.75 of its length with the adjacent penis-valve shaft; hair of T6–7 orange-red at the base and white at the tips.................***B. ladakhensis***

– Genitalia with the penis-valve head with the recurved inner hook not fused for less than 0.5 of its length with the adjacent penis-valve shaft; hair of T6–7 orange-red at the base and usually orange at the tips.................10

10. (9) Hair of the thoracic dorsum in part *either* white *or* cream...***B. separandus***

– Hair of the thoracic dorsum *either* in part yellow *or* entirely black.........11

11.(10) Eye distinctly enlarged relative to eye of a female bumblebee; hair of the face predominantly black with a few yellow hairs intermixed………………… ……………………………………………………………***B. semenovianus***

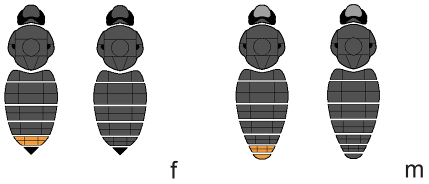
– Eye similar in relative size to eye of a female bumblebee; hair of the face predominantly yellow……………………………………………………………12

12.(11) Hair of T3 entirely black…………………………………………***B. tibeticus***

– Hair of T3 black with yellow hairs laterally……………………***B. keriensis***

16.9.1. *Bombus* (*Melanobombus*) *eximius* Smith, 1852

Bombus eximius Smith 1852a: 47. Holotype queen by monotypy NHMUK, examined.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020).

Identification. Very large body (queen length 23–30 mm includes the largest bumblebees in the world; worker 13–20 mm; male 16–19 mm) and medium length tongue. Similar in colour pattern to *B.* (*Pr.*) *flavescens*, *B.* (*Ag.*) *genalis* with bright orange legs. Females can be distinguished: (cf. *B. flavescens*) by the labrum in the middle having a very broad rectangular lamella; and (cf. *B. genalis*) by the mandible having two anterior teeth and a broadly rounded distal margin. Male genitalia are uniquely diagnostic: by the gonostylus being 'S'-shaped and the penis-valve head being turned inwards but with a very broad outer flat expansion or flange.

Habitat. Uncommon in the lower forests.

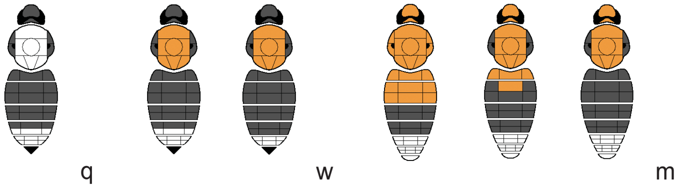
Distribution. Eastern Himalaya, southern China, and Southeast Asia (global distribution extent mapped by Williams *et al.* 2020).

16.9.2. *Bombus* (*Melanobombus*) *festivus* Smith, 1861

Bombus festivus Smith 1861: 152. Lectotype queen by designation of Tkalců (1974) NHMUK, examined.

Bombus atrocinctus Smith 1870: 193. Holotype male NHMUK, examined.

Bombus terminalis Smith 1870: 193. Lectotype worker by designation of Williams *et al.* (2009) NHMUK, examined.



Colour patterns of the hair of females (queens left, workers centre) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020). Size/caste-related colour variation in females involving white (queen) or brown (worker and male) hair on the thorax.

Identification. Large body (queen length 22–26 mm; worker 12–17 mm; male 13–16 mm) and medium length tongue. Similar in colour pattern to *B.* (*Pr.*) *bryorum*, *B.* (*Pr.*) *abnormis*. Females can be distinguished: (cf. *B. bryorum*) by having dark wings; and (cf. *B. abnormis*) by the the ocello-ocular area being extensively smooth and shining. Male genitalia are uniquely diagnostic: by the gonostylus being broadly triangular with its interior basal process extended posteriorly under and parallel to the inner margin.
Habitat. Common in forests across a broad range of elevations. Nest described from underground (Ito *et al.* 1984).

Distribution. Central and eastern Himalaya, eastern QTP, and southern China (global distribution extent mapped by Williams *et al.* 2020).

16.9.3. *Bombus* (*Melanobombus*) *simillimus* Smith, 1852

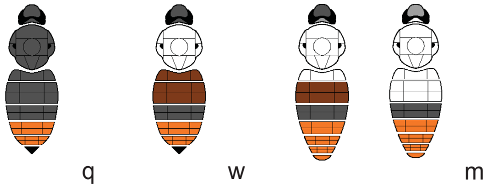
Bombus simillimis Smith 1852a: 48. Lectotype queen by designation of Williams (1991) NHMUK, examined.

Bremus oculatus Frison 1933: 335. Holotype male by original designation ZSC, examined.

Sibiricobombus tonsus Skorikov 1933a: 248. Lectotype queen by designation of Williams (1991) ZIN, examined.

Bombus oculatus var. [subsp.] *haemorrhous* Richards 1934: 87. Holotype worker by original designation NHMUK, examined.

Bombus (*Melanobombus*) *simillimus* Smith; Williams 1991: 99. Justified emendation.



Colour patterns of the hair of females (*queens left*, *workers centre*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020). Size/caste-related colour variation in females involving black (queen) or white (worker and male) hair on the thorax, and black (queens) or brown (workers and most males) on T2.

Identification. Large body (queen length 25–27 mm; worker 12–17 mm; male 16–18 mm) and medium length tongue. Worker similar in colour pattern to *B.* (*Bo.*) *tunicatus* (see also *B.* (*Sb.*) *longiceps*). Females can be distinguished: (cf. *B. tunicatus*, *B. longiceps*) by T1 being brown and the thorax white (worker) or by T1 and the thorax being black (queen). Males can be distinguished: (cf. *B. tunicatus*) by the eye being greatly enlarged relative to female bumblebees, by the penis-vale head being turned inwards in a sickle shape, and by the gonostylus being robust with the posterior edge concave and the inner corners right-angled; (cf. *B. longiceps*) by the antenna being short like a female bumblebee.

Habitat. Locally common in lower forests. Entrance to an underground nest seen in an earth bank.

Distribution. Endemic to the western Himalaya (global distribution extent mapped by Williams *et al.* 2020).

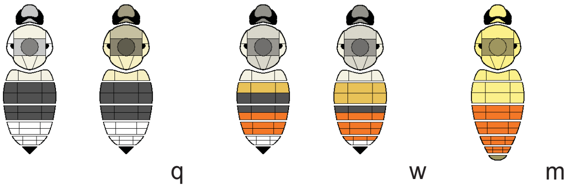
16.9.4. ***Bombus*** **(*Melanobombus*)** ***miniatus*** **Bingham, 1897**

Bombus flavothoracicus Bingham 1897: 552 (not of Hoffer 1889: 49 = *B. campestris* (Panzer)). Lectotype queen by designation of Tkalců (1974) NHMUK, examined.

Bombus miniatus Bingham 1897: 553. Holotype male by original designation NHMUK, examined.

Bombus stenothorax S.-F. Wang 1982: 439. Holotype queen by original designation IOZ, examined.

[*Bombus* (*Melanobombus*) *pyrosoma* Morawitz; Williams 1991: 101 (in part), misidentification].



Colour patterns of the hair of females (queens left, workers centre) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest , recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020). Size/caste-related colour variation in females involving black (queen) or yellow-brown (worker) hair on T2.

Identification. Large body (queen length 21–28 mm; worker 11–16 mm; male 17 mm) and medium length tongue. Closely similar in colour pattern to *B.* (*Ml.*) *eurythorax* and difficult to distinguish reliably from *B. eurythorax* without COI barcodes (see also *B.* (*Pr.*) *lepidus*). Females can be distinguished: (cf. *B. eurythorax*) by the many pale hairs being intermixed in the black band between the wing bases and T1 being cream or grey-white; (cf. *B. lepidus*) by T5 having some white hair. The males can be distinguished: (cf. *B. eurythorax*) by T3–6 lacking yellow posterior fringes. The male genitalia are closely similar to *B. eurythorax*.

Habitat. One of the most abundant species in the mid elevation and upper forests, occurring in smaller numbers in the subalpine zone.

Distribution. Eastern Himalaya likely to extend into Burma (global distribution extent mapped by Williams *et al.* 2020).

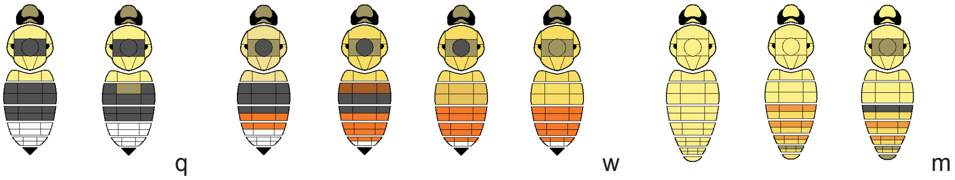
16.9.5. *Bombus* (*Melanobombus*) *eurythorax* Wang, 1982

Bombus eurythorax S.-F. Wang 1982: 439. Holotype queen by original designation IOZ, examined.

[*Bombus* (*Melanobombus*) *pyrosoma* Morawitz; Williams 1991: 101 (in part), misidentification; Saini *et al.* 2015: 116 misidentification].

[*Bombus* (*Melanobombus*) *miniatus* Morawitz; Williams *et al.* 2010: 125, misidentification; Saini *et al.* 2015: 96 misidentification].

[*Bombus* (*Mendacibombus*) *avinoviellus* (Skorikov); Saini *et al.* 2015: 240, fig. 403 (in part), misidentification].



Colour patterns of the hair of females (queens left, workers centre) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) upper forest, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020). Size/caste-related colour variation in females involving black (queen) or yellow-brown (worker) hair on T2.

Identification. Large body (queen length 21–24 mm; worker 10–16 mm; male 15–16 mm) and medium length tongue. Closely similar in colour pattern to *B.* (*Ml.*) *miniatus* and difficult to distinguish reliably without COI barcodes (see also *B.* (*Pr.*) *hilaris*). Females can be distinguished: (cf. *B. miniatus*) by the few pale hairs being intermixed in the black band between the wing bases and T1 being brownish, golden, or greenish yellow; (cf. *B. hilaris*) by T5 having some white hair. Males can be distinguished: (cf. *B. miniatus*) by T3–6 having yellow posterior fringes. Male genitalia are closely similar to *B. miniatus*.

Habitat. One of the most abundant species in the mid elevation and upper forests, occurring in smaller numbers in the subalpine zone. Entrance to an underground nest seen in an earth bank.

Distribution. Endemic to the western and central Himalaya (global distribution extent mapped by Williams *et al.* 2020). A record from Zanskar (as *B. miniatus*, Saini *et al.* 2015) needs to be confirmed.

16.9.6. *Bombus* (*Melanobombus*) *rufofasciatus* Smith, 1852

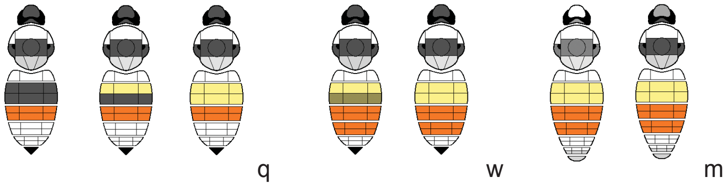
Bombus rufo-fasciatus Smith 1852a: 48. Lectotype queen by designation of Tkalců (1974) NHMUK, examined.

Bombus rufofasciatus var. [subsp.] *championi* Richards 1928a: 107. Holotype queen by original designation NHMUK, examined.

Bombus waterstoni Richards 1934: 88. Holotype queen by original designation NHMUK, examined.

[*Bombus* (*Pyrobombus*) *lemniscatus* Skorikov; Saini *et al.* 2015: 203, fig. 147 (in part), misidentification].

[*Bombus* (*Bombus*) *tunicatus* Smith; Saini *et al.* 2015: 242, fig. 416 (in part), misidentification].



Colour patterns of the hair of females (queens left, workers centre) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020). Size/caste-related colour variation in females involving black (queen) or yellow (worker and male) hair on T2, although queens from the west of the range in Pakistan often have T2 with at least some yellow.

