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Original article

A simplified subgeneric classification of the bumblebees (genus *Bombus*)*

Paul H. Williams[1], Sydney A. Cameron[2], Heather M. Hines[2], Bjorn Cederberg[3],
Pierre Rasmont[4]

[1] Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK
[2] Department of Entomology, University of Illinois, Urbana, IL 61801, USA
[3] Swedish Species Information Centre, University of Agricultural Sciences, PO Box 7007, 750 07 Uppsala, Sweden
[4] Laboratory of Zoology, University of Mons-Hainaut, Avenue Maistriau 19, 7000 Mons, Belgium

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Abstract – A system of subgenera has been widely used for nearly a century to communicate ideas of relationships among bumblebee species. However, with 38 subgenera in recent lists for about 250 species, the system has come to be seen as too complicated. In this paper we suggest four criteria to guide the process of simplifying the subgeneric system, so that ideally subgenera should become: (1) monophyletic; (2) fewer; (3) diagnosable from morphology; and (4) names for important behavioural and ecological groups. Using a new strongly-supported estimate of phylogeny for almost all bumblebee species, we apply these criteria to reduce the system to 15 subgenera, and we assess the consequences. Ten new subgeneric synonyms are recognised. Keys to identify adult bumblebees to the simplified subgenera are provided for both sexes.

bumblebee / *Bombus* / subgenera / phylogeny / classification

1. INTRODUCTION

Bumblebees are a group of about 250 species, now placed in a single genus, *Bombus* (Latreille, 1802). To summarise various kinds of relationships among these species, a system of subgenera has been developed over the last century (e.g. Dalla Torre, 1880; Radoszkowski, 1884; Robertson, 1903; Vogt, 1911; Skorikov, 1914, 1923; Krüger, 1920; Richards, 1929) and is now in common use. A review of the history of the development of bumblebee subgeneric systems is given by Ito (1985), while a unified world list of subgeneric names with their included species is summarised by Williams (1998), and keys to recently accepted subgenera are provided by Richards (1968) and Michener (2000, 2007). Now that we have a strongly supported estimate of relationships among almost all bumblebee species world-wide (Cameron et al., 2007), some minor revision will be unavoidable to ensure that the subgeneric nomenclature recognises only monophyletic groups.

However, the recent form of the bumblebee subgeneric system (e.g. as summarised by Michener, 2000, 2007) is widely regarded as unnecessarily complicated. This is exacerbated because the keys to subgenera are difficult to use and do not work well for many species. Consequently, a simplification of the subgeneric system is desirable (Kruseman, 1952; Milliron, 1961; Menke and Carpenter, 1984; Williams, 1998; Michener, 2000; Cameron et al., 2007). When using the new estimate of phylogeny to ensure monophyletic subgenera, we have an opportunity

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Corresponding author: P.H. Williams,
paw@nhm.ac.uk

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to make a more extensive rationalisation of the system. Previous attempts to make radical changes (Milliron, 1961; Tkalců, 1972) have been largely ignored because their advantages were not widely appreciated (e.g. Richards, 1968; Michener, 2000), and because the subgeneric keys (Milliron, 1971, 1973a, b) were even more difficult to use.

In this paper, we identify the principal purposes for which bumblebee subgenera are useful and then examine how we might modify the subgeneric system to make it better suited to meeting explicit and widely held aims.

2. AIMS

Bumblebee subgenera could be useful in meeting three main aims:

1. to reflect and be consistent with phylogenetic relationships;
2. to aid identification, as a stepping stone to identifying species (especially important when dealing with unfamiliar or poorly known faunas); and
3. to predict (interpolate) poorly sampled behavioural and ecological characteristics.

The primary aim in using bumblebee subgenera has changed through time. Formal subgeneric names were first introduced for bumblebees by Dalla Torre (1880, 1882), originally to group bees with similar colour patterns. Radoszkowski (1884) used informal species-group names, but applied them instead to groups of species recognised for morphological similarities in their male genitalia. This morphological system was then largely re-invented by Vogt (1911), who introduced his own set of formal subgeneric names. Skorikov (e.g. 1914, 1922, 1923, 1931) adopted Vogt's system and names and then greatly elaborated it, establishing most of the current subgeneric system (although as a mix of subgeneric and generic names, in many cases published without descriptions or diagnoses). Skorikov also extended the role of bumblebee subgenera to discussing phylogeny and the evolution of behaviour, ecology, and distribution patterns, a subject of interest to many recent researchers (e.g. Hobbs, 1964; Williams, 1985; Cameron and Williams, 2003; Kawakita et al., 2004; Hines, in press). Some authors, while recognising subgenera, have focussed instead on a few much larger groups or 'sections', either when considering morphology (Robertson, 1903; Krüger, 1917; Frison, 1927), or when considering behaviour and ecology (Sladen, 1912; Plath, 1927, 1934). According to the *International Code of Zoological Nomenclature* (ICZN, 1999: Article 10.4), if only a single genus of bumblebees is to be recognised and if these section names are required for use as formal names below the rank of genera, then they have to be treated as names for taxa at the rank of subgenera (Williams, 1998).

However, subgenera are no longer needed for communicating ideas of phylogenetic relationship among bumblebees. The use of tree diagrams for summarising relationships has the advantage over subgenera that trees can show many more levels of grouping or phylogenetic clades. Authors of subgenera had tried to keep track of the improving knowledge of morphology and concepts of relationship as bumblebees became better known world-wide by splitting subgenera to recognise progressively finer divisions. This has caused problems because the pattern of splitting subgenera has become highly asymmetric and many subgenera (11 of 38) are monotypic. These convey little information on relationships. To some extent this asymmetry is inevitable because phylogenetic trees are rarely symmetric. But in some cases the problem goes beyond this. In one example (Williams, 1998), there are two large clades that occur in both North and South America: a broad *fervidus*-group and a broad *robustus*-group, each with 20 species. But whereas the former clade has been treated recently as a single subgenus, the latter clade has been split into 10 subgenera.

Similarly, subgenera might appear to have been superseded by phylogenetic trees when seeking to communicate the distribution of character states among species. Trees have often been used to map the evolution of characters (e.g. Krüger, 1920; Kawakita et al., 2004; Cameron et al., 2007; Hines, in press). In addition, trees mapped with illustrations of morphological characters (e.g. Williams, 1985: his

Fig. 6) could, at least in principle, be used as an aid (or key) for species identification, although this has not been used in practice for bumblebees.

Nonetheless, subgenera have real advantages. Some discussions of bumblebee ecology continue to find subgeneric names useful as short-hand pointers to groups with particular behavioural and ecological characters (e.g. Hobbs, 1964; Sakagami, 1976; Plowright, 1977). It is more convenient for field biologists to remember names for a few large clades of species with characteristic behaviour and ecology, rather than having to remember an entire phylogenetic tree with all of the characters mapped upon it. Second, phylogenetic trees are often unsuited for use to structure routine identification aids, because not all clades conveniently share easily observed and unambiguous morphological characters (see below). Decisions in traditional identification keys have their pathways set by the authors (Walter and Winterton, 2007). They can be ordered pragmatically to minimise the risk of misidentification, with the least ambiguous characters in their earlier couplets. These keys frequently use subgenera as a convenient intermediate stage or stepping stone to species identification (e.g. Pittioni, 1939; Løken, 1973; Thorp et al., 1983). But above all, subgeneric names have the advantage over generic names that they can be ignored by non-specialists who do not need to use them. Subgeneric names can still be used by specialists when they find them helpful.

3. CRITERIA

From the aims listed above, we can identify four criteria that should be useful to guide changes to the bumblebee subgeneric system. Subgenera should become:

1. monophyletic;
2. fewer;
3. diagnosable from morphology;
4. names for principal behavioural and ecological groups.

Not all of these criteria are easy to satisfy, and the advantages of any changes must be balanced against the cost of instability from frequent changes. When moving from general aims to specific operational criteria, there are also potential conflicts among the criteria, as discussed below.

Monophyly. This is widely accepted as a minimum requirement of higher taxa such as subgenera and is more important than stability. Recent estimates of bumblebee phylogeny (Cameron et al., 2007) show that not all current subgenera are monophyletic, and indeed some are polyphyletic. Because the supporting evidence is strong, we feel obliged to modify the subgeneric system to avoid polyphyly. Furthermore, we prefer strict monophyly over paraphyly because it ensures that classifications are most likely to be predictive for those characters not used in their construction (whether of morphology, behaviour, or ecology), because of the underlying evolutionary model of descent with modification (e.g. Kitching et al., 1998). Because there are many possible ways of modifying the system while ensuring monophyly, it is useful to identify subsidiary criteria that help to achieve the greatest overall benefit.

Fewer. The precise choice of level within a phylogenetic tree for labelling a supraspecific taxon with a particular nomenclatural rank is essentially arbitrary, and there is a large literature discussing this problem (e.g. Stevens, 2006). For bumblebees, there is a broad perception that there are too many subgenera and that a substantial reduction in their number would be desirable (Kruseman, 1952; Milliron, 1961; Menke and Carpenter, 1984; Williams, 1998; Michener, 2000; Cameron et al., 2007). Given a well-resolved and strongly supported estimate of bumblebee phylogeny, then the number of subgenera can be reduced while remaining consistent with monophyly. Among a small e-mail poll of bumblebee ecologists in Europe and North America (12 respondents), the idea of a reduced number of larger subgenera was supported enthusiastically. The primary criterion of monophyly requires that some monotypic subgenera (*Kallobombus*) or small subgenera (*Bombias*) continue to be recognised (Cameron et al., 2007). Reducing the number of subgenera would not prevent authors from recognising informal species groups in an ad-hoc manner when necessary.

Morphological diagnosability and behavioural/ecological groups. Conflicts among criteria might arise particularly if behavioural and ecological characteristics were associated with clades that were established from DNA evidence but which have no known diagnostic morphological characters (a phenomenon familiar from work on the higher classification of plants, e.g. Stevens, 2006). This is the most serious challenge to our efforts to recognise useful subgenera for bumblebees. It can be studied by plotting the distribution of morphological/behavioural/ecological characters on phylogenetic trees and looking for concentrations of character-state changes at particular nodes (which is not necessarily the same as long branch lengths based on DNA divergences). We find that many small terminal groups of bumblebee species are easily diagnosed by morphological characters, but in some parts of the tree there remains a morass of relatively undifferentiated more 'basal' species (this is particularly a problem with early-diverging species within the proposed broader concepts of the subgenera *Thoracobombus*, *Melanobombus*, and *Cullumanobombus*, see below). One solution is to recognise paraphyletic 'stem' groups, although this has been avoided here. Another possible solution would be to ignore behaviour and ecology and maintain the traditional precedence of morphological diagnosability as the criterion for recognising subgenera. We choose to exclude geographical distribution from use as a character, because biogeography cannot be analysed for subgenera if distribution is used in their diagnosis without the logic of the biogeographic analysis becoming circular. Concentrating on morphological diagnosability allows subgenera to be more useful in an intermediate stage in the identification process. Precedence of morphological diagnosability should also promote nomenclatural stability, because morphology can largely be known now, whereas we can only hope that our patchy current knowledge of behaviour and ecology worldwide (e.g. Sakagami, 1976) will improve in the future. Fortunately, at least in some cases, behavioural and ecological groups do correspond conveniently to morphologically diagnosable subgenera (see the Assessment section).

