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An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini)

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CONTENTS

SYNOPSIS. Bumble bees are among the minority of groups of organisms for which there is some evidence that most species have already been described. Nonetheless, a synoptic revision of the group has been delayed, in part by the difficulties imposed by an unusually high ratio of names to species (averaging more than 11). To explore some of the factors contributing to this phenomenon, historical and geographical trends in the naming of bumble bees are summarised. This shows that most taxa were named by European authors, beginning with the most widespread European species, moving later to not only the more narrowly distributed species and to species from other parts of the world, but also to taxa at progressively lower nomenclatural ranks, particularly within the more widespread European species. Nearly half of all of these names have been published since the last world-wide checklist in 1922. In attempting to bring this up to date, the present checklist adopts broad interpretations of species and recognises a total of 239 recent species (including the social parasites but excluding fossil taxa), with 24 new synonyms and 29 provisional synonyms. The list also includes notes on alternative interpretations of taxonomic status and on nomenclatural problems, drawing attention to those cases where further research is most urgently needed. In particular, suggestions are presented for an application to the International Commision on Zoological Nomenclature to use its Plenary Power in order to conserve current usage of the commonly used names *atratus, balteatus, distinguendus, flavifrons, humilis, hyperboreus, mesomelas, mixtus, norvegicus, polaris, pyrenaeus, soroeensis* and *variabilis*.

INTRODUCTION

Bumble bees have long been popular with collectors. Just as with butterflies, part of the attraction may be explained by their bright colours, large body size, activity during daylight hours, and abundance in the north-temperate regions where most collectors have lived. As a result, large samples of bumble bee specimens have now been assembled, even from remote parts of the world.

A problem for biologists trying to identify bumble bee species, all the more apparent because of the large amount of material available, is that while bumble bees can be described as morphologically relatively 'monotonous' (Michener, 1990), they are often extraordinarily variable in the colour patterns of their pubescence. The situation is made worse by a strong tendency for species to converge locally on different colour patterns (Plowright & Owen, 1980).

Faced with this variation, generations of taxonomists since the starting point of Linnaean nomenclature in 1758 have described differing individuals under a plethora of more than 2800 formal names (Williams, unpublished catalogue, including names for species, subspecies and synonyms, as well as infrasubspecific names, misspellings and other unavailable names). Most of these names are for taxa below the rank of species, and just 239 taxa are interpreted here as separate species. Arguably, the nomenclatural burden of more than 11 names per species (median 5, maximum 186) has slowed progress towards a complete revision of the group. Hence there is a need for an overview which, although bound to require revision, will provide an improved framework for more detailed regional studies. It is also important to understand any regional or taxon-directed bias in patterns of taxonomic description when seeking to interpret patterns in diversity, ecology and biogeography. The present checklist begins to address these needs.

Past lists of species

There have been few attempts to present complete revisions, catalogues or checklists of all bumble bee species from which to see summaries of past views. Latreille (1809) included 13 species in his genus *Bombus*. Most of the early lists included just those species seen by their authors, usually from particular collections, and often from just one region. For example, Smith (1854) catalogued 87 bumble bee species (79 *Bombus* + 8 *Apathus* [= *Psithyrus*]) in the collection of the British Museum. The only truly synoptic catalogue of bumble bees was published by Dalla Torre (1896), with 255 (non-fossil) species (228 *Bombus* + 27 *Psithyrus*). It included many varietal names, synonyms and early references. The reason why Dalla Torre's species count exceeds the total now recognised as described before 1899 (159 species, Fig. 1) is of course that many of his species are now treated as synonyms or subspecies. Later, Skorikov (1922*a*) listed 237 species (plus 70 '*Bombi incertae sedis*'), but with few synonyms and without including *Psithyrus*. Nonetheless, Skorikov's list did arrange most of the known species within his genera and subgenera, which form the basis of the current subgeneric system (Richards, 1968).