Identification. Large body (queen length 20–23 mm; worker 10–15 mm; male 14–16 mm) and medium length tongue. Closely similar in colour pattern to *B.* (*Ml.*) *prshewalskyi* and difficult to distinguish reliably without COI barcodes (see also *B.* (*Ag.*) *kashmirensis*, *B.* (*Ag.*) *sikkimi*, *B.* (*Ml.*) *ladakhensis*, *B.* (*Pr.*) *B. hilaris*, *B.* (*Pr.*) *lemniscatus*, *B.* (*Pr.*) *biroi*, *B.* (*Md.*) *himalayanus*). Females can be distinguished: (cf. *B. prshewalskyi*) by the lighter colour pattern having fewer black hairs generally, but especially on the scutellum and on T2 posteriorly;

(cf. *B. kashmirensis*, *B. ladakhensis*) by the separation of red and white hair on different terga; (cf. *B. hilaris*, *B. lemniscatus*, *B. sikkimi*, *B. biroi*, *B. himalayanus*) by T5 having white hair. Males can be distinguished: (cf. *B. prshewalskyi*) by the gonostylus having the inner distal corner with two almost equally pronounced acute teeth; (cf. *B. kashmirensis*, *B. ladakhensis*, *B. hilaris*, *B. lemniscatus*, *B. sikkimi*, *B. biroi*, *B. himalayanus*) by the greatly enlarged eye relative to female bumblebees.

Habitat. One of the most abundant species in the alpine and subalpine flower-rich grasslands. Entrance to an underground nest seen among rocks.

Distribution. Endemic to the western and central Himalaya but absent from the western QTP (global distribution extent mapped by Williams *et al.* 2020).

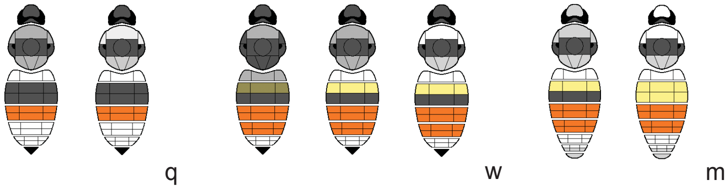
16.9.7. *Bombus* (*Melanobombus*) *prshewalskyi* Morawitz, 1880

Bombus Prshewalskyi Morawitz 1880: 342. Syntype worker (not queen) and male (Williams 1991) ZIN, not seen but identity not in doubt.

Bombus rufocinctus Morawitz 1880: 343 (not of Cresson 1863: 106 = *B. rufocinctus* Cresson). Syntype queen (Williams 1991) ZIN, not seen but identity not in doubt.

Bombus chinensis von Dalla Torre 1890 [June 25]: 139 (not of Morawitz 1890[April 30]: 352), replacement name for *rufocinctus* Morawitz 1880.

[*Bombus* (*Melanobombus*) *rufofasciatus* Smith; Williams 1991: 105 (in part), misidentification; Streinzer *et al.* 2019: table 1, misidentification].



Colour patterns of the hair of females (*queens left*, *workers centre*) *and males* (*right*).

Male genitalia from the dorsal view (*cf. Fig. 20*), *posterior towards the upper part of the image.*

Core habitat (*left: cf. Fig. 4*) *alpine and Trans-Himalayan alpine, recorded by province* (*right: cf. Fig. 3*) *from specimens* (*dark*), *likely interpolation* (*mid*), *or no records* (*light*).

Taxonomy and variation. Williams *et al.* (2020). Size/caste-related colour variation in females involving black (queen) or yellow (worker and male) hair on T2. Queens never have T2 yellow.

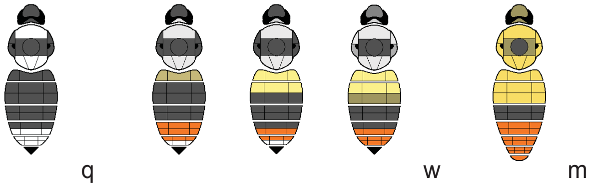
Identification. Large body (queen length 19–23 mm; worker 10–15 mm; male 13–17 mm) and medium length tongue. Closely similar in colour pattern to *B.* (*Ml.*) *rufofasciatus* (see also *B.* (*Ml.*) *richardsiellus*, *B.* (*Ml.*) *ladakhensis*, *B.* (*Ag.*) *kashmirensis*, *B.* (*Ag.*) *sikkimi*). Females can be distinguished: (cf. *B. rufofasciatus*) by the darker colour pattern having more black hairs generally, but especially on the scutellum and on T2 posteriorly; (cf. *B. richardsiellus*) by T1 being white; (cf. *B. kashmirensis*, *B. sikkimi*) by the mandible having just two anterior teeth; (cf. *B. ladakhensis*) by the lower side of the thorax being black. Males can be distinguished: (cf. *B. rufofasciatus*) by the gonostylus having the inner distal corner with the proximal tooth slightly shorter than the distal tooth; (cf. *B. richardsiellus*) by the thorax having the pale bands white; (cf. *B. kashmirensis*, *B. sikkimi*) by the mandible having just two teeth; (cf. *B. ladakhensis*) by the recurved part of the penis-valve headbeing not fused to the shaft.

Habitat. One of the most abundant species in the alpine and subalpine flower-rich grasslands extending into the Trans-Himalaya in the east.

Distribution. Eastern Himalaya and eastern QTP extending into northern Burma (global distribution extent mapped by Williams *et al.* 2020).

16.9.8. *Bombus* (*Melanobombus*) *richardsiellus* (Tkalců, 1968)

Pyrobombus richardsiellus Tkalců 1968a: 42. Holotype queen by original designation NHMUK, examined.



Colour patterns of the hair of females (queens left, workers centre) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image (left volsella, shown right, damaged).

Core habitat (left: cf. Fig. 4) subalpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020). Size/caste-related colour variation in females involving black (queen) or yellow (worker) hair on T1–2.

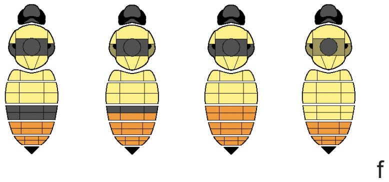
Identification. Large body (queen length 20–21 mm; worker 10–15 mm; male 12 mm) and medium length tongue. Similar in colour pattern to *B.* (*Ml.*) *prshewalskyi* (see also *B.* (*Pr.*) *lemniscatus*, *B.* (*Pr.*) *lepidus*). Females can be distinguished: (cf. *B. prshewalskyi*, *B. lemniscatus*, *B. lepidus*) by T1 being black or yellow. Males can be distinguished: (cf. *B. prshewalskyi*, *B. lemniscatus*, *B. lepidus*) by the gonostylus having the inner distal corner with a single-pointed spine.

Habitat. Rare in subalpine flower-rich grasslands.

Distribution. Likely to occur in very restricted parts of the far eastern Himalaya (global distribution mapped by Williams *et al.* 2020) because it is known from a small part of the border area just inside the eastern QTP and northern Burma.

16.9.9. ***Bombus* (*Melanobombus*) *tanguticus* Morawitz, 1887**

Bombus tanguticus Morawitz 1887: 200. Lectotype queen by designation of Williams (2018) ZIN, examined.



Colour patterns of the hair of females (males currently unknown).

Male genitalia image unavailable.

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams (2018), Williams *et al.* (2020). The male remains unknown.

Identification. Large body (queen length 22–28 mm; worker 12–13 mm) and medium length tongue. Most similar in to some *B.* (*Sb.*) *semenovi* (see also *B.* (*Sb.*) *longiceps*, *B.* (*Ml.*) *tibeticus*, *B.* (*Ml.*) *keriensis*, *B.* (*Ml.*) *separandus*). Females can be distinguished: (cf. *B. semenovi*, *B. longiceps*, *B. tibeticus*, *B. keriensis*, *B. separandus*) by the hind basitarsus being long and narrow, nearly 4× longer than its greatest breadth, the labrum having the median furrow unusually narrow, 0.2× the breadth of the labrum.

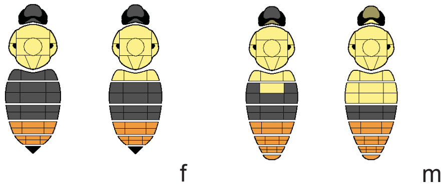
Habitat. Rare in high alpine flower-rich semi-desert grassland. One of the highest recorded bumblebee species in the world (Williams 2018).

Distribution. Trans Himalaya in Ladakh, where it is known from a single specimen (global distribution mapped by Williams *et al.* 2020) extending broadly but patchily across the central QTP.

16.9.10. *Bombus* (*Melanobombus*) *semenovianus* (Skorikov, 1914)

Lapidariobombus semenovianus Skorikov 1914a: 127. Syntype queen (Williams 1991) ZIN, examined.

Bombus lapidarius subsp*. problematicus* Bischoff 1935: 255. Holotype worker by monotypy ZMHB, examined.



Colour patterns of the hair of females (*left*) *and males* (*right*).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020).

Identification. Medium size body (queen length 17–21 mm; worker 11–15 mm; male 12–16 mm) and medium length tongue. Most similar to some *B.* (*Md.*) *marussinus*, *B.* (*Md.*) *avinoviellus* (see also *B.* (*Sb.*) *longiceps*, *B.* (*Pr.*) *subtypicus* and *B.* (*Pr.*) *kotzschi*). Females can be distinguished: (cf. *B. marussinus*, *B. avinoviellus*) by the labrum having a median furrow; (cf. *B. longiceps*) by the oculo-malar area being only very slightly longer than the basal breadth of the mandible; and (cf. *B. subtypicus*, *B. kotzschi*) by the hind basitarsus having dense pale short feathered hair on the outer surface. The male is distinctive within *Melanobombus* for its combination of: eyes being slightly enlarged with the thoracic dorsum being uniformly yellow. Males can be distinguished: (cf. *B. marussinus*, *B. avinoviellus*, *B. longiceps*, *B. subtypicus*, *B. kotzschi*) by the slightly enlarged eye relative to female bumblebees.

Habitat. Uncommon in alpine and subalpine flower-rich semi-desert grassland.

Distribution. Western Trans-Himalaya, Hindu Kush (global distribution extent mapped by Williams *et al.* 2016).

16.9.11. *Bombus* (*Melanobombus*) *ladakhensis* Richards, 1928

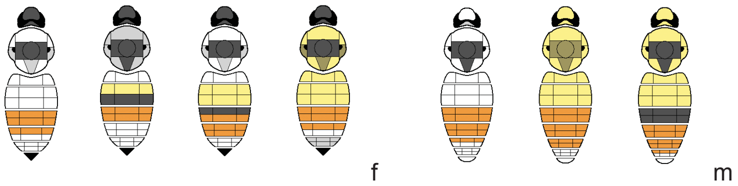
Bombus rufofasciatus var. [not subsp.] *ladakhensis* Richards 1928b: 336, but not infrasubspecific after Tkalců (1974) (ICZN 1999: Art. 45.6.4.1). Holotype queen (not worker) by monotypy NHMUK, examined.

Bombus rufofasciatus var. [not subsp.] *phariensis* Richards 1930: 642, but not infrasubspecific after Tkalců (1974) (ICZN 1999: Art. 45.6.4.1). Holotype queen by original designation NHMUK, examined.

Bombus variopictus Skorikov 1933a: 248. Syntype queen ZIN, examined.

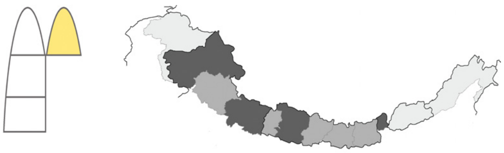
Bombus variopictus subsp. *bianchii* Skorikov 1933a: 248. Syntype queen and worker ZIN, examined.

Bombus reticulatus Bischoff 1936: 7. Lectotype queen by designation of Tkalců (1974), not seen but identity not in doubt.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.



Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020). The species includes both white-banded (eastern *e.g.*, Nepal) and yellow-banded (western *e.g.*, Zanskar) colour patterns.

Identification. Medium size body (queen length 16–19 mm; worker 9–13 mm; male 11–13 mm) and medium length tongue. Most similar in to some *B.* (*Ag.*) *kashmirensis*, *B.* (*Ml.*) *rufofasciatus* and *B.* (*Ml.*) *prshewalskyi* (see also *B.* (*Pr.*) *lemniscatus*, *B.* (*Pr.*) *lepidus*). Females can be distinguished: (cf. *B. rufofasciatus*, *B. prshewalskyi*, *B. lemniscatus*, *B. lepidus*) by their combination of T5 being white and the side of the thorax having yellow or white extending ventrally to the leg bases. Male genitalia are uniquely diagnostic: by the penis-valve having the recurved head fused to the shaft for most of its length; (cf. *B. rufofasciatus*, *B. prshewalskyi*) by the eye being not enlarged relative to female bumblebees.

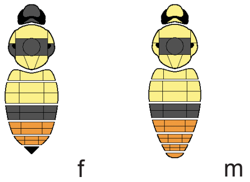
Habitat. Uncommon in high alpine flower-rich grassland.