4. APPLICATION

Monophyly of subgenera should now be achievable because we have a highly resolved estimate of phylogeny for almost all bumblebee species that is strongly supported by evidence from the DNA sequences of five genes (Cameron et al., 2007; largely compatible with more restricted DNA analyses by Pedersen, 2002; Cameron and Williams, 2003; Kawakita et al., 2003; Hines et al., 2006). Here we use a tree redrawn from Cameron et al. (2007: their Fig. 2), which recognises only the clades with the strongest support (Bayesian posterior probabilities $\geqslant 0.95$, Fig. 1) at or above the rank of the existing subgenera.

For most of the last two centuries, most authors have placed bumblebees in two genera: *Bombus* (for the truly social species) and *Psithyrus* (for the cuckoo bumblebees, all obligate social parasites of other bumblebees). Both morphological and molecular evidence shows that a genus *Bombus* excluding *Psithyrus* is paraphyletic (Williams, 1995; Cameron et al., 2007), a situation that should be avoided (see above). If all bumblebees, including the parasitic species, were to be included in a single genus *Bombus*, this would have the advantage that it emphasises both the many shared homologies of the group, on the one hand, and the shared differences from other groups of corbiculate bees, on the other. This proposal (Williams, 1991) has gained widespread acceptance and stability.

Psithyrus has been split previously by Frison (1927), Popov (1931) and Pittioni (1949) into eight smaller subgenera (*Psithyrus* in the narrow sense, plus *Allopsithyrus*, *Ashtonipsithyrus*, *Ceratopsithyrus*, *Eopsithyrus*, *Fernaldaepsithyrus*, *Laboriopsithyrus*, *Metapsithyrus*, see Williams, 1998). These smaller subgenera have been considered less distinct from one another than have the other subgenera of *Bombus* (Pittioni, 1939; Ito, 1985; Williams, 1985; Michener, 1990) and have

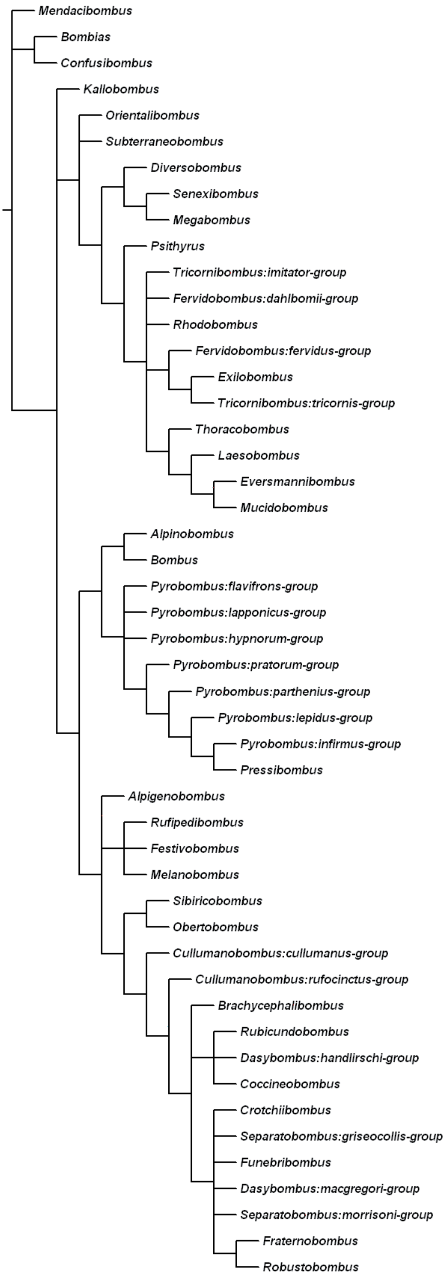

Figure 1. Recently listed bumblebee subgenera (e.g. Michener, 2000, 2007; divided into species-groups where necessary to recognise only strictly monophyletic clades, some of which may consist of a single species) showing the estimate of phylogeny redrawn from Cameron et al. (2007). Only clades with strong support (Bayesian posterior probability ⩾ 0.95) are shown.

been synonymised with a genus (Milliron, 1961) or subgenus (Williams, 1991) *Psithyrus*. Some authors have preferred to continue to use these subgenera (e.g. Rasmont, 1983). But in recognition of the importance of the many morphological and behavioural homologies among *Psithyrus* in the broad sense (e.g. Williams, 1995), more than for any other single clade, we agree that a single subgenus *Psithyrus* should be retained for the cuckoo bumblebees. This has also gained widespread acceptance and stability.

If *Psithyrus* is to remain as a single subgenus, then from the best current estimate of bumblebee phylogeny (Fig. 1), the minimum total number of subgenera required if all subgenera were to be monophyletic would be nine (*Mendacibombus*, *Bombias, Kallobombus*, *Orientalibombus*, *Subterraneobombus*, *Megabombus*, *Thoracobombus*, *Psithyrus*, and a large *Bombus* s. str.). Among these subgenera, four are accepted here in the recent sense because they are then unavoidably required to maintain monophyly once *Psithyrus* is accepted: *Mendacibombus*, *Kallobombus*, *Orientalibombus*, and *Subterraneobombus*. The others are discussed below.

Bombias: *Bombias* + *Confusibombus*. The subgenus *Confusibombus* has been seen previously as part of a 'section' *Bombias* by Kruseman (1952) (and the section *Boopobombus* Frison was synonymised with the subgenus *Bombias* by Williams, 1995). The possible argument in favour of retaining a split between them is that this represents an early divergence, dating to nearly half of the age of the inclusive *Bombus* clade (Hines, in press). Our argument in favour of lumping is that with so few species (three), uniting them within a single subgenus *Bombias* is useful to emphasise their unusual shared morphological character states of both sexes, such as the combination of male short antennae, large eyes, straight penis valves, and gonostyli and volsellae with inner processes (see the keys in Appendices).

Megabombus: *Diversobombus* + *Senexibombus* + *Megabombus.* These subgenera have been synonymised previously (Milliron, 1961) (the 'section' *Odontobombus* Krüger has also been synonymised with the subgenus *Megabombus* by Milliron, 1961, and Williams,

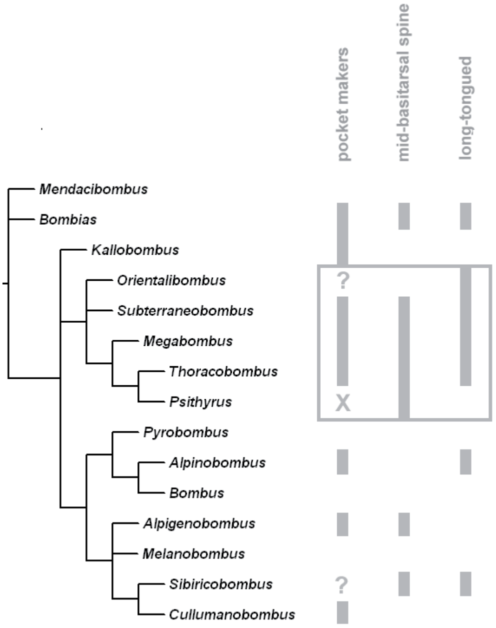

Figure 2. Proposed simplified bumblebee subgenera showing the estimate of phylogeny redrawn from Cameron et al. (2007). Only clades with strong support (Bayesian posterior probability ⩾ 0.95) are shown. Three characters that are traditionally associated with the group marked with the grey box (*Orientalibombus* + *Subterraneobombus* + *Megabombus* + *Thoracobombus* + *Psithyrus*) are mapped against the tree using data from Table III and from Appendix 1 ('?' is used for unknown [*Orientalibombus*, *Sibiricobombus*] states and 'X' for unobservable [*Psithyrus*] states).

1995). Our argument in favour of treating this clade as a single subgenus is that it recognises a group for many of the species with the longest tongues among bumblebees.

Thoracobombus: *Tricornibombus* + *Exilobombus* + *Fervidobombus* + *Rhodobombus* + *Laesobombus* + *Eversmannibombus* + *Mucidobombus* + *Thoracobombus.* This very large clade includes eight subgenera in some recent publications, although *Laesobombus*, *Eversmannibombus* and *Mucidobombus* have been synonymised previously with *Thoracobombus* (Tkalců, 1972; Reinig, 1981; Rasmont, 1983). The oldest available names for the large clade are *Thoracobombus* and *Rhodobombus*, of which we choose *Thoracobombus* as the valid name by the principle of the First Reviser (ICZN, 1999). DNA evidence shows that there are two weakly-supported similarly-sized subclades (Cameron et al., 2007: their Fig. 1), one predominantly Old World and one predominantly New World. A few species of each of these two subclades (e.g. *B. pascuorum* and *B. fervidus* respectively) are well known from their respective regions, and these species give the impression that the two subclades are strongly distinct. However, some of the less well known species of each subclade show the character states of the sister clade (i.e. both subclades show similar broad ranges in characters such as aggressiveness, colony size, nest position relative to ground level) so that there is overlapping variation between both subclades. In the DNA tree (Fig. 1), five subclades remain unresolved at a basal level in this large clade. Most of these are currently morphologically undiagnosable in one or both sexes when all known species are examined. A few small subclades (e.g. the former subgenus *Rhodobombus*) are easily diagnosable from morphological characters, but recognising these as separate subgenera would leave large paraphyletic subgenera. In addition, former concepts of some subgenera (*Fervidobombus*, *Tricornibombus*) are recognised now as polyphyletic. We have a precedent for a similarly large and diverse subgenus in the long-accepted *Pyrobombus*.

In recent publications, the remaining bumblebees include several medium to large, well-diagnosed subgenera and many small and poorly-diagnosed subgenera. The first category consists of the subgenera *Alpinobombus*, *Bombus* (in the narrow sense), *Pyrobombus*, and *Alpigenobombus*, which we accept as separate without change (the 'section' *Anodontobombus* Krüger was synonymised with the subgenus *Pyrobombus* by Milliron, 1961, and Williams, 1995). The one change to *Pyrobombus* (Cameron et al., 2007) is that the uniquely divergent, single species of *Pressibombus* is now recognised as a part of *Pyrobombus*. Our argument in favour of maintaining the separation of these four larger subgenera is that each is distinctive and reasonably homogeneous in the morphology of both sexes (see Appendices).

Melanobombus: *Rufipedibombus* + *Festivobombus* + *Melanobombus*. Our argument in favour of lumping these clades is that they are morphologically similar in both sexes (see Appendices).

Sibiricobombus: *Sibiricobombus* + *Obertobombus*. These subgenera have been synonymised previously (Richards, 1968; Williams, 1991). Our argument in favour of lumping these clades is that they have very long tongues (Williams, 1991) and are otherwise morphologically similar in both sexes (see Appendices).

Cullumanobombus: *Cullumanobombus* + *Brachycephalibombus* + *Rubicundobombus* + *Coccineobombus* + *Dasybombus* + *Crotchiibombus* + *Separatobombus* + *Funebribombus* + *Fraternobombus* + *Robustobombus*. In recent publications, most of these subgenera include just one or two species, although many of the subgenera have been synonymised previously by Milliron (1961). Two small subgroups are distinctive. The first subgroup includes *B. rufocinctus* and the *cullumanus*-group, but this may or may not form a monophyletic clade (Cameron et al., 2007). Whereas males of most species of *Cullumanobombus* in the broad sense have eyes enlarged relative to the females, males in this subgroup (of small steppe species) have their eyes relatively unenlarged. The second subclade includes *B. handlirschi* and the *coccineus*-group, which are mountain bumblebees, but which also have less strongly enlarged male eyes. While there is morphological heterogeneity in the larger inclusive clade, especially in the males, the females are morphologically more similar.