Taken together, the few past lists of bumble bees show that the number of taxa accepted as species at a particular date grew rapidly during the nineteenth century, but has since remained relatively stable, with a slight decline to the conservative estimate of 239 species in the present list. Undoubtedly part of the explanation for this decline lies in the relatively conservative species concept accepted at present (see below). This reflects a gradual shift in emphasis among criteria for recognising species from the use of colour characters to the use of morphological characters, particularly to using characters of the male genitalia (see the introductory comments by Radoszkowski, 1884). A similar pattern of growth and decline has been found for past numbers of milkweed butterfly species (Ackery & Vane-Wright, 1984). However, there might now be another period of rapid growth if molecular characters and phylogenetic species concepts (discussed below) were to be applied (cf. discussion of the number of bird species by Martin, 1996; Patterson, 1996; Zink, 1996, 1997; Snow, 1997).

History of discovery of species

The dates of first formal description for the currently recognised bumble bee species show that the highest rates of species discovery were in the latter half of the nineteenth century through to the First World War (Fig. 1, median date 1877). These species are recognised retrospectively from the present list, rather than as the numbers accepted within each time period. The larger dips in overall rate of discovery may be associated with factors such as war and its aftermath (e.g. Napoleonic and Second World Wars), presumably through constraints on resources and on freedom of travel.

Some authors described many more bumble bee species than others: 45% of presently accepted species were described by just 10% of the authors who described these species (Smith 32 species, Skorikov 19, Cresson 17, Morawitz 15, Radoszkowski 13, and Friese 12). Similarly, Gaston, Scoble & Crook (1995) found a skewed pattern of activity among authors describing geometrid moths. But of the six authors who described the most bumble bee species, only Ezra Cresson (Snr) actually worked in the New World, whereas the other five were based in Europe (including European Russia).

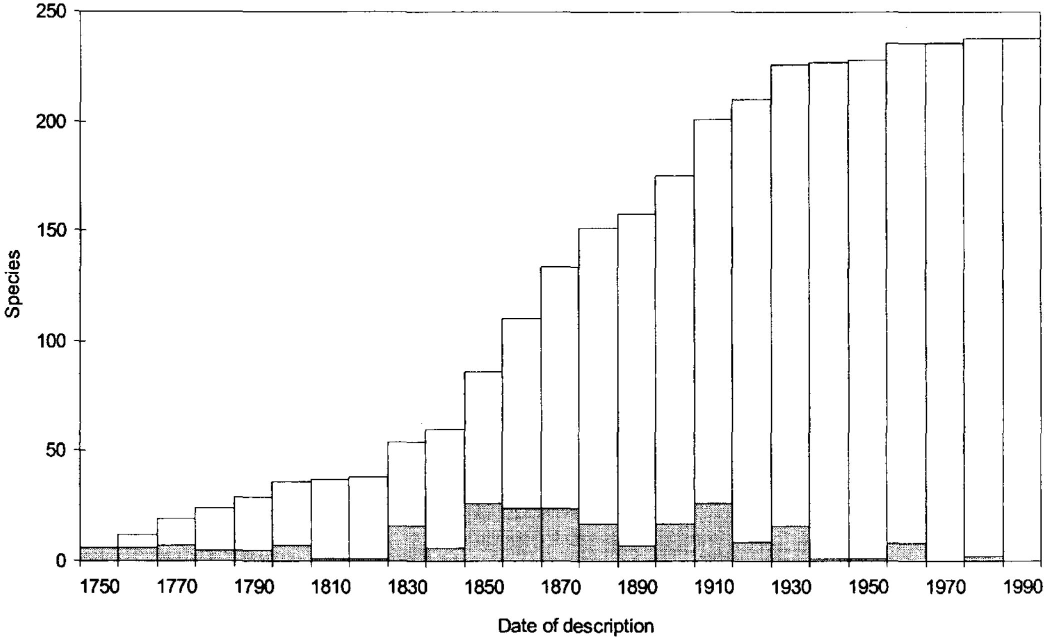

Fig. 1 Rate (lower grey) and cumulative number (upper white) of first formal descriptions of presently recognised bumble bee species (dates from the oldest available names in the sense of ICZN, 1985).

Rates of discovery of bumble bee species vary to some extent among biogeographic regions (Fig. 2). Again, this was also found for geometrid moths by Gaston, Scoble & Crook (1995). For bumble bees, the recent proportional discovery rates have been lowest in the New World and highest in the Oriental Region. The Neotropical Region appears to have a small known bumble bee fauna for its large area. There is no obvious evidence that descriptive effort has been lacking, although detailed revisionary work is needed and species with small range sizes may remain to be discovered. In contrast, the Oriental Region's high recent proportional rate of species discovery, despite its smaller area than the other regions, is possibly explained in part because it has been studied intensively for a shorter period.