Distribution. Trans Himalaya in Ladakh and extending broadly across the QTP (global distribution extent mapped by Williams *et al.* 2020).

16.9.12. ***Bombus*** **(*Melanobombus*)** ***tibeticus*** **Williams, 2020**

Bombus tibeticus Williams in Williams *et al.* 2020: 83. Holotype worker by original designation IOZ, examined.

[*Bombus* (*Melanobombus*) *keriensis* Morawitz; Williams 1991: 96 (in part), misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020).

Identification. Medium size body (queen length 17–20 mm; worker 10–14 mm; male 12–15 mm) and medium length tongue. Most similar in to *B.* (*Ml.*) *keriensis*, *B.* (*Ml.*) *separandus*, and *B.* (*Ml.*) *tanguticus* (see also *B.* (*Sb.*) *longiceps*, *B.* (*Sb.*) *semenovi*). Females can be distinguished: (cf. *B. tanguticus*) by the hind basitarsus being short and broad, 3× longer than its greatest breadth; (cf. *B. keriensis*, *B. separandus*) by the clypeus in its central area having scattered large, medium, and small punctures; (cf. *B. longiceps*, *B. semenovi*) by the oculo-malar distance being nearly equal to the breadth of the mandible at its base, and the hind basitarsus proximal posterior process on its outer surface being without a dense brush of feathered hair. Male genitalia are closely similar to *B. keriensis* and *B. separandus*.

Habitat. Locally common in high alpine flower-rich semi-desert grassland. One of the highest recorded bumblebee species in the world (under the name *B. keriensis*, Williams 2018).

Distribution. Likely to occur in parts of the eastern Himalaya (global distribution mapped by Williams *et al.* 2020) because it is known from the border area just inside the eastern QTP, where it is widespread (global distribution extent mapped by Williams *et al.* 2020).

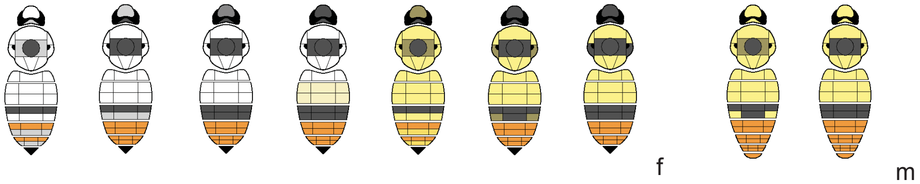
16.9.13. *Bombus* (*Melanobombus*) *keriensis* Morawitz, 1887

Bombus keriensis Morawitz 1887: 199. Lectotype queen by designation of Williams *et al.* (2020) ZIN, examined.

Lapidariobombus separandus subsp*. meridialis* Skorikov 1914a: 127. Holotype queen by monotypy, not seen but identity not in doubt.

Bombus trilineatus S.-F. Wang 1982: 441. Holotype queen by original designation IOZ, examined.

Pyrobombus keriensis subsp*. karakorumensis* Tkalců 1989: 57. Holotype queen by original designation ZSM, examined.



Colour patterns of the hair of females (*left*) *and males* (*right*), *variation shown* (*approximately*) *from west to east.*

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) alpine and Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020). The species includes both white-banded (outer humid zone of the Great Himalaya) and yellow-banded (outer humid zone and semi-arid Trans Himalaya) colour patterns.

Identification. Medium size body (queen length 17–21 mm; worker 9–14 mm; male 11–15 mm) and medium length tongue. Without COI barcodes this species is difficult to distinguish reliably from *B.* (*Ml.*) *separandus.* Most similar in to *B.* (*Ml.*) *tibeticus*, *B.* (*Ml.*) *separandus*, and *B.* (*Ml.*) *tanguticus* (see also *B.* (*Sb.*) *longiceps*, *B.* (*Sb.*) *semenovi*). Females can be distinguished: (cf. *B. tanguticus*) by the hind basitarsus being short and broad, 3x longer than its greatest breadth; (cf. *B. tibeticus*) by the clypeus in its central area having only scattered small punctures; (cf. *B. separandus*) by the face, leg bases, and T3 laterally usually having at least a few pale hairs; (cf. *B. longiceps*, *B. semenovi*) by the oculo-malar distance being nearly equal to the breadth of the mandible at its base, and the hind basitarsus proximal posterior process on its outer surface being without a dense brush of feathered hair. Male genitalia are closely similar to *B. tibeticus* and *B. separandus*.

Habitat. High alpine flower-rich grassland.

Distribution. Western Himalaya (uncommon) and Trans Himalaya (uncommon) extending into Afghanistan (global distribution extent mapped by Williams *et al.* 2020).

16.9.14. ***Bombus* (*Melanobombus*) *separandus* Vogt, 1909**

Bombus lapidarius form [subsp.] *separandus* Vogt 1909: 61. Lectotype queen by designation of Williams (1991) ZIN, examined.

Bombus lapidarius form [subsp.] *kohli* Vogt 1909: 61 (not of Cockerell 1906: 75 = *B. morio* (Swederus)). Syntype worker (Williams 1991) RMNH, examined.

Bombus kozlovi Skorikov 1910b: 413, replacement name for *kohli* Vogt 1909: 61.

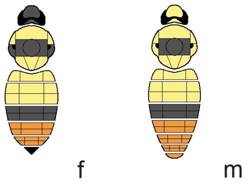
Bombus lapidarius var. [subsp.] *tenellus* Friese 1913: 86. Syntype females and male (Williams 1991) ZMHB, not seen but identity not in doubt.

Bombus tenellus var. [not subsp.] *alpivagus* Richards 1930: 639, but not infrasubspecific after Reinig 1935: 333 (ICZN 1999: Art. 45.6.4.1). Holotype queen by original designation NHMUK, examined.

Bombus keriensis f.g. [subsp.] *richardsi* Reinig 1935: 341 (not of Frison 1930: 6 = *B. rufipes* Lepeletier). Holotype queen by original designation RMNH, examined.

Bombus tenellus subsp. *tibetensis* S.-F. Wang 1982: 439, replacement name for *richardsi* Reinig, 1935: 341.

[*Bombus* (*Melanobombus*) *keriensis* Morawitz; Williams 1991: 96 (in part), misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Williams *et al.* (2020).

Identification. Medium size body (queen length 17–20 mm; worker 9–14 mm; male 10–15 mm) and medium length tongue. Without COI barcodes this species is difficult to distinguish reliably from *B.* (*Ml.*) *keriensis.* Most similar to *B.* (*Ml.*) *tibeticus*, *B.* (*Ml.*) *keriensis*, and *B.* (*Ml.*) *tanguticus* (see also *B.* (*Sb.*) *longiceps*, *B.* (*Sb.*) *semenovi*). Females can be distinguished: (cf. *B. tanguticus*) by the hind basitarsus being short and broad, 3x longer than its greatest breadth; (cf. *B. tibeticus*) by the clypeus in its central area having only scattered small punctures; (cf. *B. keriensis*) by the face, leg bases, and T3 laterally being without pale hairs; (cf. *B. longiceps*, *B. semenovi*) by the oculo-malar distance being nearly equal to the breadth of the mandible at its base, the hind basitarsus having the proximal posterior process on its outer surface without a dense brush of feathered hair. Male genitalia are closely similar to *B. keriensis* and *B. tibeticus*.

Habitat. Common in high alpine flower-rich semi-desert grassland.

Distribution. Western Trans Himalaya in Ladakh, extending into Central Asia and Mongolia (global distribution extent mapped by Williams *et al.* 2020).

16.10. Subgenus *SIBIRICOBOMBUS*

These bumblebees are associated with high alpine grasslands, grasslands and semi-deserts. Long tongue-length bumblebees visiting deep flowers. Nests are underground or above ground in cavities. Older larvae are likely to be reared separately, as non-pocket makers, although this has not been recorded. Males of most species have enlarged eyes relative to the females and perch before racing after potential mates while avoiding contact with other males, so that they are not truly territorial (Williams 1991).

Species of *Sibiricobombus* have often been mistaken for species of *Subterraneobombus*.

FEMALES: key to SPECIES

1. Hair of T3 entirely yellow……………………………………………***B. sibiricus***
– Hair of T3 *either* black *or* orange *or* both……………………………………………2

2. (1) Antennal A3 length 4× greatest breadth; hair of thoracic dorsum *either* yellow *or* white, *either* with *or* without a black band between the wing bases……………………………………***B. longiceps***
– Antennal A3 length 2× greatest breadth; hair of the thoracic dorsum yellow with a black band between the wing bases………***B. semenovi***

MALES: key to SPECIES

1. Hair of T3 entirely yellow……………………………………………***B. sibiricus***
– Hair of T3 *either* black *or* orange……………………………………………2

2. (1) Eye greatly enlarged relative to eye of a female bumblebee, from the dorsal view the eye separated from the lateral ocellus by 1x ocellar breadth; volsella with the outer terminal corner shorter than the inner terminal curved process………………………***B. longiceps***
– Eye not enlarged relative to eye of a female bumblebee, from the dorsal view the eye separated from the lateral ocellus by 3x the ocellar breadth; volsella with the outer terminal pointed corner projecting further than the inner terminal rounded corner……………***B. semenovi***

16.10.1. *Bombus* (*Sibiricobombus*) *semenovi* Morawitz, 1887

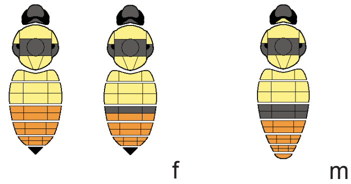
Bombus Semenovi Morawitz 1887: 198. Syntype queen (Williams 1991) ZIN, examined.

Bombus (*Sibiricobombus*) *xionglaris* S.-F. Wang 1982: 432. Holotype male by original designation IOZ, examined.

Bombus (*Subterraneobombus*) *duanjiaoris* S.-F. Wang 1982: 444. Holotype worker by original designation IOZ, examined.

Bombus (*Subterraneobombus*) *zhadaensis* S.-F. Wang 1982: 444. Holotype queen by original designation IOZ, examined.

[*Bombus* (*Sibiricobombus*) *oberti* Morawitz; Williams 1991: 92 (in part), misidentification; Saini *et al.* 2015: 105, misidentification].



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams (1991), although analyses of COI barcodes and of the morphology of the male volsella (with the inner distal corner projecting posteriorly almost as far as the outer distal corner) now support this species as separate from the Central Asian *B.* (*Sb.*) *oberti* Morawitz (which has the volsella with an even shorter and more broadly rounded inner distal corner) (Williams *et al.* 2015).

Identification. Large body (queen length 22–24 mm; worker 13–16 mm; male 16 mm) and long tongue. Most similar to *B.* (*Sb.*) *longiceps*, *B.* (*Ml.*) *tanguticus* (see also *B.* (*Ml.*) *tibeticus*, *B.* (*Ml.*) *keriensis*, and *B.* (*Ml.*) *separandus*). Females can be distinguished: (cf. *B. longiceps*) by large size and the A3 length being only

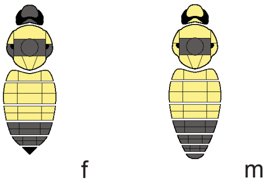
2× greatest breadth; (cf. *B. tanguticus*) by the hind basitarsus being short and broad, 3× longer than its greatest breadth, the labral furrow broad; (cf. *B. tibeticus*, *B. keriensis*, *B. separandus*) by the oculo-malar area having many scattered fine punctures and being much longer than the basal breadth of the mandible, and by the proximal posterior process of the hind basitarsus having many branched hairs on its outer surface. Males can be distinguished: (cf. *B. longiceps*) by the unenlarged eye relative to female bumblebees; (cf. *B. tibeticus*, *B. keriensis*, *B. separandus*) by the volsella having the process on the inner terminal corner short and very broadly rounded, not projecting distally as far as the pointed outer distal corner.

Habitat. Uncommon in high alpine flower-rich semi-desert grassland.

Distribution. Trans Himalaya in Zanskar extending into the central QTP (global distribution mapped by Williams 1991).

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

Apis ſibirica Fabricius 1781: 478. Syntype female (small queen?) NHMUK, examined.
Bombus flaviventris Friese 1905: 514. Syntype queen and worker ZMHB, examined.
Bombus flaviventris subsp. *ochrobasis* Richards 1930: 655. Holotype queen by original designation NHMUK, examined.



Colour patterns of the hair of females (left) and males (right).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams (1998a), although analysis of COI barcodes now confirms that the black-tailed taxon *flaviventris* is part of a single species *B. sibiricus* that includes the red-tailed colour patterns in North China and Mongolia (Williams *et al.* 2015).