Our proposed simplified subgeneric classification is summarised with the phylogeny in Figure 2 and listed with the necessary nomenclatural changes in Table I. A full synonymic list of bumblebee subgeneric names with minor corrections from Sandhouse (1943), Richards (1968), Michener (1997, 2000, 2007), and Williams (1998) can be found at <http://www.nhm.ac.uk/research-curation/projects/bombus/groups.html>. The keys were prepared from a survey of morphological characters by mapping character-state changes onto the molecular estimate of the phylogenetic tree in order to identify which states diagnose subgenera or groups of subgenera.

5. ASSESSMENT

We can assess the degree of success of the proposed subgeneric system (Fig. 2) in meeting each of the criteria listed above as follows:

Monophyly. All bumblebee subgenera in Figure 2 are monophyletic according to the strongly supported published evidence (Cameron et al., 2007).

Fewer. The number of bumblebee subgenera world-wide is reduced from 38 to 15. The consequences of this simplification for continental counts of indigenous subgenera are shown in Table II.

Morphological diagnosability. Illustrated keys for the identification of the bumblebee subgenera from the morphological characters of both sexes are included here (Appendices). Our tests show that, while many of the characters are not as easy to use as we would wish, the diagnoses give correct subgeneric determinations for all but a few of the smallest specimens tested so far.

The keys include exceptions for the characters of a few early-diverging species within the enlarged subgenera *Melanobombus*, *Sibiricobombus*, and *Cullumanobombus*. These species could be recognised as separate subgenera with the available names *Rufipedibombus*, *Festivobombus*, *Obertobombus*, *Rufocinctobombus*, and *Cullumanobombus* (in the narrow sense, which would then have to be distinguished from an enlarged *Robustobombus*). However, several of these former subgenera are undiagnosable by morphology in one of the sexes. None is known to be particularly strongly differentiated in behavioural or ecological characters. Consequently, at present we see no substantial benefit in separating them from their larger sister groups in a series of monotypic or near-monotypic subgenera. We see greater benefit in recognising the broader homologies across the larger, more inclusive subgenera.

Behavioural and ecological groups. Subgenera in the simplified system can in many

Table I. Summary of nomenclature for the proposed simplified subgeneric system.

	Proposed simplified subgenera	No. of species*	Synonyms among recent subgenera**
1	***Mendacibombus*** Skorikov	12	
2	***Bombias*** Robertson	3	
			Confusibombus Ball **syn. n.**
3	***Kallobombus*** Dalla Torre	1	
4	***Orientalibombus*** Richards	3	
5	***Subterraneobombus*** Vogt	10	
6	***Megabombus*** Dalla Torre	22	
			Diversobombus Skorikov
			Senexibombus Frison
7	***Thoracobombus*** Dalla Torre	50	
			Eversmannibombus Skorikov
			Exilobombus Skorikov **syn. n.**
			Fervidobombus Skorikov **syn. n.**
			Laesobombus Krüger
			Mucidobombus Krüger
			Rhodobombus Dalla Torre **syn. n.**
			Tricornibombus Skorikov **syn. n.**
8	***Psithyrus*** Lepeletier	30	
9	***Pyrobombus*** Dalla Torre	50	
			Pressibombus Frison **syn. n.**
10	***Alpinobombus*** Skorikov	5	
11	***Bombus*** *s. str.*	10	
12	***Alpigenobombus*** Skorikov	7	
13	***Melanobombus*** Dalla Torre	17	
			Festivobombus Tkalců **syn. n.**
			Rufipedibombus Skorikov **syn. n.**
14	***Sibiricobombus*** Vogt	7	
			Obertobombus Reinig
15	***Cullumanobombus*** Vogt	23	
			Brachycephalibombus Williams **syn. n.**
			Coccineobombus Skorikov
			Crotchiibombus Franklin
			Dasybombus Labougle & Ayala **syn. n.**
			Fraternobombus Skorikov
			Funebribombus Skorikov
			Robustobombus Skorikov
			Rubicundobombus Skorikov
			Separatobombus Frison

* Complete list of nomenclature and species at <http://www.nhm.ac.uk/research-curation/projects/bombus/groups.html>.
** From the most recent published list in Michener (2000, 2007).

cases be associated with particular combinations of behavioural and ecological character states (these are summarised crudely in Table III, but published information is far from adequate). For example, species of *Mendacibombus* and *Bombias* have distinctive nest-building behaviour (Hobbs, 1965; Haas, 1976). Many (but not all) species of *Megabombus* have the longest tongues among bumblebees and specialise in visiting particularly deep flowers, sometimes of very few plant species (e.g. Løken, 1973). Species of

Table II. Geographical distribution of recent and proposed bumblebee subgenera.

	Continent/region	No. of species*	Recent subgenera**	Proposed simplified subgenera
1	Western Palaearctic	72	18	14
2	Eastern Palaearctic	96	20	14
3	Oriental	108	19	11
4	Nearctic	58	14	8
5	Neotropical	25	7	3

* From the list of species at <http://www.nhm.ac.uk/research-curation/projects/bombus/groups.html>.
** From the most recent published list in Michener (2000, 2007).

Thoracobombus in the new broad sense (both Old World and New World) often have moderately long tongues and include all of the species described by Sladen (1912) as 'carder bees'. Many of these species build nests on the surface of the ground, covered only by herbaceous plant material, such as grass stems (broadly similar behaviour is also known for some of the South American tropical lowland forest species, e.g. Cameron and Whitfield, 1996; other species build nests underground). Although social parasitism occurs elsewhere in the genus, *Psithyrus* species are very distinctive for their particular kind of parasitic behaviour (e.g. Sladen, 1912). *Alpinobombus* species are well known for being specialists in high arctic (and a few alpine) environments (e.g. Richards, 1973). *Bombus* s. str. species are regarded as having a distinctive social biology that makes them particularly well suited to management for pollination (e.g. Winter et al., 2006). *Pyrobombus* is a large and diverse clade, but includes many small species with short colony cycles and which forage particularly often from hanging flowers (Prys-Jones and Corbet, 1987). *Alpigenobombus* species are distinctive for having six large triangular teeth on each mandible and for habitually using them to bite through flower corollas to rob nectar (e.g. Løken, 1973; Williams, 1991). *Melanobombus* species are predominantly mountain bees (Williams, 1991; although the best known species, the European *B. lapidarius* and *B. sichelii*, are exceptional for being widespread in the lowlands in large parts of their ranges) that nest underground, and at least in some cases, have a preference for composite inflorescences. *Sibiricobombus* species are steppe and mountain bees with unusually long tongues (Williams, 1991; Rasmont et al., 2005). *Cullumanobombus* species are predominantly mountain species, although there are a few lowland species.

Combining former subgenera brings together species with similar characteristics, so that generally intra-subgeneric variation appears to be less than inter-subgeneric variation. A few small clades (e.g. the *pomorum*-group within *Thoracobombus* and some of the *rufofasciatus*-group within *Melanobombus*) are divergent, particularly in morphological characters relating to male mate-searching behaviour (e.g. Terzo et al., 2005, 2007a, b, and Williams, 1991: his Fig. 10, respectively). However, recognising these as separate subgenera would leave large paraphyletic subgenera. We consider that it is premature to attempt a more quantitative assessment of behavioural and ecological data at present because: (1) data are available from relatively few species, with a strong bias towards those from north-western Europe and from North America (Sakagami, 1976); (2) character states have not been defined in a consistent manner in the literature (Sakagami, 1976); and (3) characters are often variable within species and may depend upon environmental influences in ways that are not yet fully understood (Sakagami, 1976; Plowright, 1977).

There would be potential pitfalls in pursuing simplification of the subgeneric system too far. If we exclude from this discussion the parasitic species of the subgenus *Psithyrus*, then many authors (often faced with restricted regional faunas) have regarded the remaining social bumblebees as being divided into two broad groups. However, Figure 2 shows that different versions of the two groups based on

Table III. Behavioural/ecological characters listed for the proposed simplified subgenera.

	Md*	Bi	Kl	Or	St	Mg	Th	Ps	Pr	Al	Bo	Ag	Ml	Sb	Cu
Tongue length: S short; M medium; L long**	M	ML	S	L	L	ML	ML	SM	SM	ML	S	S(M)	SM(L)	L	SM
Principal nest site of a species: U underground/enclosed; S surface/exposed	U	US	U	?	U(S)	U(S)	(U)S	X	US	US	U	U	U	U	U(S)
Frequent nest-material assemblers: N non-carder bees; C carder bees	N	N	N	?	N	N	C	X	N	N	N	N	N	?	N
Egg laying: I isolated; C compact	I	I	C	?	C	C	C	C	C	C	C	C	C	?	C
Pollen priming of brood: P primer; N non-primer	?	P	[P]N	?	PN	P	[P]N	X	(P)/[P]N	[P]N	[P]N	(P)/[P]N	[P]N	?	[P]N
Pollen storage: P pocket maker (indirect feeding); N non-pocket maker or pollen storer (direct feeding)	N	[P]N	[P]N	?	P	P	P/[P]N	X	N	[P]N	N	[P]N	N	?	[P]N
Nectar storage: O outside brood envelope; I inside brood envelope	O	I	I	?	I	I	I	X	I	I	I	I	I	?	I
Male mate-searching behaviour: N nest entrance; P patrolling; R racing/territorial/cruising	R	R	P	P	N	P	NP	P	P	P	P	P(R)	P(R)	R	(P)R
Principal habitat of a species: A alpine/arctic; F montane/temperate forest; G prairie/steppe; D desert; T lowland tropical forest	A	AG	AG	F	AGD	AFG(T)	(AF)GDT	AFG	AFGD(T)	A	AFG	AF	AFG(T)	AGD	AG

* Abbreviations for subgeneric names: *Md*, *Mendacibombus*; *Bi*, *Bombias*; *Kl*, *Kallobombus*; *Or*, *Orientalibombus*; *St*, *Subterraneobombus*; *Mg*, *Megabombus*; *Th*, *Thoracobombus*; *Ps*, *Psithyrus*; *Pr*, *Pyrobombus*; *Al*, *Alpinobombus*; *Bo*, *Bombus s. str.*; *Ag*, *Alpigenobombus*; *Ml*, *Melanobombus*; *Sb*, *Sibiricobombus*; *Cu*, *Cullumanobombus.*

** Data sources: Sladen, 1912; Plath, 1934; Medler, 1962; Hobbs, 1964, 1965; Richards, 1975; Haas, 1976; Sakagami, 1976; Plowright, 1977; Rasmont, 1988; Williams, 1991; Kearns and Thomson, 2001; Hagen and Aichhorn, 2003; original observations by the authors. Where a minority of species frequently show an opposing character state, these are placed in parentheses; where character states expressed are only by the first or early broods, these are shown in brackets. 'X' marks unobservable characters of *Psithyrus*.

each of three popular characters are not monophyletic, even if the early-diverging subgenera *Mendacibombus*, *Bombias*, and *Kallobombus* (Fig. 2) were also excluded from consideration. First, Sladen's (1912) group of 'pocket makers' is now known to include not only the subgenera *Subterraneobombus, Megabombus*, and *Thoracobombus*, as originally described, but also *Alpinobombus*, *Alpigenobombus*, and *Cullumanobombus*, at least as far as the early stages of nest development are concerned (Fig. 2). Second, Krüger's (1917) group of bumblebees with a spine on the mid basitarsus (his 'section' *Odontobombus*), which excited much interest because it was seen as being associated with Sladen's original group of pocket makers (*Subterraneobombus*, *Megabombus*, and *Thoracobombus*), also includes *Alpigenobombus* and *Sibiricobombus*, but excludes *Orientalibombus*, *Alpinobombus* and *Cullumanobombus* (Fig. 2). Third, tongue length (e.g. Medler, 1962), which is so important for governing food-plant preferences (e.g. Harder, 1983), is not only long as widely recognised (e.g. Kawakita et al., 2004; Cameron et al., 2007) for the group of subgenera *Orientalibombus*, *Subterraneobombus*, *Megabombus*, and some *Thoracobombus*, but is also long for a few *Melanobombus*, some *Alpinobombus*, and is characteristically long for *Sibiricobombus* (Fig. 2). As long ago as 1977, Plowright (1977) cast doubt on the supposed association between the two major taxonomic divisions of Krüger (1917) on the one hand and the two traditional groups of bumblebees by brood-rearing behaviour (Sladen, 1912) on the other.