The world-wide rate of discovery of genuinely unknown bumble bee species appears now to be slowing down (Fig. 1). Undiscovered species are very likely to remain, although there is no evidence that large numbers of species are awaiting description in collections (although some known subspecific taxa might yet be recognised as species if changes were to occur in species concepts or in the availability of character evidence, see Martin, 1996; Patterson, 1996; Zink, 1996). The sigmoidal pattern of species discovery in Fig. 1 is also shown by a few other relatively well known groups such as birds, although for most large groups (including Hymenoptera as a whole) the rates of description continue to be high or are even increasing (Hammond in Groombridge, 1992; Tennessen, 1997).

History of publication of names

The present checklist is intended only to address the question of taxa at the rank of species (see below). For this purpose it is not necessary to consider concepts of taxa at the rank of subspecies and below and subspecific names may be treated in analyses as further synonyms of species (Gaston & Mound, 1993). This is not to say that subspecific taxa ought not to be recognised if they were considered useful in the context of other studies. In addition, some authors have applied classical names to taxa at even lower nomenclatural ranks, for example in referring to 'varieties' or 'forms' within subspecies. These are now interpreted as infrasubspecific names and are 'unavailable' for use in the sense of the *International Code of Zoological Nomenclature* (ICZN, 1985). They have had to be included in a manuscript catalogue (unpublished) in order to avoid confusion by explicitly resolving questions of nomenclatural status and availability. Infrasubspecific names are included in this analysis as a category separate from specific or subspecific names because of their particular significance for understanding historical patterns in the description of diversity at the lowest nomenclatural ranks.

Bumble bees have the highest known levels of synonymy (83%, or 92% if infrasubspecific names were to be included) in comparison with the range of insect taxa reviewed by Gaston & Mound (1993). Their results showed synonymy levels ranging from 7% for Siphonaptera to 80% for Papilionidae and

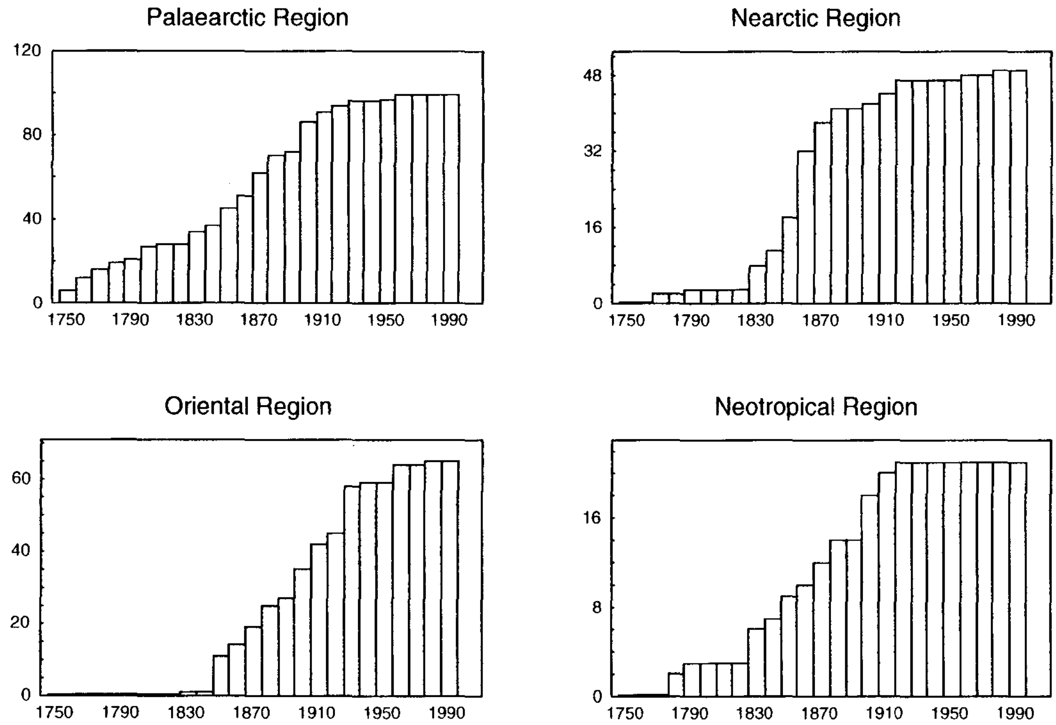
Palaearctic Region
Nearctic Region
Oriental Region
Neotropical Region