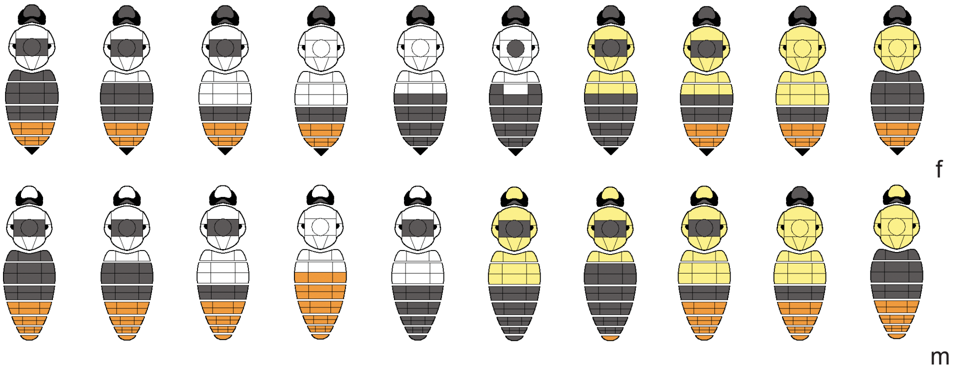
Identification. Large body (queen length 18–20 mm; worker 12–16 mm; male 15–16 mm) and long tongue. Most similar to *B.* (*Sb.*) *longiceps* (see also *B.* (*St.*) *difficillimus*). Females can be distinguished: (cf. *B. longiceps*) by T3 being entirely yellow; (cf. *B. difficillimus*) by T3 being yellow, the clypeus having many small punctures. Males can be distinguished: (cf. *B. longiceps*) by the volsella having the inner distal curved hook broad but projecting distally beyond the outer distal corner, and by the eye being not greatly enlarged relative to female bumblebees.

Habitat. Uncommon in high alpine flower-rich semi-desert grassland.

Distribution. Likely to occur in parts of the eastern Himalaya (global distribution mapped by Williams *et al.* 2020) because it is known from the border area just inside the eastern QTP where it is widespread, extending into northern China and Mongolia.

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

Bombus longiceps Smith 1878b: 8. Syntype worker and male ZSC, examined.
Sibiricobombus flavodorsalis Skorikov 1933a: 248. Syntype queens ZIN, not seen but identity not in doubt.
Sibiricobombus oshanini Skorikov 1933a: 248. Syntype queens and male ZIN, not seen but identity not in doubt.
[*Bombus* (*Sibiricobombus*) *asiaticus* Morawitz; Williams 1991: 87 (in part), misidentification; Burger *et al.* 2009: 456, misidentification; Williams *et al.* 2010: 125, misidentification; Saini *et al.* 2015: 19, misidentification; Jaffar *et al.* 2019: 983, misidentification].
[*Bombus* (*Pyrobombus*) *lepidus* Skorikov; Saini *et al.* 2015 :203, fig. 152 (in part), misidentification; Jaffar *et al.* 2019: 983, fig. 11 (in part), misidentification].
[*Bombus* (*Pyrobombus*) *semenovianus* (Skorikov); Saini *et al.* 2015: 214, fig. 235 (in part), misidentification; Jaffar *et al.* 2019: 983 fig. 22 (in part), misidentification].
[*Bombus* (*Pyrobombus*) *subtypicus* (Skorikov); Saini *et al.* 2015: 217, fig. 257 (in part), misidentification].



Colour patterns of the hair of females (above) and males (below).

Male genitalia from the dorsal view (cf. Fig. 20), posterior towards the upper part of the image.

Core habitat (left: cf. Fig. 4) lower and upper forest, alpine and Trans-Himalayan alpine, recorded by province (right: cf. Fig. 3) from specimens (dark), likely interpolation (mid), or no records (light).

Taxonomy and variation. Most recently by Williams (1991), although recent species-coalescent (PTP) analysis of a MrBayes phylogenetic tree for COI barcodes and morphological differences including the female especially weakly punctured clypeus and ocello-ocular area with an especially large unpunctured area now support *B. longiceps* as a species separate from the other closely similar species in this *asiaticus*-complex: *B.* (*Sb.*) *miniatocaudatus* Vogt (Mongolia, Russia); *B.* (*Sb.*) *falsificus* Richards (Qinghai and Xizang); and *B.* (*Sb.*) *asiaticus* Morawitz *s.str.* (Central Asia). The Himalayan species *B. longiceps* includes both white-banded (outer humid forest zone of the Great Himalaya) and yellow-unbanded (western semi-arid Trans Himalaya) colour patterns.

Identification. Medium size body (queen length 17–20 mm; worker 12–14 mm; male 14–16 mm) and long tongue. Most similar to *B.* (*Sb.*) *sibiricus* and *B.* (*Sb.*) *semenovi* (see also *B.* (*Ml.*) *semenovianus*, *B.* (*Ml.*) *tibeticus*, *B.* (*Ml.*) *keriensis*, *B.* (*Ml.*) *separandus*, *B.* (*Md.*) *marussinus B.* (*St.*) *difficillimus*). Females can be distinguished: (cf. *B. sibiricus*) by T3 being black; (cf. *B. semenovi*, *B. marussinus*) by A3 length being 4× its greatest breadth; (cf. *B. semenovianus*, *B. tibeticus B. keriensis*, *B. separandus*) by the oculo-malar distance being much greater than the breadth of the mandible at its base and this area having many small punctures; (cf. *B. difficillimus*) by the clypeus having many small punctures. Males can be distinguished: (cf. *B. semenovi*) by the volsella being elongated and strongly narrowed distally beyond the gonostylus with the inner distal hook being long, curved and narrow, projecting distally beyond the rounded outer corner; and (cf. *B. sibiricus*, *B. semenovi*, *B. semenovianus*, *B. tibeticus*, *B. keriensis*, *B. separandus*, *B. difficillimus*) by the eye being greatly enlarged relative to female bumblebees.

Habitat. One of the most abundant and widespread species, especially in open areas in the upper forest zone and in the Trans Himalaya including semi-desert grassland. Entrance to an underground nest seen among rocks.

Distribution. Western and central Himalaya and Trans Himalaya in Zanskar and Ladakh, extending into Afghanistan and the western QTP.

16.11. Summary of species distribution records

Table 3. Table summarising the occurrence of bumblebee species in areas of the Himalaya (Fig. 3) and in north-east Indian mountain states. Records (‘1’) are based on specimens examined in collections and reliable literature records. Expected occurrences (‘?’) are interpolations based on the presence of suitable habitat and recorded occurrence in neighbouring areas (including the QTP: Williams *et al.* 2015).

No.	**Subgenus**	**Species**	**Area**													**Range (recorded)**
			Pakistan	Kashmir	Himachal Pradesh	Uttarakhand	Nepal	Sikkim	West Bengal	Bhutan	Arunachal Pradesh	Nagaland	Manipur	Mizoram	Meghalaya	
1.1	*Md*	*waltoni*		1	?	?	1	?		?	?					2
2		*marussinus*	1													1
3		*avinoviellus*	1	1	1	1	1									5
4		*himalayanus*	1	1	1											3
2.1	*St*	*personatus*	1	1	1	?	1	1		?	?					5
2		*melanurus*	1	1	1	1	1	1								6
3		*difficillimus*	1	1	?	?	?	1		?	?					3
3.1	*Mg*	*montivagus*			1	?	?	?	?	?	1	?	1	?	1	4
2		*albopleuralis*	1	1	1	1	1	1	1	1	1					9
4.1	*Or*	*funerarius*				1	1	1	1	1	1					6
2		*haemorrhoidalis*	1	1	1	1	1	1	1	1	1	?	?	1	1	11
5.1	*Ps*	*cornutus*			1	1	1	?		1	1					5
2		*turneri*					1	?	?	?	1					2
3		*novus*	1	1	1	?	1	?		?	1					5
4		*branickii*	1	1	1	?	1	1								5
5		*ferganicus*	1	1	1											3
6		*morawitzianus*	1	1												2
7		*bohemicus*	1													1
8		*skorikovi*	1	1	?	?	1	1		?	?					4
6.1	*Pr*	*subtypicus*	1	1												2
2		*bryorum*	1	1	?	?	1	1		1	1					6
3		*abnormis*					1	1		?	1					3
4		*mirus*					1	1		?	1					3
5		*lemniscatus*		1	?	1	1	1		1	1					6
6		*hilaris*	1	1												2
7		*lepidus*			1	?	1	?		?	?					2
8		*infirmus*						1		1	?					2

No.	**Subgenus**	**Species**	**Area**													**Range** **(recorded)**
			Pakistan	Kashmir	Himachal Pradesh	Uttarakhand	Nepal	Sikkim	West Bengal	Bhutan	Arunachal Pradesh	Nagaland	Manipur	Mizoram	Meghalaya	
9		*pressus*				1	1	1	1	1	1					6
10		*parthenius*			1	1	1	1	1	1	1					7
11		*luteipes*					1	1	1	1	1				1	6
12		*biroi*	1	1	1											3
13		*kotzschi*	1	1												2
14		*rotundiceps*			1	1	1	1	1	?	?				1	6
15		*flavescens*				1	1	1	1	1	1					6
7.1	*Bo*	*tunicatus*	1	1	1	1	1	1	1							7
2		*longipennis*						1		1	?					2
3		*reinigi*		1	1	1	1									4
4		*jacobsoni*		1												1
5		*cryptarum*	1													1
8.1	*Ag*	*kashmirensis*	1	1	1	1	1	1								6
2		*rainai*	1	1												2
3		*sikkimi*			1	1	1	1		?	1					5
4		*genalis*						1	1	?	1				1	4
5		*breviceps*		1	1	1	1	1	1	1	1				1	9
6		*grahami*					1	1	?	1	1				1	5
9.1	*Ml*	*eximius*					1	1	1	1	1				1	6
2		*festivus*			1	1	1	1	1	1	1					7
3		*simillimus*	1	1	1	1										4
4		*miniatus*						1		1	1					3
5		*eurythorax*	1	1	1	1	1									5
6		*rufofasciatus*	1	1	1	1	1									5
7		*prshewalskyi*						1		?	1					2
8		*richardsiellus*									?					0
9		*tanguticus*		1			?	1		?						2
10		*semenovianus*	1	1												2
11		*ladakhensis*		1	?	1	1	1								4
12		*tibeticus*					?	?		?						0
13		*keriensis*	1	1	1											3
14		*separandus*	1	1												2
10.1	*Sb*	*semenovi*		1												1
2		*sibiricus*					?	?								0
3		*longiceps*	1	1	1	1	1	1								6
		Species richness (recorded)	30	34	26	22	33	32	13	17	23	0	1	1	8	

17. References

Square brackets indicate insertions, especially for corrected publication dates and translations of titles.

ALFORD D.V. 1975. *Bumblebees*. Davis-Poynter, London. xii+352 pages.

ASHMEAD W.H. 1905. Additions to the recorded Hymenopterous fauna of the Philippine Islands, with descriptions of new species. *Proceedings of the United States National Museum* 28: 957-971.

BHUSAL D.R. 2020. Insect Pollinators, Threats For Survival and Ecosystem Service: An Outlook From Hindu-Kush Himalaya Region. *In:* Regmi G. & Huettmann F. (eds), *Hindu Kush-Himalaya Watersheds Downhill: Landscape Ecology and Conservation Perspectives*. Springer, Cham, pp. 565-576. https://doi.org/10.1007/978-3-030-36275-1_27

BHUSAL D.R., GHIMIRE K.C., DULAI S., BANIYA P. & THAKURI S. 2019. Spatial relation of bumblebees (Hymenoptera-Apidae) with host-plant and their conservation issues: an outlook from urban ecosystem of Kathmandu Valley, Nepal. *European Journal of Ecology* 5: 1-7. https://doi.org/10.2478/eje-2019-0008

BINGHAM C.T. 1897. *The Fauna of British India*, *including Ceylon and Burma. Hymenoptera. Vol. I. Wasps and Bees*. Taylor & Francis, London. xxix+579 pages.

BISCHOFF H. 1935. Genus BOMBUS (Apidae, Hymen.). *In: Wissenschaftliche Ergebnisse der niederländischen Expedition in den Karakorum und die angrenzenden Gebiete in den Jahren 1922*, *1925 und 1929/30*. C. Visser & J. Visser-Hooft, Leipzig, pp. 255-256.