In summary, we find that while it is straightforward to recognise monophyletic subgenera and to reduce their number, it is more difficult to choose clades that are either easily diagnosed morphologically, or clades that share important behavioural and ecological characters. In part this may be because 'the [morphological] homogeneity of the species in the genus is outstanding' (Michener, 2000, 2007). But from Figure 2, it also appears that there may be substantial homoplasy in behavioural characters. We consider that the proposed simplified subgenera reflect the pattern of variation in these characters more closely than recent subgeneric systems. What is needed now is to collect information on these characters in a consistent way and from many more species so that they can be mapped onto the phylogenetic tree more precisely in order to clarify this relationship.

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Classification simplifiée des sous-genres de bourdons (genre *Bombus*).

***Bombus* / sous-genre / phylogénie / classification**

Zusammenfassung – Eine vereinfachte Klassifikation der Untergattungen der Hummeln (Gattung *Bombus*). Hummeln sind farblich sehr variabel, morphologisch ansonsten aber relativ einheitlich. Um die Variation sinnvoll zu ordnen, besteht eine lange Tradition die Arten in Untergattungen zusammenzufassen und sich hierbei zunächst auf die Färbung, dann auf die Morphologie und neuerdings auch auf DNA Sequenzen zu stützen. Allerdings wurde bei 38 Unterarten in den derzeitigen Listungen die Notwendigkeit einer Vereinfachung des Systems gesehen. Wir besprechen die weiterhin bestehende Nützlichkeit des Systems von Untergattungen und erörtern vier mögliche als Leitlinie für Änderungen nutzbare Kriterien. Wir schlagen vor, dass Untergattungen (1) monophyletisch, (2) weniger, (3) aus der Morphologie erkennbar werden sollten und (4) zur Namensgebung wichtiger verhaltensmäßiger oder ökologischer Gruppen dienlich sein sollten. Unter Nutzung einer fast alle Hummeln einschließenden gut fundierten Abschätzung der Phylogenie besprechen wir Konflikte in der Nutzung dieser Kriterien und schlagen ein vereinfachtes System aus 15 Untergattungen vor, in der 10 neue Untergattungssynonyme anerkannt werden. Wir fanden es leicht, monophyletische Subgenera zu erkennen und ihre Anzahl zu reduzieren. Dagegen wurde es mit zunehmender Artenzahl immer schwieriger, Untergattungen zu definieren, die sowohl morphologisch leicht zu unterscheiden waren als auch einige der oft als besonders wichtig angesehenen verhaltensmässigen und ökologischen Eigenschaften teilen. Dies war deshalb der Fall, da entsprechend unserer vorläufigen Analyse einzelne Ausprägungen dieser Eigenschaften nicht ausschließlich von allen Arten einer morphologischen Gruppe geteilt werden.

Hummeln / *Bombus* / Untergattungen / Phylogenie / Klassifikation

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APPENDIX 1

Key to simplified subgenera of the genus **Bombus** *for female bumblebees*

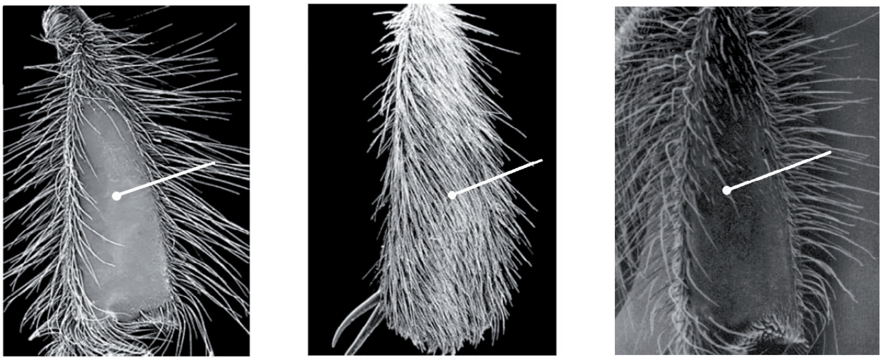
Paul H. WILLIAMS

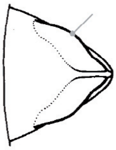
With SEM images by Michael Terzo, Pierre Rasmont, Paul Williams.

The keys have been simplified as far as possible to make them easier to use. Keys will generally be easier to use for larger and younger (less worn) individuals, and if they have had their mandibles opened and are cleaned of debris. Differences in the mid-basitarsal spine and face length are clearer for larger individuals and may be relatively undifferentiated for smaller individuals.

1 Hind tibia with the outer surface broad, almost flat, most of the outer surface in the distal half without moderate to long hairs (Fig. 3a arrow), but fringed with stout hairs that form a pollen basket (corbicula), the inner distal margin with a comb of stout spines (rastellum); gastral sternum 6 without ventro-lateral keels 2

- Hind tibia with the outer surface strongly and uniformly convex and uniformly densely covered with moderate to long stout hairs throughout (Fig. 3b arrow), the fringing hairs often poorly differentiated and not forming a pollen basket (corbicula), the inner distal margin without a comb of stout spines (rastellum); gastral sternum 6 with ventro-lateral keels (Fig. 4 arrow). (Holarctic, Oriental) ***Psithyrus***


3a 3b 3c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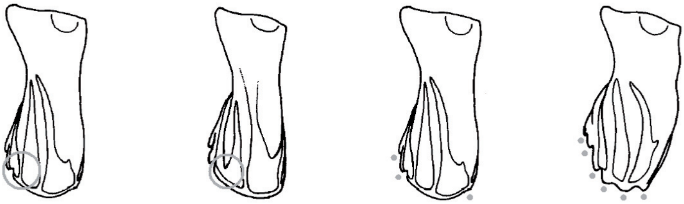
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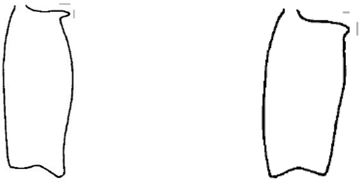
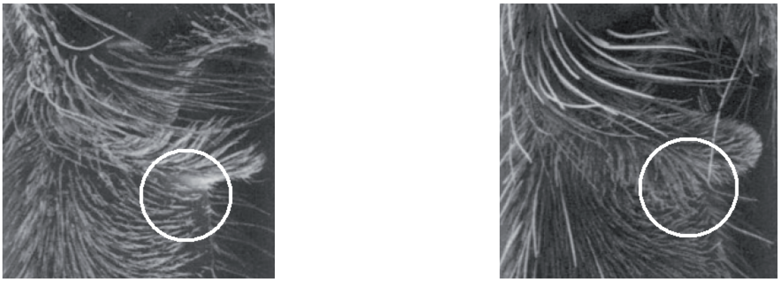
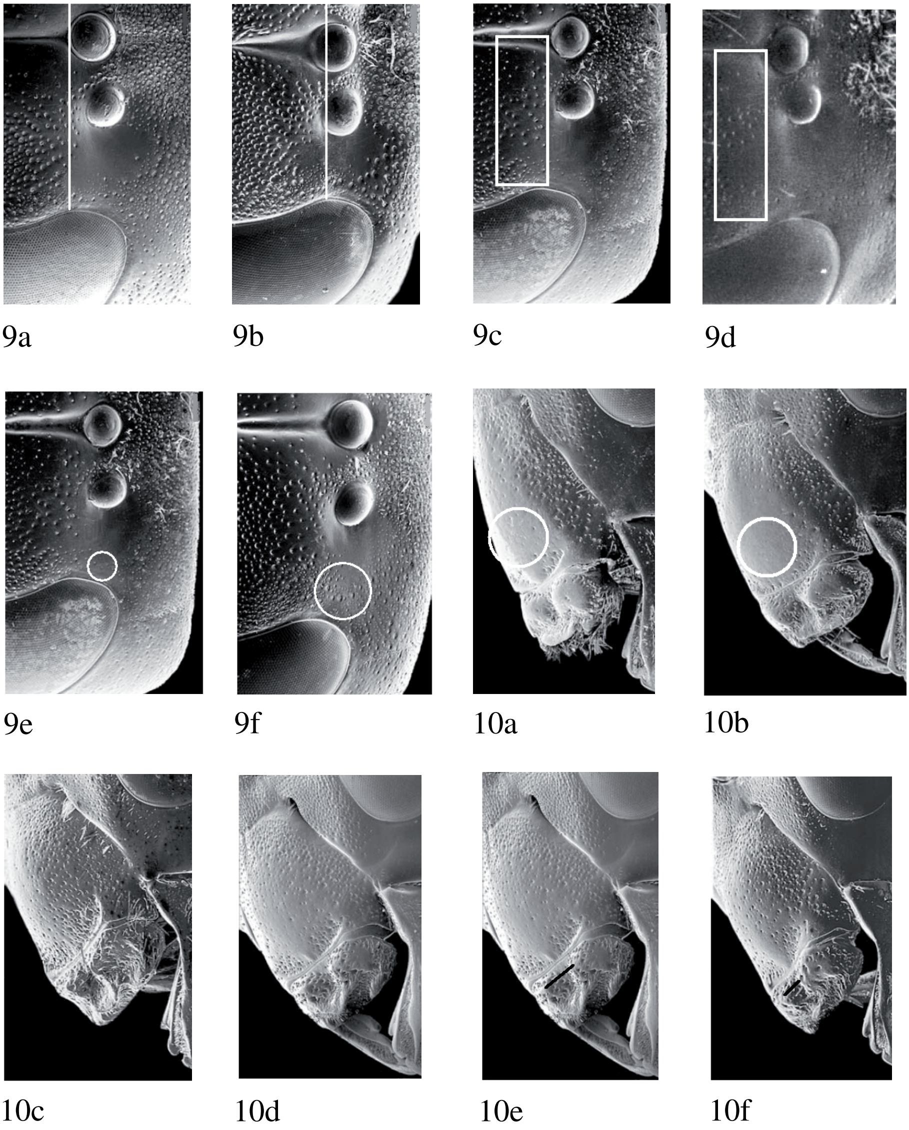

6a 6b

7a 7b


8a 8b

Figures 3–8. 3: Female left hind tibia from the outer lateral aspect for (a) *B.* (*Pr.*) *pratorum*; (b) *B.* (*Ps.*) *campestris*; (c) *B.* (*Md.*) *avinoviellus*. 4: Female sternum 6 from the ventral aspect for *B.* (*Ps.*) *morawitzianus*. 5: Female left mandible from the outer lateral aspect for (a) *B.* (*Ml.*) *rufofasciatus*; (b) *B.* (*Md.*) *avinoviellus*; (c) *B.* (*Ml.*) *rufofasciatus*; (d) *B.* (*Ag.*) *kashmirensis*. 6: Female left hind tibia from the outer lateral aspect for (a) *B. (Pr.) subtypicus*; (b) *B.* (*Md.*) *avinoviellus*. 7: Female left mid basitarsus from the outer lateral aspect for (a) *B.* (*Mg.*) *trifasciatus*; (b) *B.* (*Or.*) *haemorrhoidalis*. 8: Female proximal third of the left hind basitarsus from the outer lateral aspect of (a) *B.* (*Ml.*) *semenovianus*; (b) *B.* (*Sb.*) *oberti*. For all figures, anterior is towards the left of the page and posterior is towards the right. For explanations of the arrows and circles, see the text.