Fig. 2 Cumulative number of first formal descriptions of presently recognised bumble bee species with centres of area of occupancy (so species lists do not overlap) in each of the four principal biogeographic regions occupied by bumble bees (dates from the oldest available names in the sense of ICZN, 1985; regions defined in Williams, 1996*b*: fig. 1; Oriental includes northern and southern Oriental Regions; Nearctic includes northern, central and southern Nearctic Regions; Neotropical includes northern, central and southern Neotropical Regions; the Arctic Region is excluded; species that are exclusively peri-Tibetan Oriental but which nevertheless have range centres in Palaearctic central Tibet by simple range averaging are included as Oriental species).

Pieridae combined. It must be born in mind that the insect taxa that they surveyed are all more speciose than the bumble bees by a factor of at least four, and extreme values for larger groups are less likely. Nonetheless, Gaston & Mound (1993) also noted that the two families of most brightly coloured butterflies have the highest levels of synonymy and that these families have many more subspecific names than the smaller and duller-coloured hesperiid butterflies. R. I. Vane-Wright (pers. com.) suggests that synonymy rates may be particularly high among the large, colourful butterflies of the Danainae and *Parnassius*.

In contrast to the discovery of currently recognised species, the greatest activity in publishing names for all supposed bumble bee taxa at the rank of species and below was concentrated slightly later than for presently recognised species, in the first half of the twentieth century (Fig. 3, median date 1922). This difference may be explained in part by the logical inevitability that synonyms and names for taxa below the rank of species can only be published subsequently to valid species names (i.e. the oldest available names, excluding junior homonyms, in the sense of ICZN, 1985). If these names were in effect to represent the redescription of known species at random, then the earlier described species might be expected to have accumulated more names. Studies of other taxa have also shown that both the date of first description and the number of synonyms per species may be affected by variation in the size of a species' geographic range (as well as by other factors such as body size). Large range size is likely to affect the date of first description because it contributes to a greater 'apparency' of the species to collectors (Gaston, Blackburn & Loder, 1995), particularly as broad correlations between range size and abundance suggest that widespread species also tend to have higher local densities (Brown, 1984; Gaston, 1994; for bumble bees, see Hanski, 1982; Williams, 1988). Apart from enhancing the chances of random redescription, large range size is also likely to affect the number of synonyms because there is a greater likelihood that specimens collected in one area will be regarded as