BISCHOFF H. 1936. Schwedisch-chinesische wissenschaftliche Expedition nach den nordwestlichen Provinzen Chinas, unter Leitung von Dr. Sven Hedin und Prof. Sü Ping-chang. Insekten gesammelt vom schwedischen Arzt der Expedition Dr. David Hummel 1927-1930. 56. Hymenoptera. 10. Bombinae. *Arkiv för zoologi* 27A: 1-27.

BISCHOFF H. & HEDICKE H. 1931. Über einige von Illiger beschriebene Apiden (Hym.). *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* 1930: 385-392.

BURGER F., CREUTZBURG F., HARTMANN J. & HARTMANN M. 2009. Die Hummeln von Nepal (Insecta: Hymenoptera: Apidae: *Bombus*). *In:* Hartmann M. & Weipert J. (eds), *Biodiversität und Naturausstattung im Himalaya III*. Verein der Freunde und Förderer des Naturkundemuseums Erfurt e.V., Erfurt, pp. 455-462.

CAMERON S.A., HINES H.M. & WILLIAMS P.H. 2007. A comprehensive phylogeny of the bumble bees (*Bombus*). *Biological Journal of the Linnean Society* 91: 161-188.

CAMERON S.A. & SADD B.M. 2020. Global trends in bumble bee health. *Annual Review of Entomology* 65: 209-232.

COCKERELL T.D.A. 1905. Descriptions and records of bees. - I. *Annals and Magazine of Natural History* (7) 16: 216-225.

Cockerell T.D.A. 1906. Descriptions and records of bees. - XII. *Annals and Magazine of Natural History* (*7*) 18: 69-75.

Cockerell T.D.A. 1909. Descriptions and records of bees. - XXIII. *Annals and Magazine of Natural History* (*8*) 4: 393-404.

Cockerell T.D.A. 1910. Some bees from high altitudes in the Himalaya mountains. *Entomologist* 43: 238-239.

Cockerell T.D.A. 1917. New social bees. *Psyche* 24: 120-128.

Cockerell T.D.A. 1922. Bees in the collection of the United States National Museum. -4. *Proceedings of the United States National Museum* 60: 1-20.

Cresson E.T. 1863. List of the North American species of *Bombus* and *Apathus*. *Proceedings of the Entomological Society of Philadelphia* 2: 83-116.

Dar G.H., Khuroo A.A., Reddy C.S. & Malik A.H. 2012. Impediment to taxonomy and its impact on biodiversity science: an Indian perspective. *Proceedings of the National Academy of Sciences*, *India Section B: Biological Sciences* 82: 235-240. https://doi.org/10.1007/s40011-012-0031-3

de Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* 56: 879-886. https://doi.org/10.1080/10635150701701083

Dias B.S.F., Raw A. & Imperatri-Fonseca V.L. 1999. International Pollinators Initiative: the São Paulo declaration on pollinators. Report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees. Brazilian Ministry of the Environment, Brasília.

Eberhard W.G. 1985. *Sexual Selection and Animal Genitalia*, London. xvii+ 244 pages.

Estoup A., Solignac M., Cornuet J.-M., Goudet J. & Scholl A. 1996. Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. *Molecular Ecology* 5: 19-31.

Eversmann E. 1846. Hymenopterorum Rossicorum species novæ vel parum cognitæ, descriptæ et ex parte depictæ. *Byulleten*' *Moskovskogo obshchestva ispytatelei prirody* 19: 436-443.

Fabricius J.C. 1775. *Systema entomologiae*, *sistens insectorum classes*, *ordines*, *genera*, *species*, *adiectis synonymis*, *locis*, *descriptionibus*, *observationibus*. Flensburgi and Lipsiae. 32+832 pages.

Fabricius J.C. 1781. *Species insectorum exhibentes eorum differentias specificas*, *synonyma auctorum*, *loca natalia*, *metamorphosin adiectis observationibus*, *descriptionibus* (Vol. 1), Hamburg. viii+552 pages.

Favre A., Paeckert M., Pauls S.U., Jaehnig S.C., Uhl D., Michalak I. & Muellner-Riehl A.N. 2015. The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. *Biological Reviews* 90: 236-253.

Fisher R.M. 1987. Queen-worker conflict and social parasitism in bumble bees (Hymenoptera: Apidae). *Animal Behaviour* 35: 1026-1036.

Friese H. 1904. Beiträge zur Bienenfauna von Chile, Peru und Ecuador. *Zeitschrift für Systematische Hymenopterologie und Dipterologie* 4: 180-188.

Friese H. 1905. Neue oder wenig bekannte Hummeln des russischen Reiches (Hymenoptera). *Ezhegodnik Zoologicheskago muzeya* 9: 507-523.

Friese H. 1909. Neue Varietäten von *Bombus* (Hym.). *Deutsche Entomologische Zeitschrift* 1909: 673-676.

Friese H. 1913. Über einige neue Apiden (Hym.). *Archiv für Naturgeschichte* 78: 85-89.

Friese H. 1916. Über einige neue Hummelformen. *Bombus* 1916: 107-110.

Friese H. 1918. Über Hummelformen aus dem Himalaja. *Deutsche Entomologische Zeitschrift* 1918: 81-86.

Frison T.H. 1930. The bumblebees of Java, Sumatra and Borneo (Bremidae: Hymenoptera). *Treubia* 12: 1-22.

Frison T.H. 1933. Records and descriptions of *Bremus* and *Psithyrus* from India (Bremidae: Hymenoptera). *Record of the Indian Museum* 35: 331-342.

Frison T.H. 1935. Records, notes and descriptions of *Bremus* from Asia (Bremidae: Hymenoptera). *Record of the Indian Museum* 37: 339-363.

Gaira K.G., Rawal R.S. & Singh K.K. 2016. Variations in pollinator density and impacts on large cardamom (*Amomum subulatum* Roxb.) crop yield in Sikkim Himalaya, India. *Journal of Asia-Pacific Biodiversity* 9: 17-21. https://doi.org/10.1016/j.japb.2015.12.010

Gauld I. & Bolton B. 1988. *The Hymenoptera*. Oxford University Press, Oxford. xi+332 pages.

Giangrande A. 2003. Biodiversity, conservation, and the ‘Taxonomic impediment’. *Aquatic Conservation* 13: 451-459. https://doi.org/10.1002/aqc.584

Goulson D. 2010. *Bumblebees*, *Behaviour*, *Ecology*, *and Conservation* (2 ed.). Oxford University Press, Oxford. x+317 pages.

Gribodo G. 1892. Contribuzioni imenotterologiche. Sopra alcune specie nuove o poco conosciute di imenotteri antofili (generi *Ctenoplectra*, *Xylocopa*, *Centris*, *Psithyrus*, *Trigona*, e *Bombus*). *Bolletino della Società Entomologica Italiana* 23: 102-119.

Haas A. 1976. Paarungsverhalten und Nestbau der alpinen Hummelart *Bombus mendax* (Hymenoptera: Apidae). *Entomologica Germanica* 3: 248-259.

Handlirsch A. 1888. Die Hummelsammlung des k. k. naturhistorischen Hofmuseums. *Annalen des Naturhistorischen Museums in Wien* 3: 209- 250.

Heinrich B. 1979. *Bumblebee Economics*. Harvard University Press, Cambridge (Massachusetts). viii+245 pages.

Hines H.M. 2008. Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera: Apidae: *Bombus*). *Systematic Biology* 57: 58-75.

HINES H.M. & WILLIAMS P.H. 2012. Mimetic colour pattern evolution in the highly polymorphic *Bombus trifasciatus* (Hymenoptera: Apidae) species complex and its comimics. *Zoological Journal of the Linnean Society* 166: 805-826. https://doi.org/10.1111/j.1096-3642.2012.00861.x

HOFFER E. 1889. Die Schmarotzerhummeln Steiermarks. Lebensgeschichte und Beschreibung derselben. *Mitteilungen des Naturwissenschaftlichen Vereins für Steiermark* 25: 82-158.

HOSKEN D.J. & STOCKLEY P. 2004. Sexual selection and genital evolution. *Trends in Ecology and Evolution* 19: 87-93.

HUANG J.-X., AN J.-D., WU J. & WILLIAMS P.H. 2015. Extreme food-plant specialisation in *Megabombus* bumblebees as a product of long tongues combined with short nesting seasons. *PLoSONE*: 1-15. https://doi.org/10.1371/journal.pone.0132358

ICZN 1999. *International Code of Zoological Nomenclature* (4 ed.). International Commission on Zoological Nomenclature, London. xxix+306 pages.

ILLIGER J.C.W. 1806. William Kirby's Familien der bienenartigen Insekten, mit Zusätzen, Nachweisungen und Bemerkungen. *Magazin für Insektenkunde* 5: 28-175.

ITO M., MATSUMURA T. & SAKAGAMI S.F. 1984. A nest of the Himalayan bumblebee *Bombus* (*Festivobombus*) *festivus*. *Kontyu* 52: 537-539.

JAFFAR S., ALI S., IMTIAZ H., HASSAN M.A., YASIN M., RIZVI S.A.H., DILBAR D.A. & ALI A. 2019. New records of *Bombus* Latreille, 1802 (Hymenoptera: Apidae) from the Himalayan range of Pakistan. *Journal of Entomology and Zoology Studies* 7: 981-985.

JAFFAR S., SHAH F., ALI S., YASEEN M., RIZVI S.A.H. & HASSAN M.A. 2019. Taxonomy and distribution of bumblebees (Hymenoptera: Apidae) of district Skardu, Gilgit Baltistan *Journal of Entomology and Zoology Studies* 7: 83-89.

KAWAKITA A., SOTA T., ITO M., ASCHER J.S., TANAKA H., KATO M. & ROUBIK D.W. 2004. Phylogeny, historical biogeography, and character evolution in bumble bees (*Bombus*: Apidae) based on simultaneous analysis of three nuclear gene sequences. *Molecular Phylogenetics and Evolution* 31: 799-804. https://doi.org/10.1016/j.ympev.2003.12.003

KEARNS C.A. & THOMSON J.D. 2001. *The Natural History of Bumblebees, a Sourcebook for Investigations*. University Press of Colorado, Boulder. xiv+130 pages.

KEN T., MARMA A., MUNAWAR M.S., PARTAP T., PARTAP U., PHARTIYAL P., SHARMA H.K. & TAMANG N.B. 2012. Value of Insect Pollinators to Himalayan Agricultural Economies. *International Centre for Integrated Mountain Development* (*ICIMOD*), 70 pages.

KUMAR A. & CHANDEL P. 2002. Distribution and zoogeographical affinities of the bumblebee species from northwest Himalaya. *Indian Journal of Entomology* 64: 227-230.

KUMAR A. & LALL A. 2004. New species of bumblebee (Hymenoptera: Apidae: Bombinii) recorded from North-West Himalaya. *Entomon 2004 September*; 29(3): 235-243.

LATREILLE P.A. 1802. *Histoire naturelle*, *générale et particulière des crustaces et des insectes.* (Vol. 3), Paris. xii+467 pages.

LEE C.K.F., WILLIAMS P.H. & PEARSON R.G. 2019. Climate change vulnerability higher in arctic than alpine bumblebees. *Frontiers of Biogeography*. https://doi.org/10.21425/F5FBG42455

LEPELETIER A.L.M. 1832. Observations sur l'ouvrage intitulé: 'Bombi scandinaviae monographice tractato, etc., à Gustav. Dahlbom.'. *Annales de la Société Entomologique de France* 1: 366-382.

LEPELETIER A.L.M. [1835]. *Histoire naturelle des insectes. Hyménoptères* (Vol. 1), Paris (1836).

LHOMME P. & HINES H.M. 2018. Ecology and Evolution of Cuckoo Bumble Bees. *Annals of the Entomological Society of America* 112: 122-140. https://doi.org/10.1093/aesa/say031

LINNAEUS C. 1758. *Systema naturae per regna tria naturae*, *secundum classes*, *ordines*, *genera*, *species*, *cum characteribus*, *differentiis*, *synonymis*, *locis*, Holmiae. 823 pages.

LØKEN A. 1966. Notes on Fabrician species of *Bombus* Latr. and *Psithyrus* Lep., with designations of lectotypes (Hym., Apidae). *Entomologiske Meddelelser* 34: 199-206.

MAA T. 1948. On some eastern Asiatic species of the genus *Psithyrus* Lepel. (Hymenoptera: Bombidae). *Notes d'entomologie chinoise* 12: 17-37.