Figures 9–10. 9: Left half of the female head from the anterio-dorsal aspect of (a) *B.* (*Th.*) *pomorum*; (b) *B.* (*Sb.*) *niveatus*; (c) *B.* (*Pr.*) *pratorum*; (d) *B.* (*Or.*) *haemorrhoidalis;* (e) *B.* (*Pr.*) *pratorum*; (f) *B.* (*Kl.*) *soroeensis*. 10: Left ventral part of the female head from the anterio-lateral aspect of (a) *B.* (*Th.*) *pascuorum*; (b) *B.* (*St.*) *subterraneus*; (c) *B.* (*Bo.*) *terrestris*; (d) *B.* (*Cu.*) *cullumanus appolineus*; (e) *B.* (*Cu.*) *cullumanus appolineus*; (f) *B.* (*Kl.*) *soroeensis*. For all figures, anterior is towards the left of the page and posterior is towards the right. For explanations of the lines and circles, see the text.

2 (1) Mandible with the anterior keel reaching and continuous with the distal margin (Fig. 5a circled); hind basitarsus with the proximal posteriorly-directed process usually narrow and pointed, longer than its breadth proximally where it joins the basitarsus (Fig. 6a lines), or if it is shorter than broad then either the lateral ocellus diameter equal to half or less than half of the distance separating the lateral ocellus from the inner margin of the eye (e.g. some of the *hypnorum*-group of *Pyrobombus* and some *Melanobombus*, from the Palaearctic and Oriental), or the hair on the side of tergum 2 is longer than the breadth of the hind basitarsus and the labrum has a strong longitudinal median furrow and ventral transverse lamella (the rare parasitic *B.* (*Th.*) *inexspectatus*, from the Alps), or the hind basitarsus narrows distally to 0.66–0.75 times the proximal breadth just distal to the proximal process (*B.* (*Cu.*) *rubicundus* and *B.* (*Cu.*) *handlirschi*, from the Andes) 4

- Mandible with the anterior keel not reaching and separated from the distal margin (Fig. 5b circled); hind basitarsus with the proximal posteriorly-directed process broad and blunt, usually shorter than its breadth proximally where it joins the basitarsus (Fig. 6b lines); lateral ocellus diameter always nearly three quarters or more of the distance separating the lateral ocellus from the inner margin of the eye; either the hair on the side of tergum 2 is shorter than half of the breadth of the hind basitarsus, or the labrum lacks a distinct longitudinal median furrow and ventral transverse lamella, or both; hind basitarsus nearly equal in breadth distally and proximally beyond the proximal process 3

3 (2) Hind tibia with the outer surface coarsely sculptured (imbricate), matt and not shining, 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 (Fig. 3c arrow). (Palaearctic) . . . . ***Mendacibombus***

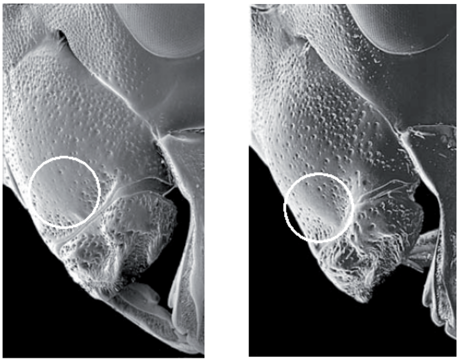
- Hind tibia with the outer surface weakly sculptured (reticulate coriaceous), smooth and brightly shining, and without long stout hairs in the middle of the proximal half beyond the proximal quarter (similar to Fig. 3a arrow). (Holarctic) . . . . ***Bombias***

4 (2) Mandible distally broadly rounded, with two anterior teeth and often a posterior tooth (Fig. 5c spots); hind basitarsus with the longest erect hairs near the anterior margin of the outer surface shorter than the narrowest breadth of the basitarsus 5

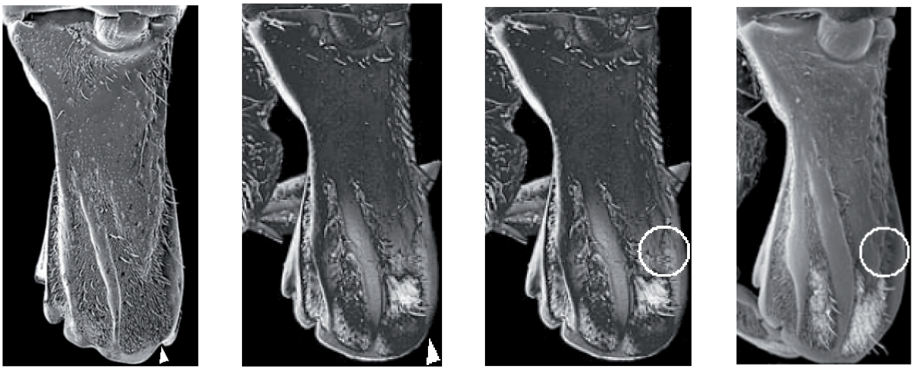
- Mandible distally not broadly rounded, but with six evenly-spaced large triangular teeth (which may become worn down) (Fig. 5d spots); hind basitarsus with the longest erect hairs near the anterior margin of the outer surface as long or longer than the narrowest breadth of the basitarsus (but which may become broken off). (Palaearctic, Oriental) . . . . ***Alpigenobombus***

5 (4) Mid basitarsus with the distal posterior corner extended to form a sharp angle of 45° or less, often produced as a narrow tooth or spine (Fig. 7a lines) (it may be less pronounced in some of the smallest individuals), or if borderline then the ocello-ocular area with the unpunctured and shining areas occupying less than half of the distance between the lateral ocellus and the inner margin of the eye (e.g. *B.* (*Th.*) *digressus*, from Central America, and *B.* (*Sb.*) *sibiricus*, from the eastern Palaearctic and Oriental). (Note: oculo-malar distance approximately 1.0–2.5 times the breadth of the mandible proximally between the outer ends of its articulations [condyles].) 6

- Mid basitarsus with the distal posterior corner broadly or narrowly rounded, but forming an angle of more than 45°, and without a narrow tooth or spine (Fig. 7b lines), or if borderline then the ocello-ocular area with the unpunctured and shining areas occupying three quarters of the distance between the lateral ocellus and the inner margin of the eye (e.g. *B.* (*Pr.*) *hypnorum*, from the Palaearctic and Oriental). (Note: oculo-malar distance approximately 0.5–1.6 times the breadth of the



10g 10h



11a 11b 11c 11d

Figures 10–11. 10: Left ventral part of the female head from the anterio-lateral aspect of (g) *B.* (*Cu.*) *cullumanus appolineus*; (h) *B.* (*Kl.*) *soroeensis*. 11: Female left mandible from outer lateral aspect of (a) *B.* (*Bo.*) *terrestris*; (b) *B.* (*Kl.*) *soroeensis*; (c) *B.* (*Kl.*) *soroeensis*; (d) *B.* (*Cu.*) *cullumanus appolineus*. For all figures, anterior is towards the left of the page and posterior is towards the right. For explanations of the arrows and circles, see the text.

mandible proximally between the outer ends of its articulations [condyles].) 9

6 (5) 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, or at most the outer surface with widely scattered rather decumbent short hairs with broad shining areas between them (Fig. 8a circled); median ocellus with its anterior margin lying on a line linking the corners between the anterior and dorsal margins of each compound eye (Fig. 9a line)............................7

- 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 a dense erect brush of moderately long branched hairs that obscures the outer surface of the basitarsus between them (Fig. 8b circled); median ocellus with its anterior margin lying anterior to a line linking the corners between the anterior and dorsal margins of each compound eye (Fig. 9b line). (Palaearctic, Oriental) .... ***Sibiricobombus***

7 (6) Clypeus with scattered large medium or small punctures over most of its area

(Fig. 10a circled), or at least extending onto the outer quarters of the weakly flattened, bulbous, central area (e.g. *B.* (*Mg.*) *hortorum*, from the Palaearctic), or forming very dense patches in the lateral depressions adjacent and parallel to the ventral labral margin (e.g. *B.* (*Mg.*) *senex*, from Sumatra); if the corbicular fringes are shorter than the greatest breadth of the hind tibia then the proximal half of the outer surface of the hind tibia has long hairs in the centre (and the body hair is all black: *B.* (*Th.*) *brevivillus*, from north-eastern Brazil); sternum 6 without a raised median longitudinal ridge in the posterior one third, or if a strong ridge is present then either the clypeus has medium and large punctures (e.g. *B.* (*Th.*) *muscorum*, from the Palaearctic) or antennal segment 4 is shorter than broad (e.g. *B.* (*Mg.*) *trifasciatus*, from the Oriental) 8

- Clypeus predominantly smooth and shining, the strongly flattened central area with only widely scattered micro-punctures (Fig. 10b circled), larger punctures only at the edges, or if more extensively covered with many small and medium punctures then the corbicular fringes are shorter than the greatest breadth of the hind tibia and the proximal half of the outer surface of the hind tibia has no long hairs in the centre beyond the proximal quarter (and the dorsal body hair is extensively yellow: *B. fragrans*, *B. fedtschenkoi*, and *B. amurensis*, from the central and eastern Palaearctic); sternum 6 with a raised and often shiny median longitudinal keel in the posterior one third. (Holarctic, Oriental) .... ***Subterraneobombus***

8 (7) Sternum 2 usually slightly bulging between the anterior and posterior margins in a weak rounded transverse ridge; hind tibia with the corbicular surface at least moderately convex anteriorly and often swollen and almost lacking any posterior concavity in the distal half, or if flatter then either the clypeus is densely punctured (e.g. *dahlbomii*-group, from the Neotropics), or the ocello-ocular area with the unpunctured and shining areas occupying two thirds of the distance between the lateral ocellus and the inner margin of the eye (e.g. *B. pomorum*, from the Palaearctic); clypeus dorsally uniformly convex and always without a deep dorsal median longitudinal groove with many punctures, clypeus in its central half with a few large punctures and sometimes densely punctured, or if it has only sparsely scattered fine punctures then there is no dorsal groove and the dorsal thoracic hair is largely orange-brown and segment 4 of the antenna is longer than broad (e.g. *B. pascuorum*, from the Palaearctic). (Note: oculo-malar distance approximately 1.0–1.5 times the breadth of the mandible proximally between the outer ends of its articulations [condyles].) (Holarctic, Oriental, Neotropics) .... ***Thoracobombus***