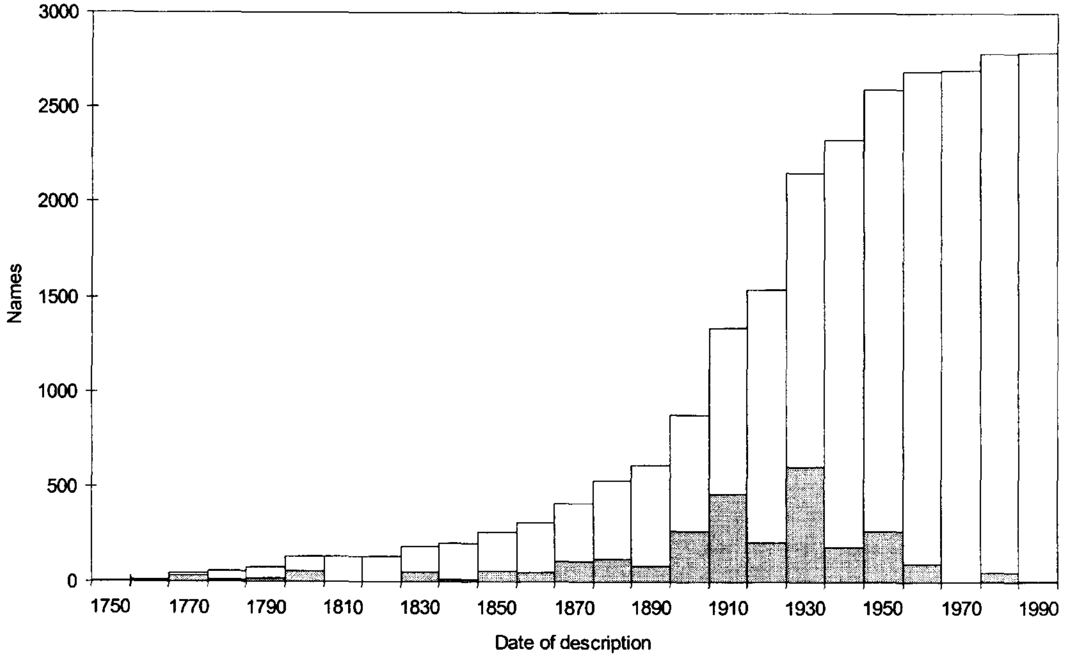

Fig. 3 Rate (lower grey) and cumulative number (upper white) of all descriptions with classical names for bumble bee species, subspecies and infrasubspecies since the starting point of zoological nomenclature in 1758 (from a manuscript catalogue, unpublished).

distinct from specimens collected from another distant area, because character variation is apt on average to be greater (Gaston, Blackburn & Loder, 1995).

For the bumble bee catalogue data, the number of synonyms (including subspecies, but excluding infrasubspecies) is correlated with both the date of first description and the range size of a species independently of one another, although slightly more of the variation is explained by variation in range size (partial *r*, Table 1). Many of the species with large range sizes, early dates of first formal description and many synonyms are found in western Europe (i.e. triangles at the left and upper part of Fig. 4). Most of these species occur in either the lowland areas of Europe where early naturalists were most active, such as Britain, or else are nearly circumpolar in their distribution.

Curiously, all of the infrasubspecific names (34% of all names as interpreted at present) belong to the bumble bee species of the Old World (Fig. 5). Species of the Old World also have more synonyms and subspecies per species than do the species of the New World (numbers of names log-transformed and excluding 6 Holarctic species, t_{232}= 3.81 with separate variance estimates, p< 0.001).

One possible explanation for the greater numbers of names per species for bumble bees of the Old World is that they might have broader distributions than the species of the New World (see above). This could arise because the Old World has a slightly larger total area of suitable habitat (bumble bees occupy 131 of the 611,000 km^2 grid cells in the Old World and 117 in the New), which is apparently subdivided into fewer well differentiated biogeographic assemblages of bumble bee species (e.g. Williams, 1996*b*: fig. 1). However, this explanation is not strongly supported by the bumble bee data, which show the difference in range sizes between the two hemispheres to be not significant, (range sizes log-transformed and excluding 6 Holarctic species, t_{232}= –1.24 with separate variance estimates, p= 0.22). Consequently, while an effect of differences in habitat area will deserve future consideration, other effects are likely to be more important.

A second possibility is that whereas bumble bee taxa of uncertain rank may have tended to be regarded more often as subspecies in the Old World, in the New World they may have tended to be regarded as species (see the discussion below of criteria to recognise species). While this factor could have contributed to the observed patterns, it is unlikely to explain why (at a lower rank) so many infrasubspecific names were described exclusively for taxa from the Old World.

A third possibility is that the diversity of languages used for taxonomic publications in the Old World may

Table 1 Results of multiple regression of numbers of synonyms/subspecific names (infrasubspecific names are excluded; from a manuscript catalogue, unpublished) on date of first formal description for presently accepted species and range size (number of occupied 611,000 km² grid cells world-wide). Partial *r* values indicate the correlations with the synonyms variable after adjusting for the other predictor variable in each case.

$\log_{10}(\text{synonyms}+1) = 6.316(\pm 0.969) - 0.003(\pm 0.0005).\text{date} + 0.401(\pm 0.057).\log_{10}(\text{range})$

	multiple $r = 0.72$	$F_{(2,236)} = 129.76$	$p < 0.0001$
	partial r	t_{236}	p
date	−0.390	−6.51	< 0.0001
$\log_{10}$(range)	0.418	7.08	< 0.0001