MALLET J. 2013a. Species, concepts of. *In: Encyclopedia of Biodiversity*. Elsevier, pp. 679-691. https://doi.org/10.1016/B978-0-12-384719-5.00131-3

MALLET J. 2013b. Subspecies, semispecies, superspecies. *In: Encyclopedia of Biodiversity*. Elsevier, pp. 45-48. https://doi.org/10.1016/B978-0-12-384719-5.00138-6

MAYR E. 1963. *Animal Species and Evolution*, Massachusetts. xiv+797 pages.

MEDLER J.T. 1962a. Morphometric analyses of bumblebee mouthparts. *Transactions of the 11th International Congress of Entomology*, *Vienna* 2: 517-521.

MEDLER J.T. 1962b. Morphometric studies on bumble bees. *Annals of the Entomological Society of America* 55: 212-218.

MICHENER C.D. 1979. Biogeography of the bees. *Annals of the Missouri Botanical Garden* 62: 335-353.

MICHENER C.D. 2007. *The Bees of the World* (2 ed.). John Hopkins University Press, Baltimore. xiv+913 pages.

MORAWITZ F.F. 1875. Bees. (Mellifera). *In: Reise in Turkestan*, *A. P. Fedtschenko. II Zoologischer Teil*. Izvestiya Imp. Obshch. Ljubit. Estestvozn., Anthrop. Ethnogr., t. 19, no. 2, Moscow, p. ii+160.

MORAWITZ F.F. 1880. Ein Beitrag zur Bienen-Fauna mittel-Asiens. *Izvêstiya Imperatorskoi akademii nauk* 26: 337-379.

MORAWITZ F.F. 1887. Insecta in itinere cl. N. Przewalskii in Asia centrali novissime lecta. I. Apidae. *Trudy Russkago éntomologicheskago obshchestva* 20(1886): 195-229.

MORAWITZ F.F. 1890. Insecta a cl. G. N. Potanin in China et in Mongolia novissime lecta. XIV. Hymenoptera Aculeata. II). III. Apidae. *Trudy Russkago éntomologicheskago obshchestva* 24: 349-385.

MORAWITZ F.F. 1893. Supplement zur Bienenfauna Turkestans. *Trudy Russkago éntomologicheskago obshchestva* 28(1894): 3-87.

OLLERTON J. 2020. *Pollinators & Pollination: Nature and Society*. Pelagic Publishing Exeter. ix+286 pages.

ORR M., HUGHES A., CHESTERS D., PICKERING J., ZHU C.-D. & ASCHER J. 2021. Global patterns and drivers of bee distribution *Current Biology* 31: 1-8. https://doi.org/10.1016/j.cub.2020.10.053

PAKRASHI A., KUNDU S., SAINI J., TYAGI K., CHANDRA K. & KUMAR V. 2020. Molecular identification of selected bees from the Indian Himalaya: a preliminary effort. *Journal of Asia-Pacific Entomology* 23: 883-889. https://doi.org/10.1016/j.aspen.2020.07.001

PANFILOV D.V. 1957. [On the geographical distribution of bumblebees (*Bombus*) in China]. *Acta Geographica Sinica* 23: 221-239.

PATERSON H.E.H. 1985. The recognition concept of species. *In:* Vrba E.S. (ed), *Species and Speciation*, Pretoria, pp. 21-29.

PÉREZ J. 1884. Contribution à la faune des apiaires de France. Deuxième partie. Parasites. *Actes de la Société linnéenne de Bordeaux* 37: 205-380.

PESENKO Y.A. & ASTAFUROVA Y.V. 2003. Annotated bibliography of Russian and Soviet publications on the bees (Hymenoptera: Apoidea; excluding *Apis mellifera*): 1771-2003. *Denisia* 11: 1-616.

PITTIONI B. 1949. Beiträge zur Kenntnis der Bienenfauna SO-Chinas. Die Hummeln und Schmarotzerhummeln der Ausbeute J. Klapperich (1937/38). (Hym., Apoidea, Bombini). *Eos* 25: 241-284.

POPOV V.B. 1927. New forms of the genus *Psithyrus* Lep. *Konowia* 6: 267-274.

POPOV V.B. 1931. Zur Kenntnis der paläarktischen Schmarotzerhummeln (*Psithyrus* Lep.). *Eos* 7: 131-209.

POULTON E.B. 1904. What is a species? *Proceedings of the Entomological Society of London* 1903: lxxvii-cxvi.

PRYS-JONES O.E. & CORBET S.A. 2011. *Bumblebees*. Pelagic Publishing, Exeter. 144 pages.

RADOSZKOWSKI O. 1860. Sur quelques hyménoptères nouveaux ou peu connus de la collection du Musée de l'Académie des sciences de St. Pétersbourg. *Byulleten' Moskovskogo obshchestva ispytatelei prirody* 32(1859): 479-486.

RADOSZKOWSKI O. 1862. Sur quelques hyménoptères nouveaux ou peu connus. *Byulleten' Moskovskogo obshchestva ispytatelei prirody* 35: 589-598.

RADOSZKOWSKI O. 1884. Révision des armures copulatrices des mâles du genre *Bombus*. *Byulletin' Moskovskogo obshchestva ispytatelei prirody* 59: 51-92.

RADOSZKOWSKI O. 1893. Descriptions d'hyménoptères nouveaux. *Revue d'entomologie* 12: 241-245.

RASMONT P., COPPÉE A., MICHEZ D. & MEULEMEESTER T.D. 2008. An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). *Annales de la Société entomologique de France* 44: 243-250.

REINIG W.F. 1930. Untersuchungen zur Kenntnis der Hummelfauna des Pamir-Hochlandes. Zoologische Ergebnisse der deutsch-russischen Alai-Pamir-Expedition der Notgemeinschaft der Deutschen Wissenschaft und der Akademie der Wissenschaften der U.d.S.S.R. *Zeitschrift für Morphologie und Ökologie der Tiere* 17: 68-123.

REINIG W.F. 1935. On the variation of *Bombus lapidarius* L. and its cuckoo, *Psithyrus rupestris* Fabr., with notes on mimetic similarity. *Journal of Genetics* 30: 321-356.

REINIG W.F. 1939. Die Evolutionsmechanismen, erläutert an den Hummeln. *Verhandlungen der Deutschen zoologischen Gesellschaft* (*supplement*) 12: 170-206.

REINIG W.F. 1940. Beiträge zur Kenntnis der Hummelfauna von Afghanistan. (Hym., Apid.). (Ergebnisse der Reise von H. und E. Kotzsch in den Hindukusch im Jahre 1936.). *Deutsche Entomologische Zeitschrift* 1940: 224-235.

RENNER S.S. 2016. Available data point to a 4-km-high Tibetan Plateau by 40 Ma, but 100 molecular-clock papers have linked supposed recent uplift to young node ages. *Journal of Biogeography* 43: 1479-1487.

RICHARDS O.W. 1928a. *Bombus* and *Volucella* in the Himalayas. *Entomologist's Monthly Magazine* lxiv: 107-108.

RICHARDS O.W. 1928b. On a collection of humble-bees (Hymenoptera, Bombidae) made in Ladakh by Col. R. Meinertzhagen. *Annals and Magazine of Natural History* (*10*) 2: 333-336.

RICHARDS O.W. 1929a. On two new species of humble-bees in the collection of the British Museum, constituting a new group of the genus *Psithyrus*, Lep. (Hymenoptera, Bombidae). *Annals and Magazine of Natural History* (*10*) 3: 139-143.

RICHARDS O.W. 1929b. A revision of the humble-bees allied to *Bombus orientalis*, Smith, with the description of a new subgenus. *Annals and Magazine of Natural History* (*10*) 3: 378-386.

RICHARDS O.W. 1930. The humble-bees captured on the expeditions to Mt. Everest (Hymenoptera, Bombidae). *Annals and Magazine of Natural History* (*10*) 5: 633-658.

RICHARDS O.W. 1931. A new species of Indian humble-bee in the collection of the British Museum (Hymenoptera, Bombidae). *Annals and Magazine of Natural History* (*10*) 8: 529-533.

RICHARDS O.W. 1934. Some new species and varieties of oriental humble-bees (Hym. Bombidae). *Stylops* 3: 87-90.

RICHARDS O.W. 1968. The subgeneric divisions of the genus *Bombus* Latreille (Hymenoptera: Apidae). *Bulletin of the British Museum* (*Natural History*) (*Entomology*) 22: 209-276.

SABIR A.M., SUHAIL A., AHMED S. & KHALID S. 2011. Diversity of bumblebees (Bombini, Apidae: Hymenoptera) in northern Pakistan. *International Journal of Agriculture & Biology* 13: 159-166.

SAINI M.S., RAINA R.H. & GHATOR H.S. 2015. *Indian Bumblebees*. B. Singh and M. P. Singh, Dehra Dun, India. 248 pages.

SAKAGAMI S.F. 1972. Bumble bees collected by the California Academy - Lingnan Dawn-Redwood Expedition to central west China, 1948. *Pan-Pacific Entomologist* 48: 153-174.

SAKAGAMI S.F. & ITO M. 1981. Specific and subgeneric variations in tibial corbiculation of male bumblebees (Hymenoptera: Apidae), an apparently functionless character. *Entomologica Scandinavica* (*supplement*) 15: 365-376.

SAMYN Y., KERR A., O'LOUGHLIN M., MASSIN C., PAWSON D.L., ROWE F.W.E., SMILEY S., SOLIS-MARIN F., THANDAR A.S., VANDENSPIEGEL D. & PAULAY G. 2010. Using sea cucumbers to illustrate the basics of zoological nomenclature. *SPC Beche-de-mer Information Bulletin* 30: 33-40.

SCHLICK-STEINER B.C., STEINER F.M., SEIFERT B., STAUFFER C., CHRISTIAN E. & CROZIER R.H. 2010. Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology* 55: 421-438.
https://doi.org/10.116/annurev-ento-112408-085432

SCHMIEDEKNECHT H.L.O. 1883. *Apidae Europaeae* (*Die Bienen Europa*'*s*) *per genera*, *species et varietates. Dispositae atque descriptae. Volume I fascicule 6*, Berlin.

SCHWEINFURTH U. 1957. *Die horizontale und vertikale Verbreitung der Vegetation im Himalaya*, Bonn. xii+372 pages.

SEIDL W.B. 1837. Die in Böhmen vorkommenden Hummelarten. *Beiträge zur gesammten Natur- und Heilwissenschaft* 2: 65-73.

SHEIK U.A.A., AHMAD M., AZIZ M.A., NAEEM M., BODLAH I., IMRAN M. & NASIR M. 2015. First record of genus *Bombus* Latreille (Hymenoptera: Apidae, Bombini) in Naran Kaghan valley of Pakistan and their floral host range. *Journal of Biodiversity and Environmental Sciences* 7: 215-223.

Skorikov A.S. 1910a. [Intraspecific forms of *Bombus mendax* Gerst.] (Hymenoptera, Bombidae). *Russkoe éntomologicheskoe Obozrênie* 9(1909): 328-330.

Skorikov A.S. 1910b. [New forms of bumblebees] (Hymenoptera, Bombidae). ([Preliminary diagnoses]). III. *Russkoe éntomologicheskoe Obozrênie* 9(1909): 409-413.

Skorikov A.S. 1912a. *Bombus lapponicus* (F.) et ses formes ([queens] et [workers]) (Hymenoptera, Bombidae). *Russkoe éntomologicheskoe Obozrênie* 12: 95-102.

Skorikov A.S. 1912b. Neue Hummelformen (Hymenoptera, Bombidae). IV. *Russkoe éntomologicheskoe Obozrênie* 12: 606-610.

Skorikov A.S. 1914a. Les formes nouvelles des bourdons (Hymenoptera, Bombidae). VI. *Russkoe éntomologicheskoe Obozrênie* 14: 119-129.

Skorikov A.S. 1914b. *Pratobombus leucopygos* [sic] (F. Mor.) et ses variations (Hymenoptera, Bombidae). *Russkoe éntomologicheskoe Obozrênie* 14: 293-294.

Skorikov A.S. 1923. [Palaearctic bumblebees. Part I. General biology (including zoogeography)]. *Izvestiya Severnoi oblastnoi stantsii zashchity rastenii ot vreditelei* 4(1922): 1-160.

Skorikov A.S. 1931. Die Hummelfauna Turkestans und ihre Beziehungen zur zentralasiatischen Fauna (Hymenoptera, Bombidae). *In:* Lindholm V.A. (ed), *Abhandlungen der Pamir-Expedition 1928*. Academy of Sciences of the USSR, Leningrad, pp. 175-247.

Skorikov A.S. 1933a. Zur Fauna und Zoogeographie der Hummeln des Himalaya. *Doklady Akademii nauk SSSR* 1933: 243-248.