- Sternum 2 flat between the anterior and posterior margins, with the weakly bulging transverse ridge absent; hind tibia with the corbicular surface nearly flat and only very weakly convex anteriorly and concave posteriorly in the distal half; clypeus in its dorsal third often with a deep median longitudinal groove with many punctures (*supremus-consobrinus*-group), clypeus in its central half shining with only sparsely scattered small punctures and no large or dense punctures. (Note: oculo-malar distance approximately 1.0–2.5 times the breadth of the mandible proximally between the outer ends of its articulations [condyles].) (Palaearctic, Oriental) .... ***Megabombus***

9 (5) Ocello-ocular area with the unpunctured and shining areas medium or small, the area anterior to the three ocelli unpunctured for less than the breadth of an ocellus (Fig. 9c box), or if this area is largely unpunctured then the diameter of the lateral ocellus is more than half of the distance separating the lateral ocellus from the inner margin of the eye (e.g. *B.* (*Cu.*) *brachycephalus*, from Central America) 10

- Ocello-ocular area with the unpunctured and shining areas very large and 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 (Fig. 9d box); diameter of the lateral ocellus less than or equal to half of the distance separating the lateral ocellus from the inner margin of the eye. (Oriental) . . . . ***Orientalibombus***

10 (9) Mandible distally with a notch (incisura) nearly as deep as wide (Fig. 11a arrow) separating a strong posterior tooth (which may become worn down); clypeus in the dorsal half always strongly swollen and bulging, concave ventrally with deep lateral depressions adjacent and parallel to the labral margin (Fig. 10c); diameter of the lateral ocellus less than or equal to half of the distance separating the lateral ocellus from the inner margin of the eye; labrum always with a broad median longitudinal furrow; hind tibia outer surface in the proximal half without long hairs beyond the proximal quarter 11

- Mandible distally with a notch (incisura) less than half as deep as wide, or often completely lacking (Fig. 11b arrow) and not separating a weak posterior tooth; clypeus usually weakly swollen or nearly flat throughout, with only shallow lateral depressions adjacent and parallel to the ventral labral margin (Fig. 10d), or if it is strongly swollen dorsally and concave ventrally then either the diameter of the lateral ocellus is more than half of the distance separating the lateral ocellus from the inner margin of the eye (e.g. *B.* (*Cu.*) *brachycephalus*, from Central America), or the labrum has almost no median longitudinal furrow and the hind tibia has the outer surface in its proximal half with long hairs throughout (*B.* (*Cu.*) *rubicundus*, from the Andes) 12

11 (10) Hind basitarsus with the posterior margin strongly and evenly convex; oculo-malar distance just shorter or distinctly shorter than the breadth of the mandible proximally between the outer ends of its articulations (condyles). (Holarctic, Oriental) . . . . ***Bombus*** s. str.

- Hind basitarsus with the posterior margin strongly convex in its proximal quarter, the remainder nearly straight; oculo-malar distance longer than the breadth of the mandible proximally between the outer ends of its articulations (condyles). (Holarctic) . . . . ***Alpinobombus***

12 (10) Median ocellus with its anterior margin lying on a line linking the corners between the anterior and dorsal margins of each compound eye (similar to Fig. 9a line), the diameter of the lateral ocellus less than half or equal to half of the distance separating the lateral ocellus from the inner margin of the eye, or if the ocelli are larger and situated more anteriorly then the hind basitarsus has very densely overlapping pale short plumose hairs throughout the outer surface excluding the proximal posterior process (*B.* (*Ml.*) *rufofasciatus* and *B.* (*Ml.*) *simillimus*, from the Himalaya); hind basitarsus with the posterior margin convex in the proximal quarter, the remainder nearly straight, or if it is more evenly convex then this is weak and nearly straight (e.g. *B.* (*Kl.*) *soroeensis*, from the Palaearctic); mandible with the posterior groove (sulcus obliquus) indistinct or absent (Fig. 11c circled), or if stronger then again the hind basitarsus has very densely overlapping pale yellowish short plumose hairs throughout its outer surface excluding the proximal posterior process (e.g. *B.* (*Ml.*) *lapidarius*, from Europe); oculo-malar distance nearly as long as (0.9 times) or longer than the breadth of the mandible proximally between the outer ends of its articulations (condyles) 13

- Median ocellus with its anterior margin lying anterior to a line linking the corners between the anterior and dorsal margins of each compound eye (similar to Fig. 9b line), the diameter of the lateral ocellus more than half of the distance separating the lateral ocellus from the inner margin of the eye, or if the ocelli are smaller then the hind basitarsus has the posterior margin strongly and nearly evenly convex (*cullumanus*-group, from the Palaearctic); mandible with the posterior groove (sulcus obliquus) present (Fig. 11d circled); if the hind basitarsus on its outer surface has pale yellowish short plumose hairs, then they are not densely overlapping, at least in the proximal quarter; oculo-malar distance either equal to (e.g. *B. coccineus*, from the Andes) but may be much shorter than (0.5–1.0 times) the breadth of the mandible proximally between the outer ends of its articulations (condyles). (Holarctic, Neotropics) . . . . ***Cullumanobombus***

13 (12) Ocello-ocular area with the band of punctures along the inner margin of the eye almost always with very few small punctures, only scattered large punctures separated by more than their own widths (Fig. 9e circled), the unpunctured and shining areas usually large, occupying as much as three quarters of the distance between the lateral ocellus and the inner margin of the eye, or rarely the ocello-ocular area almost completely covered with very dense intermediate-sized punctures (*B. abnormis* and *B. mirus*, from the central Himalaya). (Holarctic, Oriental, northern edge of the Neotropics) . . . . ***Pyrobombus***

- Ocello-ocular area with the band of punctures along the inner margin of the eye always with many small and large punctures intermixed and separated by less than the widths of the large punctures (Fig. 9f circled), the unpunctured and shining areas occupying about half of the distance between the lateral ocellus and the inner margin of the eye 14

14 (13) Mid basitarsus with the longest erect hairs (which may become broken off) near the proximal margin of the outer surface from the posterior aspect as long as or longer than the distal breadth of the basitarsus, or if shorter then the hind tibia with the distal posterior corner extended into a finger-like process that is longer than broad (*B. festivus*, from the Oriental); labrum with the median longitudinal furrow broad, approximately one third of the total breadth of the labrum (similar to Fig. 10e line); clypeus shining with only widely scattered and mostly fine punctures (similar to Fig. 10g circled), or if there is a clearer median ventral area then it is not narrowly raised; hind tibia with the outer corbicular surface sometimes with short or medium hairs, but any long hairs are restricted to the proximal quarter or to the outer edges. (Note: body length 9–32 mm.) (Palaearctic, Oriental) . . . . ***Melanobombus***

- Mid basitarsus with the longest erect hairs near the proximal margin of the outer surface from the posterior aspect shorter than the distal breadth of the basitarsus; hind tibia with the distal posterior corner scarcely extended into a finger-like process, which is shorter than broad; labrum with the median longitudinal furrow narrow, approximately one fifth of the total breadth of the labrum (Fig. 10f line); clypeus in the central area densely covered with large and small punctures, except in a slightly narrowly raised ventral median longitudinal band which is unpunctured and shiny (Fig. 10h circled); hind tibia with the outer corbicular surface without short or medium hairs but sometimes with one or two scattered long stout hairs near the centre in the proximal half. (Note: body length 9–18 mm.) (Palaearctic) . . . . ***Kallobombus***

APPENDIX 2

Key to simplified subgenera of the genus **Bombus** *for male bumblebees*

Paul H. Williams

With photomontage images by Andrew Polaszek.

This key is based largely on morphological characters of the male genitalia (parts labelled in Fig. 12), because these characters are more reliable and more clearly distinctive than other morphological characters.

1 Gonostylus with the inner proximal process without medium-length branched hairs (Fig. 13a arrow); volsella and gonostylus usually strongly sclerotised and mid or dark brown in colour; 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

- Gonostylus with the inner proximal process associated with many medium-length branched hairs (Fig. 13b arrow); volsella and gonostylus usually weakly sclerotised and pale yellowish in colour; volsella always without a process or hooks on its inner margin; penis valve head always nearly straight. (Holarctic, Oriental) .... ***Psithyrus***

2 (1) Antenna medium to long, reaching back at least to the anterior margin of the tegula at the wing base; penis spatha narrowly and sharply pointed at its proximal end (Fig. 14a circled), or if rounded then the spatha is broader than long (*B.* (*Th.*) *digressus*, from Central America); penis valve head either straight, or curved inwards, or curved outwards; eye either enlarged or not enlarged relative to the females 4

- Antenna short, not quite reaching back to the anterior margin of the tegula at the wing base; penis spatha rounded at its proximal end (Fig. 14b circled); penis valve head always straight; eye always strongly enlarged relative to the females...........................3

3 (2) Volsella without a process or hook on its inner margin (Fig. 13c circled); volsella with long hairs on its outer distal margin but no hairs on its inner distal margin (Fig. 13f arrows); gonostylus simple and finger-like, without an inner proximal process, at most with a broad low proximal swelling (Fig. 13h circled). (Palaearctic).......***Mendacibombus***

- Volsella with a process or hook on its inner margin, either near the mid point of its length (Fig. 13d circled) or near its distal end (Fig. 13e circled); volsella with only short hairs on its outer and inner distal margins (Fig. 13g arrows); gonostylus either with an inner proximal process (Fig. 13i circled), or divided into dorso-ventral and horizontal lamellae (Fig. 13j arrows). (Holarctic) .... ***Bombias***

4 (2) Penis valve narrow dorso-ventrally, at least in its distal third, which is slightly ventrally curved (Fig. 15a between the lines); antenna either of medium length or longer, reaching to or beyond the tegula at the wing base 5

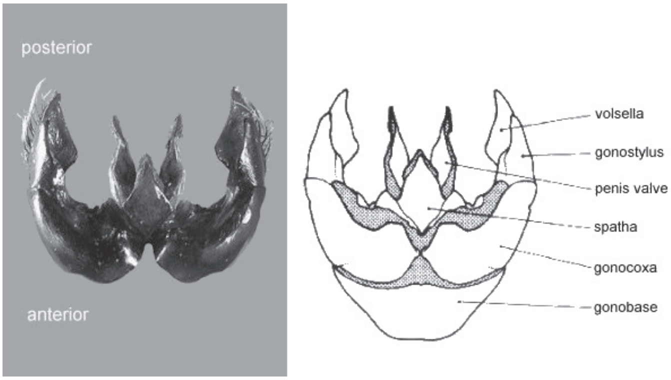
- Penis valve greatly broadened dorso-ventrally so as to form half of a broad tube (Fig. 15b between the lines), the distal end flared outwards as half of a broad funnel (Fig. 14c within the oval); antenna of medium length, not reaching back as far as the posterior margin of the tegula at the wing base. (Holarctic, Oriental) .... ***Bombus*** s. str.