Skorikov A.S. 1933b. Zur Hummelfauna Japans und seiner Nachbarländer. *Mushi* 6: 53-65.

Sladen F.W.L. 1912. *The Humble-Bee*, *its Life History and how to Domesticate it*, *with Descriptions of all the British Species of Bombus and Psithyrus*. MacMillan, London. xiii+283 pages.

Smith F. 1852a. Descriptions of some hymenopterous insects from northern India. *Transactions of the Entomological Society of London* 2: 45-48.

Smith F. 1852b. Descriptions of some new and apparently undescribed species of hymenopterous insects from north China, collected by Robert Fortune, Esq. *Transactions of the Entomological Society of London* 2: 33-45.

Smith F. 1854. *Catalogue of Hymenopterous Insects in the Collection of the British Museum. Part II. Apidae*. Trustees of the British Museum, London. pp. 199-465.

Smith F. 1861. Descriptions of new genera and species of exotic Hymenoptera. *Journal of Entomology* 1: 146-155.

Smith F. 1870. [V. Notes on the habits of some hymenopterous insects from the North-west Provinces of India. By Charles Horne, Esq., B.C.S., F.Z.S.] With an appendix, containing descriptions of some new species of Apidae and Vespidae collected by Mr. Horne: by Frederick Smith, of the British Museum. Illustrated by plates from drawings by the author of the notes. *Transactions of the Zoological Society of London* 7: 161-196.

Smith F. 1878a. List of the Hymenoptera obtained by Mr Ossian Limborg east of Maulmain, Tenasserim Provinces, during the months of December 1876, January, March and April 1877, with descriptions of new species. *Journal of the Asiatic Society of Bengal* 47: 167-169.

Smith F. 1878b. *Scientific Results of the Second Yarkand Mission. Hymenoptera*. Government Print Office, Calcutta. 22 pages.

Smith F. 1879. *Descriptions of new species of Hymenoptera in the Collection of the British Museum*. Trustees of the British Museum, London. xxi+240 pages.

Streinzer M. 2019. Bumble bees (Hymenoptera: Apidae: Apinae: Bombini) of India. *In: Indian Insects*, pp. 173-185.

Streinzer M., Chakravorty J., Neumayer J., Megu K., Narah J., Schmitt T., Bharti H., Spaethe J. & Brockmann A. 2019. Species composition and elevational distribution of bumble bees (Hymenoptera: Apidae: *Bombus*) in the East Himalaya, Arunachal Pradesh, India. *Zookeys* 851: 71-89.
https://doi.org/10.3897/zookeys.851.32956

Suhail A., Sabir A.M., Asghar M., Rafi M.A. & Qadir A. 2009. Geographic distributional patterns of the genus *Bombus* (Bombini, Apidae: Hymenoptera) in northern Pakistan. *Biological Diversity and Conservation* 2: 1-9.

Sun C., Huang J.-X., Wang Y., Zhao X.-M., Su L., Thomas G.W.C., Zhao M.-Y., Zhang X.-T., Jungreiss I., Kellis M., Vicario S., Sharakov I.V., Bondarenko S., Hasselmann M., Kim C.N., Paten B., Penso-Dolfin L., Wang L., Chang Y.-X., Gao Q., Ma L., Ma L., Zhang Z., Zhang H.-H., Ruzzante L., Robertson H.M., Zhu Y.-H., Liu Y.-J., Yang H.-P., Ding L., Wang Q.-G., Xu W.-L., Liang C., Itgen M.W., Mee L., Sadd B.M., Cao G., Zhang Z., Hahn M.W., Schaack S., Barribeau S.M., Williams P.H., Waterhouse R.M. & Mueller R.L. 2020. Genus-wide characterization of bumblebee genomes reveals variation associated with key ecological and behavioral traits of pollinators. https://doi.org/10.1101/2020.05.29.122879

Tkalců B. 1961. Zur Hummelfauna der Umgebung Kuku-Nors (Hymenoptera, Bombinae). *Casopis Ceskoslovenské spolecnosti entomologické* 58: 344-379.

Tkalců B. 1968a. Neue Arten der Unterfamilie Bombinae der paläarktischen Region (Hymenoptera, Apoidea). *Sborník Entomologického oddeleni Národního musea v Praze* 65: 21-51.

Tkalců B. 1968b. Revision der vier sympatrischen, homochrome geographische Rassen bildenden Hummelarten SO-Asiens (Hymenoptera, Apoidea, Bombinae). *Annotationes Zoologicae et Botanicae* 52: 1-31.

Tkalců B. 1969a. Beiträge zur Kenntnis der Fauna Afghanistans (Sammelergebnisse von O. Jakes 1963-64, D. Povolny 1965, D. Povolny & Fr. Tenora 1966, J. Simek 1965-66, D. Povolny, J. Geisler, Z. Sebek & Fr. Tenora 1967). Bombinae, Apoidea, Hym. *Casopis Moravského musea v Brne* 53(1968): 189-210.

TKALCŮ B. 1969b. Ergebnisse der Albanien-Expedition 1961 des Deutschen Entomologischen Institutes. 78. Beitrag. Hymenoptera: Apidae IV (Bombinae). *Beiträge zur Entomologie* 19: 887-916.

TKALCŮ B. 1974. Eine Hummel-Ausbeute aus dem Nepal-Himalaya (Insecta, Hymenoptera, Apoidea, Bombinae). *Senckenbergiana biologica* 55: 311- 349.

TKALCŮ B. 1989. Neue Taxa asiatischer Hummeln (Hymenoptera, Apoidea). *Acta entomologica bohemoslovaca* 86: 39-60.

VOGT O. 1909. Studien über das Artproblem. 1. Mitteilung. Über das Variieren der Hummeln. 1. Teil. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* 1909: 28-84.

VOGT O. 1911. Studien über das Artproblem. 2. Mitteilung. Über das Variieren der Hummeln. 2. Teil. (Schluss). *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* 1911: 31-74.

VON DALLA TORRE K.W. 1890. Hymenopterologische Notizen. *Wiener entomologische Zeitung* 9: 139.

WANG C.-S., ZHAO X.-X., LIU Z.-F., LIPPERT P.C., GRAHAM S.A., COE R.S., YI H.-S., ZHU L.-D., LIU S. & LI Y.-L. 2008. Constraints on the early uplift history of the Tibetan plateau. *Proceedings of the National Academy of Sciences of the United States of America* 105: 4987-4992.

WANG S.-F. 1979. Three new species of bomble [sic] bees from Tibet. *Acta entomologica sinica* 22: 188-191.

WANG S.-F. 1982. Hymenoptera: Apidae - *Bombus*. *In:* Sciences Q.-T.P.C.S.I.T.o.t.C.A.o. (ed), *Insects of Xizang*. Science Press, Beijing, pp. 427-447.

WILLIAMS P.H. 1985. A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae). *Systematic Entomology* 10: 239-255.

WILLIAMS P.H. 1991. The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum* (*Natural History*) (*Entomology*) 60: 1-204.

WILLIAMS P.H. 1995. Phylogenetic relationships among bumble bees (*Bombus* Latr.): a reappraisal of morphological evidence. *Systematic Entomology* 19: 327-344.

WILLIAMS P.H. 1998a. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bulletin of The Natural History Museum* (*Entomology*) 67: 79-152 [updated at www.nhm.ac.uk/bombus/ accessed 2021].

WILLIAMS P.H. 1998b. Key sites for conservation: area-selection methods for biodiversity. *In:* Mace G.M., Balmford A. & Ginsberg J. (eds), *Conservation in a Changing World*. Cambridge University Press, Cambridge, UK, pp. 211-249.

WILLIAMS P.H. 2004. Genus *Bombus* Latreille. *In:* Gupta R.K. (ed), *An Annotated Catalogue of the Bee Species of the Indian Region*. Jai Narain Vyas University, Jodhpur. Web page providing a list of bumblebees of India and adjacent countries with common synonyms and a summary of their distributions within the region.

WILLIAMS P.H. 2007. The distribution of bumblebee colour patterns world-wide: possible significance for thermoregulation, crypsis, and warning mimicry. *Biological Journal of the Linnean Society* 92: 97-118. https://doi.org/10.1111/j.1095-8312.2007.00878.x

WILLIAMS P.H. 2008. Do the parasitic *Psithyrus* resemble their host bumblebees in colour pattern? *Apidologie* 39: 637-649. https://doi.org/10.1051/apido:2008048

WILLIAMS P.H. 2018. In a group of its own? Rediscovery of one of the world's rarest and highest mountain bumblebees, *Bombus tanguticus*. *Journal of Natural History* 52: 305-321. https://doi.org/10.1080/00222933.2018.1428377

WILLIAMS P.H. 2021. Not just cryptic, but a barcode bush: PTP re-analysis of global data for the bumblebee subgenus *Bombus s.str.* supports additional species (Apidae, genus *Bombus*). *Journal of Natural History*. https://doi.org/10.1080/00222933.2021.1900444

WILLIAMS P.H., ALTANCHIMEG D., BYVALTSEV A., DE JONGHE R., JAFFAR S., JAPOSHVILI G., KAHONO S., LIANG H., MEI M., MONFARED A., NIDUP T., RAINA R., REN Z., THANOOSING C., ZHAO X. & ORR M. 2020. Widespread polytypic species or complexes of local species? Revising bumblebees of the subgenus *Melanobombus* world-wide (Hymenoptera, Apidae, Bombus). *European Journal of Taxonomy* 719: 1-120. https://doi.org/10.5852/ejt.2020.719.1107

WILLIAMS P.H., AN J.-D. & HUANG J.-X. 2011. The bumblebees of the subgenus *Subterraneobombus*: integrating evidence from morphology and DNA barcodes (Hymenoptera, Apidae, *Bombus*). *Zoological Journal of the Linnean Society* 163: 813-862.

WILLIAMS P.H., ARAÚJO M.B. & RASMONT P. 2007. Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biological Conservation* 138: 493-505.

WILLIAMS P.H., BROWN M.J.F., CAROLAN J.C., AN J.-D., GOULSON D., AYTEKIN A.M., BEST L.R., BYVALTSEV A.M., CEDERBERG B., DAWSON R., HUANG J.-X., ITO M., MONFARED A., RAINA R.H., SCHMID-HEMPEL P., SHEFFIELD C.S., SIMA P. & XIE Z.-H. 2012. Unveiling cryptic species of the bumblebee subgenus *Bombus s.str.* world-wide with COI barcodes (Hymenoptera: Apidae). *Systematics and Biodiversity* 10: 21-56. https://doi.org/10.1080/14772000.2012.664574

WILLIAMS P.H., BYSTRIAKOVA N., HUANG J.-X., MIAO Z.-Y. & AN J.-D. 2015. Bumblebees, climate and glaciers across the Tibetan plateau (Apidae: *Bombus* Latreille). *Systematics and Biodiversity* 13: 164-181. https://doi.org/10.1080/14772000.2014.982228

WILLIAMS P.H., BYVALTSEV A.M., CEDERBERG B., BEREZIN M.V., ØDEGAARD F., RASMUSSEN C., RICHARDSON L.L., HUANG J.-X., SHEFFIELD C.S. & WILLIAMS S.T. 2015. Genes suggest ancestral colour polymorphisms are shared across morphologically cryptic species in arctic bumblebees. *PLoS ONE* 10: 1-26. https://doi.org/10.1371/journal.pone.0144544

Williams P.H., Cameron S.A., Hines H.M., Cederberg B. & Rasmont P. 2008. A simplified subgeneric classification of the bumblebees (genus *Bombus*). *Apidologie* 39: 46-74.

Williams P.H., Huang J.-X. & An J.-D. 2017. Bear wasps of the Middle Kingdom: a decade of discovering China's bumblebees. *Antenna* 41: 21-24.

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

Williams P.H., Ito M., Matsumura T. & Kudo I. 2010. The bumblebees of the Nepal Himalaya (Hymenoptera: Apidae). *Insecta Matsumurana* 66: 115-151.

Williams P.H. & Jepsen S. 2020. IUCN BBSG - Bumblebee Specialist Group Report 2019. London, UK, 27 pages. https://doi.org/10.13140/RG.2.2.15618.84166

Williams P.H., Lobo J.M. & Meseguer A.S. 2017. Bumblebees take the high road: climatically integrative biogeography shows that escape from Tibet, not Tibetan uplift, is associated with divergences of present-day *Mendacibombus*. *Ecography* 41: 461-477. https://doi.org/10.1111/ecog.03074

Williams P.H. & Osborne J.L. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie* 40: 367-387.

Williams P.H., Tang Y., Yao J. & Cameron S. 2009. The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini). *Systematics and Biodiversity* 7: 101-190. https://doi.org/10.1017/S1477200008002843

Williams P.H., Thorp R.W., Richardson L.L. & Colla S.R. 2014. *Bumble Bees of North America. An Identification Guide.* Princeton University Press, Princeton New Jersey. 208 pages.

Wilson E.O. & Brown W.L. 1953. The subspecies concept and its taxonomic application. *Systematic Zoology* 2: 97-111.

Winter K., Adams L., Thorp R.W., Inouye D.W., Day L., Ascher J. & Buchmann S. 2006. Importation of non-native bumble bees into North America: potential consequences of using *Bombus terrestris* and other non-native bumble bees for greenhouse crop pollination in Canada, Mexico, and the United States. *In: A White Paper of the North American Pollinator Protection Campaign* (*NAPCC*), San Francisco. 33 pages.

Xie Z.-H., Williams P.H. & Tang Y. 2008. The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation* 12: 695-703. https://doi.org/10.1007/s10841-008-9180-3

Yin A. 2010. Cenozoic tectonic evolution of Asia: a preliminary synthesis. *Tectonophysics* 488: 293-325.

Zink R.M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society of London* (*B*) 271: 561-564.

18. Acknowledgements

Enormous thanks to J. An, L. Bailey, P. Basu, V. Belavadi, A. Brockmann, K. Chandra, S. Jaffar, V. Kalkman, T. Nidup, M. Orr, Z. Ren, S. Ryder, M. Streinzer, C. Thanoosing, and especially R. Raina, for their discussion and support. Thanks to all of the many people who have sent specimens as loans or donations and to all of those who have collected bumblebees from the Himalaya to help advance our knowledge. Thanks to A. Polaszek for photographing many bumblebee male genitalia (blue backgrounds). I am greatly indebted: to Trinity College, Cambridge, for helping to support the visit to the Himalaya in 1980; to the UK's Natural Environment Research Council for a postdoctoral research fellowship that supported visits to the Himalaya in 1985–1986; to China's SAFEA High-End Foreign Experts Recruitment Programme, to the Chinese Academy of Agricultural Sciences Institute for Apicultural Research, to the Chinese Academy of Sciences Institute of Zoology, and to the Chinese Academy of Sciences Kunming Institute of Botany for supporting work in China 2007–2019; to India's National Centre for Biological Sciences for supporting visits to collections in India; to the Biodiversity Institute of Ontario for supporting the barcoding work; and to the Natural History Museum, London, for making this work possible. Thanks to the Belgian Development Cooperation for supporting *Abc Taxa* and the publication of this work.

19. Taxonomic index

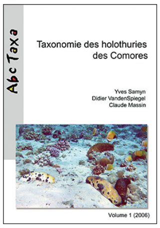
This index includes references to names of bumblebees used in the text but not to those used in the nomenclatural summary, in the keys to species, or in the lists of similar species in the comments on each species. Valid names are shown in ***bold***, names in the genus group are shown in *CAPITALS*

20. About the author

Paul Williams (1959) is a Principal Researcher at the Natural History Museum in London. His interest is the evolution, biogeography, diversity, ecology, and taxonomy of all bumblebees world-wide. He has worked particularly with bumblebees in the Himalaya and China since 1980, is author of the first quantitative analysis world-wide of bumblebee declines in 1982, and has led five global revisions of bumblebee subgenera, as well as being Chair and Co-Chair of the IUCN Bumblebee Specialist Group 2012-2021.

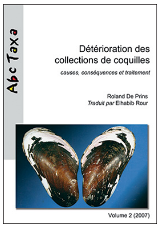
Previous volumes of Abc Taxa

Abc Taxa is a series of peer-reviewed manuals dedicated to capacity building in zoological and botanical taxonomy, in collection management and in good practices in taxonomic and curatorial research. The entire collection can be downloaded on www.abctaxa.be



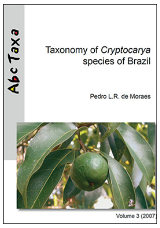
Volume 1

Samyn, Y., Vandenspiegel, D. & Massin, C. 2006. Taxonomie des holothuries des Comores. *Abc Taxa* 1: 130 pp.



Volume 2

De Prins, R. & Rour, E. 2007. Détérioration des collections de coquilles. *Abc Taxa* 2: 60 pp.

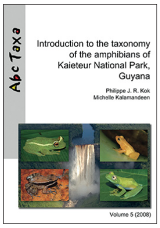


Volume 3

De Moraes, P.L.R. 2007. Taxonomy of Cryptocarya species of Brazil. *Abc Taxa* 3: 191 pp.

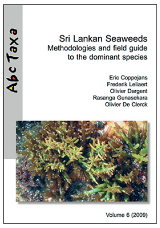
Volume 4

Diaz, L. & Cadiz, A. 2007. Guia taxonomica de los anfibios de Cuba. *Abc Taxa* 4: 294 pp.



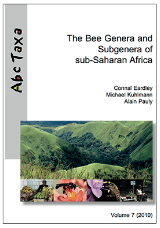
Volume 5

Kok, P.J.R. & Kalamandeen, M. 2008. Introduction to the taxonomy of the amphibians of Kaieteur National Park, Guyana. *Abc Taxa* 5: 278 pp.



Volume 6

Coppejans, E., Leliaert, F., Dargent, O., Gunasekara, R. & De Clerck, O. 2009. Sri Lankan Seaweeds – Methodologies and field guide to the dominant species. *Abc Taxa* 6: 265 pp.



Abc Taxa

The Bee Genera and
Subgenera of
sub-Saharan Africa

Connal Eardley
Michael Kuhlmann
Alain Pauly

Volume 7 (2010)

Volume 7

Eardley, C., Kuhlmann, M. & Pauly, A.. 2010. The Bee Genera and Subgenera of sub-Saharan Africa. *Abc Taxa* 7: 138 pp.

Abc Taxa

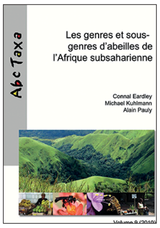
Manual on field recording
techniques and protocols
for All Taxa Biodiversity
Inventories and Monitoring

Edited by
J. Eymann, J. Degreef, Ch. Häuser
J.C. Monje, Y. Samyn and D. VandenSpiege

Volume 8, part 2 (2010

Volume 8

Eymann, J., Degreef, J., Häuser, C., Monje, J.C., Samyn, Y. & VandenSpiegel, D. 2010. Manual on Field Recording Techniques and Protocols for All Taxa Biodiversity Inventories. *Abc Taxa* 8: part 1: 1-330; part 2: 331-635.



Abc Taxa

Les genres et sous-
genres d'abeilles de
l'Afrique subsaharienne

Connal Eardley
Michael Kuhlmann
Alain Pauly

Volume 9 (2010)

Volume 9

Eardley, C., Kuhlmann, M. & Pauly, A. 2010. Les genres et sous-genres d'abeilles de l'Afrique subsaharienne. *Abc Taxa* 9: 143 pp.

Abc Taxa

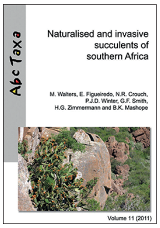
Champignons comestibles
des forêts denses
d'Afrique centrale
Taxonomie et identification

Hugues Eyi Ndong
Jérôme Degreef
André De Kesel

Volume 10 (2011)

Volume 10

Eyi Ndong, H., Degreef, J. & De Kesel, A. 2011. Les champignons comestibles des forêts denses d'Afrique centrale. *Abc Taxa* 10: 253 pp.



Abc Taxa

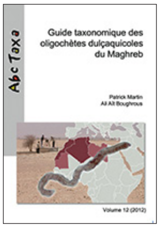
Naturalised and invasive
succulents of
southern Africa

M. Walters, E. Figueiredo, N.R. Crouch,
P.J.D. Winter, G.F. Smith,
H.G. Zimmermann and B.K. Mashope

Volume 11 (2011)

Volume 11

Walters, M., Figueiredo, E., Crouch, N.R., Winter, P.J.D., Smith, G.F., Zimmermann, H.G. & Mshope, B.K. 2011. Naturalised and invasive succulents of southern Africa. *Abc Taxa* 11: 370 pp.



Abc Taxa

Guide taxonomique des
oligochètes dulçaquicoles
du Maghreb

Patrick Martin
Ali Aït Boughrous

Volume 12 (2012)

Volume 12

Martin, P. & Boughrous, A.A. 2012. Guide taxonomique des oligochètes dulçaquicoles du Maghreb. *Abc Taxa* 12: 194 pp.

Abc Taxa

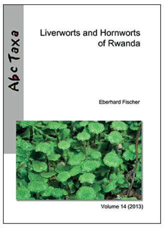
Bréviaire de taxonomie
des acariens

H.M. André and J.K. N'Dri

Volume 13 (2012)

Volume 13

André, H.M. & N'Dri, J.K. 2013. Bréviaire de taxonomie des acariens. *Abc Taxa* 13: 200 pp.



Abc Taxa

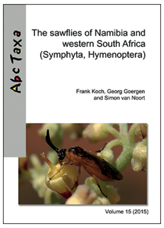
Liverworts and Hornworts
of Rwanda

Eberhard Fischer

Volume 14 (2013)

Volume 14

Fischer, E. 2013. Liverworts and Hornworts of Rwanda. *Abc Taxa* 14: 552 pp.



Abc Taxa

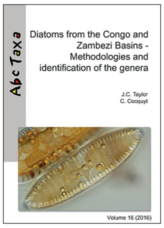
The sawflies of Namibia and
western South Africa
(Symphyta, Hymenoptera)

Frank Koch, Georg Goergen
and Simon van Noort

Volume 15 (2015)

Volume 15

Koch, F., Goergen, G. & van Noort, S. 2015. The sawflies of Namibia and western South Africa (Symphyta, Hymenoptera). *Abc Taxa* 15: 262 pp.



Abc Taxa

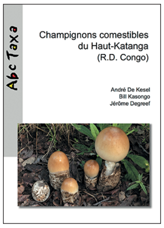
Diatoms from the Congo and
Zambezi Basins -
Methodologies and
identification of the genera

J.C. Taylor
C. Cocquyt

Volume 16 (2016)

Volume 16

Taylor, J.C. & Cocquyt, C. 2016. Diatoms from the Congo and Zambezi Basins – Methodologies and identification of the genera. *Abc Taxa* 16: 364 pp.



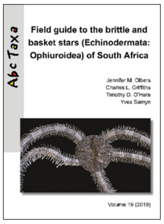
Abc Taxa

Champignons comestibles
du Haut-Katanga
(R.D. Congo)

André De Kesel
Bill Kasongo
Jérôme Degreef

Volume 17

De Kesel, A., Kasongo, B. & Degreef, J. 2017. Champignons comestibles du Haut-Katanga (R.D. Congo). *Abc Taxa* 17: 296 pp.



Abc Taxa

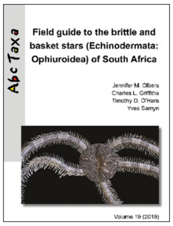
Field guide to the brittle and
basket stars (Echinodermata:
Ophiuroidea) of South Africa

Jennifer M. Olbers
Charles L. Griffiths
Timothy D. O'Hara
Yves Samyn

Volume 19 (2019)

Volume 18

Scholz, T., Vanhove, M.P.M., Smit, N., Jayasundera, Z. & Gelnar, M. (eds) 2018. A Guide to the Parasites of African Freshwater Fishes. *Abc Taxa* 18: 420 pp.



Abc Taxa

Field guide to the brittle and basket stars (Echinodermata: Ophiuroidea) of South Africa

Jennifer M. Olbers
Charles L. Griffiths
Timothy D. O'Hara
Yves Samyn

Volume 19 (2019)

Volume 19

Olbers, J.M., Griffiths, C.L., O'Hara, T.D. & Samyn, Y. 2019. Field guide to the brittle and basket stars (Echinodermata: Ophiuroidea) of South Africa. *Abc Taxa* 19: 346 pp.

Abc Taxa

Taxonomie du genre *Craterispermum* Benth.
(Gentianales – Rubiaceae) en Afrique continentale

Méthodologie de révision taxonomique chez les Angiospermes

H. Taedoumg

Volume 20 (2020)

Volume 20

Hermann, E. Taedoumg. 2020. Taxonomie du genre Craterispermum Benth. (Gentianales – Rubiaceae) en Afrique continentales. *Abc Taxa* 20: 174pp.