5 (4) Penis valve head from the dorsal aspect turned inwards distally as a distinct broad hook, either dorso-ventrally flattened in the form of a sickle (Fig. 16a circled), or as an incurved spoon (Fig. 16b circled), or if the hook is strongly reduced (Fig. 19a circled) then the penis valve shaft has the ventral angle near its mid-point absent (similar to Fig. 15c arrow) although there is still a ventral rounded angle at the proximal end of the penis valve head (*B.* (*Cu.*) *funebris* and *B.* (*Cu.*) *rubicundus,* from the Andes) 10

- Penis valve head from the dorsal aspect distally either nearly straight (Fig. 16c circled) or turned slightly outwards (Fig. 16d circled), at most with only a tiny inwardly curved narrow point...............................6

6 (5) Gonostylus with a distinct inner proximal process separate from the distal lobe (Fig. 13l circled), or if there is only one lobe or process then either it is reduced to a freely articulating transverse curved inner spine-like plate and the gonocoxa has the inner distal corner extended as a finger-like process that is more than twice as long as broad (*B.* (*Th.*) *imitator*, from southern China), or the gonocoxa just before the distal margin has a deep oval sharply-defined mid-dorsal concavity and the spatha is nearly twice as broad as long (*B.* (*Th.*) *digressus*, from Central America) 7

- Gonostylus without a narrow inner proximal process (Fig. 13k circled), at most marked with a broad shallow curve or swelling, or if there is a very small sharp inner tooth then the distal lobe has a submarginal longitudinal groove (*Alpinobombus*); gonocoxa with the inner distal corner rounded and just before its distal margin convex without a mid-dorsal oval concavity; spatha longer than broad 8



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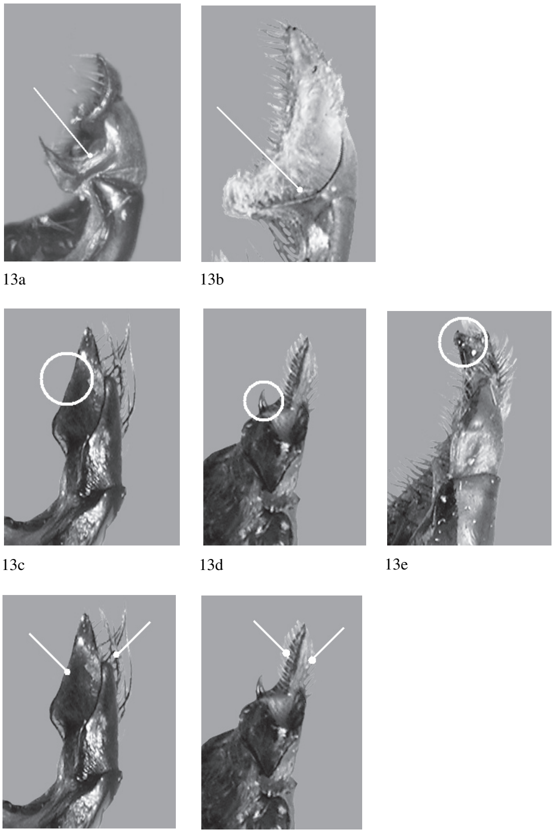
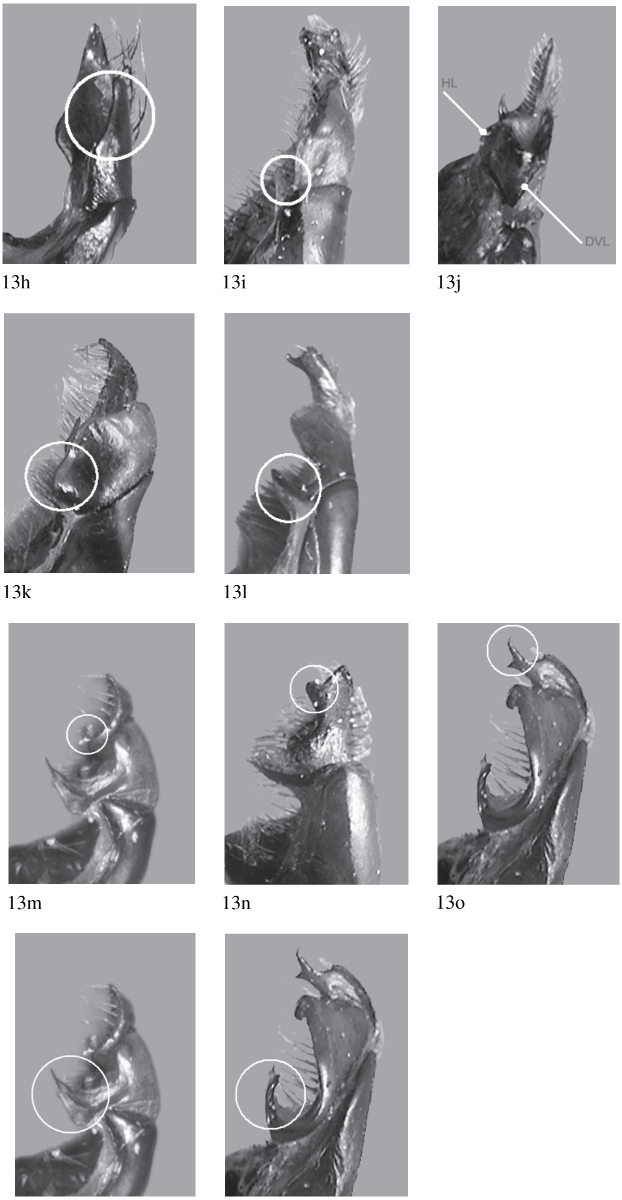


13a 13b

13c 13d 13e

13f 13g

Figures 12–13(a–g). 12: Male genital capsule from the dorsal aspect for *B.* (*Md.*) *avinoviellus*. 13: Male left gonostylus from the dorsal aspect for (a) *B.* (*Th.*) *impetuosus*; (b) *B.* (*Ps.*) *citrinus*; (c, f) *B.* (*Md.*) *avinoviellus*; (d, g) *B.* (*Bi.*) *confusus*; (e) *B.* (*Bi.*) *auricomus*. For all figures, anterior is towards the bottom of the page and posterior is towards the top. For explanations of the arrows and circles, see the text.



13h 13i 13j

13k 13l

13m 13n 13o

13p 13q

Figure 13(h–q). 13: Male left gonostylus from the dorsal aspect for (m, p) *B.* (*Th.*) *impetuosus*; (h) *B.* (*Md.*) *avinoviellus*; (j) *B.* (*Bi.*) *confusus*; (i) *B.* (*Bi.*) *auricomus*; (k) *B.* (*Or.*) *haemorrhoidalis*; (l) *B.* (*Sb.*) *asiaticus*; (n) *B.* (*Th.*) *mexicanus*; (o, q) *B.* (*Mg.*) *koreanus*. For all figures, anterior is towards the bottom of the page and posterior is towards the top. For explanations of the arrows and circles, see the text.

13r 13s

13t 13u

13v 13w

13x 13y 13z 13aa

Figures 13(r–aa). 13: Male left gonostylus from the dorsal aspect for (u, w) *B.* (*Or.*) *haemorrhoidalis*; (r, t, v) *B.* (*Kl.*) *soroeensis*; (s) *B.* (*Al.*) *alpinus*.; (x) *B.* (*Pr.*) *flavifrons*; (y) *B.* (*Pr.*) *pressus*; (z) *B.* (*Cu.*) *macgregori*; (aa) *B.* (*Cu.*) *handlirschi*. For all figures, anterior is towards the bottom of the page and posterior is towards the top. For explanations of the arrows and circles, see the text.

7 (6) Volsella in ventral aspect in its distal half broad, the inner hooks (absent in *B. persicus*, from Turkey and Iran) placed either close to the midpoint of its length between its broadest point and the distal end (Fig. 13m circled), or if close to the distal end then reduced to a broad blunt process (Fig. 13n circled); gonostylus with the inner proximal process often weakly sclerotised in the ventral part of the shelf, and if it has a long spine then this is usually nearly straight, sharp and inwardly pointed (Fig. 13p circled); hind tibia with the outer surface inside the posterior margin convex, or if concave then the penis valve head has an outer proximal hook that is longer than the breadth of the adjacent penis valve head (*B. dahlbomii* and *B. morio*, from South America). (Holarctic, Oriental, Neotropics) .... ***Thoracobombus***

- Volsella in ventral aspect in its distal half narrow, the inner hooks pointed and always placed close to the distal end (Fig. 13o circled); gonostylus with the inner proximal process uniformly strongly sclerotised and strongly re-curved away from the body midline and back towards the distal part of the gonostylus, with either at least one long strongly curved tubular spine with a blunt tip or flatter and with many teeth (Fig. 13q circled); hind tibia with the outer surface inside the posterior margin concave, or if convex then the volsella has the more proximal of the inner hooks with many radiating teeth (*diversus*-group, from eastern Asia). (Palaearctic, Oriental) .... ***Megabombus***

8 (6) Gonostylus with the inner distal margin simple, flattened, and blade-like in cross section (Fig. 13r between the lines); antenna very long, reaching distinctly beyond the wing base; hind basitarsus with the posterior fringe shorter than the greatest breadth of the basitarsus 9

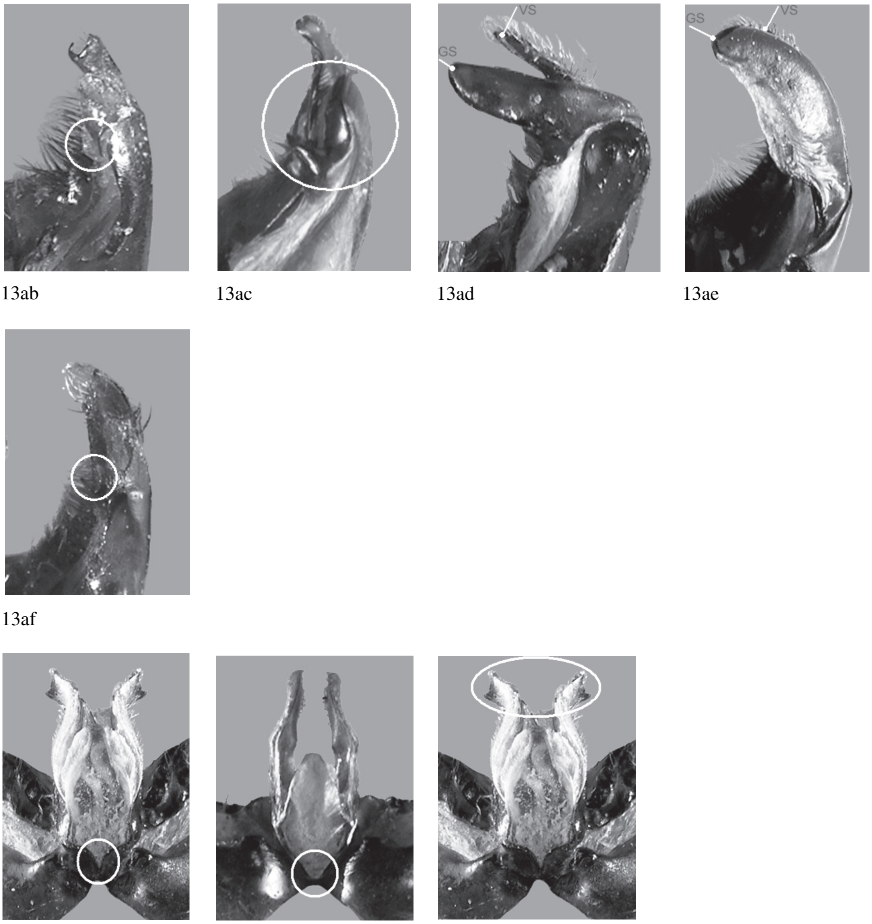
- Gonostylus with the inner distal margin thickened in cross section, with a submarginal longitudinal groove (Fig. 13s between the lines); antenna long, reaching only as far as the posterior margin of the tegula at the wing base; hind basitarsus with the posterior fringe longer than the greatest breadth of the basitarsus. (Holarctic) .... ***Alpinobombus***

9 (8) Penis valve head turned outwards and flattened like an axe head (Fig. 16d circled); gonostylus longer than broad (Fig. 13t circled); volsella narrow, the inner hook near the distal end (Fig. 13v circled); hind basitarsus with an anterior face flattened proximally, the proximal outer process at the articulation with the tibia strongly produced, as long as proximal breadth. (Palaearctic) .... ***Kallobombus***

- Penis valve head straight, narrowed, and pointed like a spear head (Fig. 16c circled); gonostylus shorter than broad (Fig. 13u circled); volsella broad, the inner hook near the mid point of its length (Fig. 13w circled); hind basitarsus with the anterior margin rounded in section proximally, the proximal outer process at the articulation with the tibia weakly produced, shorter than proximal breadth. (Oriental) .... ***Orientalibombus***

10 (5) Gonostylus usually a simple triangle, always without an inner proximal process (Fig. 13x circled), or if reduced to a single long stout pointed spine (Fig. 13y circled) then the penis valve head has an outer flange broader than the adjacent penis valve head and projecting ventrally and laterally (the rare *B. pressus*, from the central Himalaya); gonostylus with the inner distal margin at least slightly thickened in cross section with a submarginal longitudinal groove (similar to Fig. 13s between the lines). (Holarctic, Oriental, northern edge of the Neotropics) .... ***Pyrobombus***

- Gonostylus very variable in shape, but usually with a distinct inner proximal process (e.g. Fig. 13l circled), or if this is strongly reduced or absent (Fig. 13z, aa circled) then the distal lobe of the gonostylus is greatly expanded distally and projecting inwardly beyond the volsella (Fig. 13ad, ae arrows) (*B.* (*Cu.*) *macgregori*, from Central America, and *B.* (*Cu.*) *handlirschi*, from the Andes); gonostylus with the inner distal margin simple, flattened and blade-like in cross



13ab 13ac 13ad 13ae

13af

14a 14b 14c

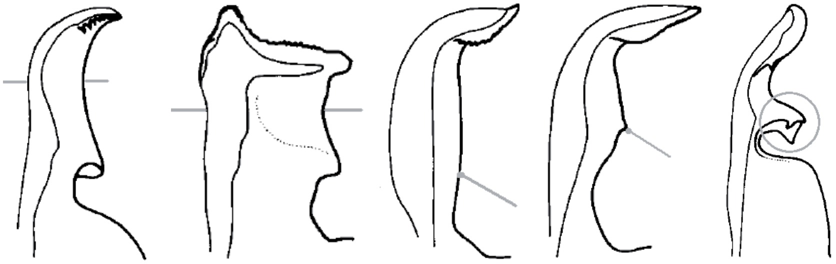
Figures 13(ab–af)–14(a–c). 13: Male left gonostylus from the dorsal aspect for (ad) *B.* (*Cu.*) *macgregori*; (ae) *B.* (*Cu.*) *handlirschi*; (ab) *B.* (*Ml.*) *festivus*; (ac) *B.* (*Ml.*) *eximius*; (af) *B.* (*Cu.*) *rufocinctus*. 14: Male spatha and penis valves from the dorsal aspect for (a, c) *B.* (*Bo.*) *patagiatus*; (b) *B.* (*Md.*) *convexus*. For all figures, anterior is towards the bottom of the page and posterior is towards the top. For explanations of the arrows and circles, see the text.

section without a submarginal longitudinal groove 11

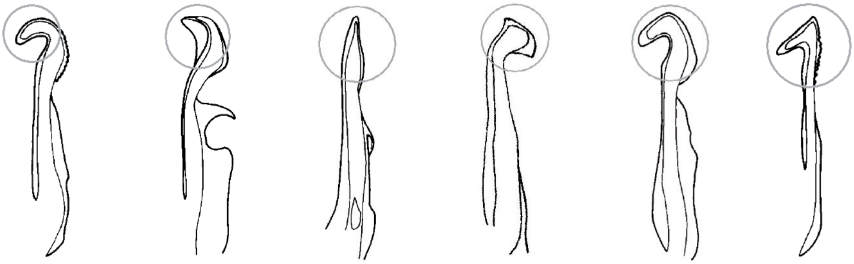
11 (10) Penis valve shaft with a ventral angle about half way along its length and distinct either as a pronounced sharp angle (Fig. 15d arrow) or produced as a larger transverse process (Fig. 15e circled) 12

- Penis valve shaft with a ventral angle about half way along its length either reduced and very broadly rounded (not sharply marked) or absent (Fig. 15c arrow), although there may be an additional ventral rounded angle at the proximal end of the penis valve head (most easily confused in e.g. *B.* (*Cu.*) *rubicundus* and *B.* (*Cu.*) *funebris*, from the Andes) 13

12 (11) Penis valve head turned inwards distally as an incurved bowl-shaped spoon (Fig. 16b circled); penis valve shaft with the ventral angle about half way along its length produced ventrally and laterally

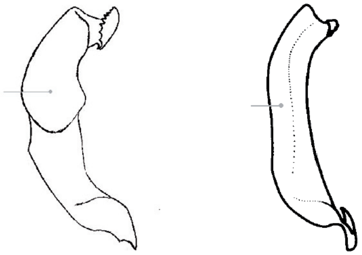


15a 15b 15c 15d 15e

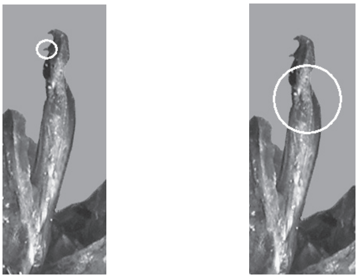


16a 16b 16c 16d 16e 16f

17



18a 18b



19a 19b

Figures 15–19. 15: Male left penis valve from the outer lateral aspect for (a) *B.* (*Mg.*) *trifasciatus*; (b) *B.* (*Bo.*) *lucorum* s.l.; (c) *B.* (*Sb.*) *asiaticus*; (d) *B.* (*Ag.*) *kashmirensis*; (e) *B.* (*St.*) *melanurus.* 16: Male left penis valve from the dorsal aspect for (a) *B.* (*Pr.*) *hypnorum*; (b) *B.* (*St.*) *melanurus*; (c) *B.* (*Or.*) *haemorrhoidalis*; (d) *B.* (*Kl.*) *soroeensis*; (e) *B.* (*Ag.*) *kashmirensis*; (f) *B.* (*Ml.*) *keriensis*. 17: Male left mandible from the outer lateral aspect for *B.* (*Ag.*) *kashmirensis*. 18: Male left volsella from the ventral aspect for (a) *B.* (*Cu.*) *robustus*; (b) *B.* (*Ml.*) *keriensis*. 19: Male left penis valve from the dorsal aspect for (a, b) *B.* (*Cu.*) *rubicundus*. For all figures except Figure 17, anterior is towards the bottom of the page and posterior is towards the top. For explanations of the arrows and circles, see the text.

as a broad transverse paddle-like process (Fig. 15e circled); mandible distally pointed and with one anterior tooth. (Holarctic, Oriental) .... ***Subterraneobombus***

- Penis valve head turned inwards distally as a dorso-ventrally flattened sickle (Fig. 16e circled); penis valve shaft with the ventral angle about half way along its length produced ventrally as a pronounced angle (Fig. 15d arrow); mandible distally pointed and with two anterior teeth (Fig. 17 spots). (Palaearctic, Oriental) .... ***Alpigenobombus***

13 (11) Mid basitarsus on its outer surface with many medium and long hairs; gonostylus with the distal lobe longer or shorter than broad; oculo-malar distance longer or shorter than the breadth of the mandible proximally between the outer ends of its articulations (condyles); antenna either medium or long, reaching to or beyond the tegula at the wing base 14

- 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; oculo-malar distance always longer than the breadth of the mandible proximally between the outer ends of its articulations (condyles); antenna usually very long, reaching distinctly beyond the wing base, or if shorter and reaching only to the posterior margin of the tegula then the recurved hook of the penis valve head is strongly club-shaped (the rare *B. oberti*, from Central Asia). (Palaearctic, Oriental) .... ***Sibiricobombus***

14 (13) Oculo-malar distance at least as long as the breadth of the mandible proximally between the outer ends of its articulations (condyles); gonocoxa with the inner proximal process about as long as broad; either the penis valve head narrowed as a short slender barbed arrow head without a dog-leg (Fig. 16f circled) (*simillimus-lapidarius*-group, from the Palaearctic and Oriental regions), or the gonostylus with the shelf of the inner proximal process membranous (Fig. 13ab circled) (*B. festivus*, from the Oriental region), or the gonostylus reduced to a narrow S-shaped band (Fig. 13ac circled) (*rufipes*-group, from the southern Oriental region); volsella, if it is thickened ventrally, then this forms only a narrow more coarsely-sculptured band extending for most of the length of the volsella (Fig. 18b arrow); antenna of medium length, not reaching beyond the posterior margin of the tegula at the wing base. (Palaearctic, Oriental) .... ***Melanobombus***

- Oculo-malar distance shorter than the breadth of the mandible proximally between the outer ends of its articulations (condyles), or if equal in length then the gonocoxa with the inner proximal processes finger-like and more than twice as long as broad (*B. coccineus*, from the Andes); penis valve head either not narrowed, or if narrowed then forming an elongated spear head with a small dog-leg proximally (Fig. 19b circled) (*B. rubicundus*, from the Andes); gonostylus either with a strongly sclerotised inner proximal process, or together with the inner distal lobe reduced to two small teeth (Fig. 13af circled) (*B. rufocinctus*, *B. cullumanus*, from the Holarctic region), or if absent then the distal lobe is strongly produced distally and inwardly beyond the volsella (Fig. 13ad, ae arrows) (*B. handlirschi* and *B. macgregori*, from the Andes and Central America); volsella expanded ventrally into a short pear-shaped coarsely-sculptured thickened pad in its distal half (Fig. 18a arrow), or if it is thickened ventrally only as a narrow more coarsely-sculptured band extending for most of the length of the volsella (similar to Fig. 18b arrow) then either the gonostylus has the inner processes reduced to two small teeth (Fig. 13af circled) (*B. rufocinctus*, *B. cullumanus*), or the gonostylus is strongly produced distally and inwardly beyond the volsella (Fig. 13ad arrows) (*B. handlirschi*, from the Andes); antenna either of medium length or longer, reaching to or beyond the tegula at the wing base. (Holarctic, Neotropics) .... ***Cullumanobombus***