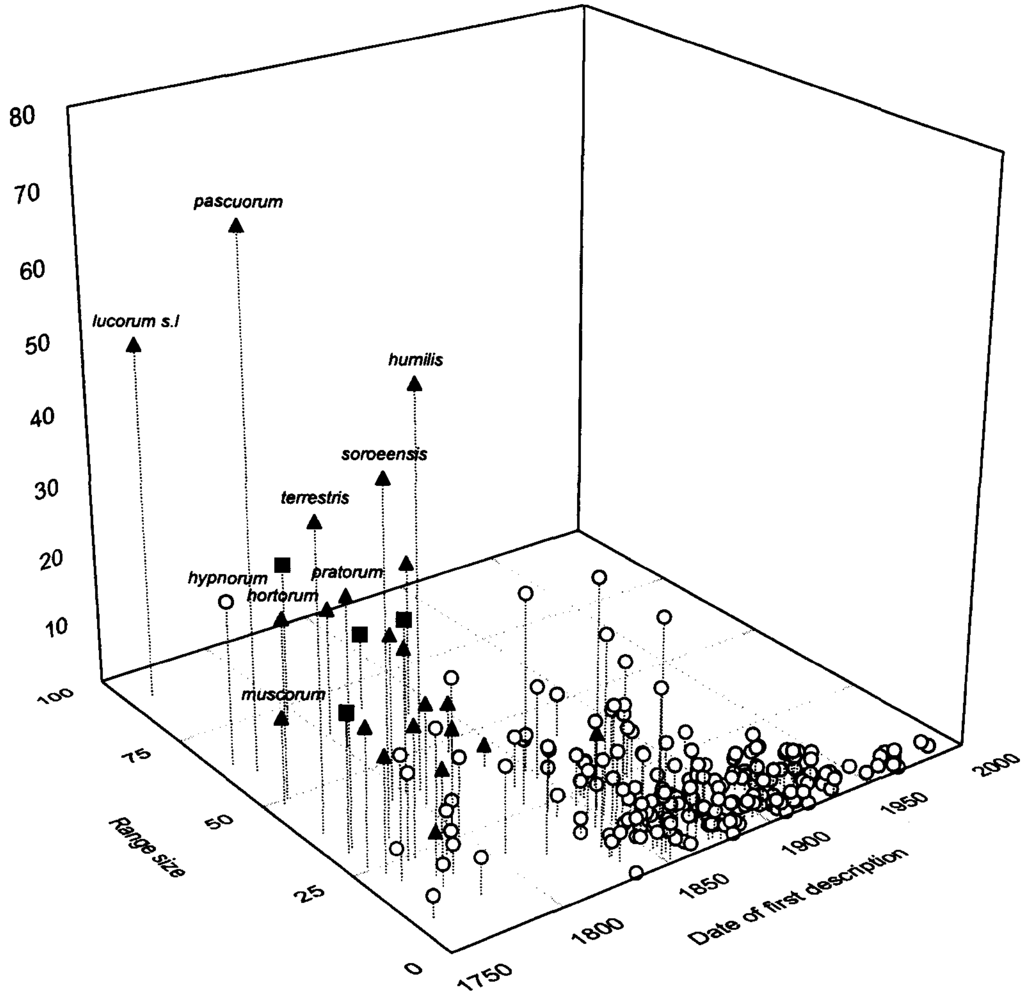

Fig. 4 Scatterplot of 239 presently accepted bumble bee species by range size (number of occupied 611,000 km² grid cells world-wide), date of first formal description and numbers of synonyms/subspecific names (infrasubspecific names are excluded; from a manuscript catalogue, unpublished). The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus, B. balteatus, B. polaris* and *B. lapponicus*) as squares, and some British and widespread European species are labelled individually.

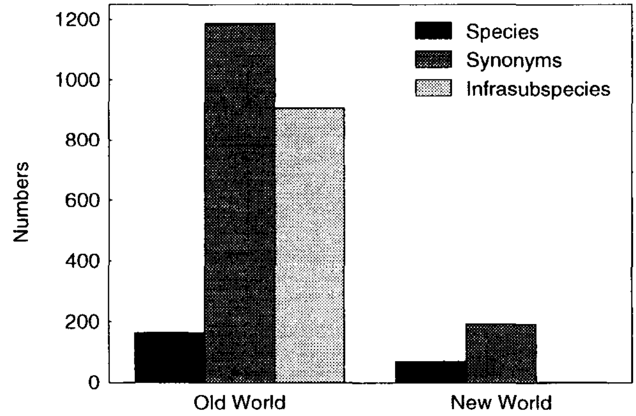

Fig. 5 Number of presently recognised bumble bee species, synonyms/subspecific names and infrasubspecific names for the Old World and the New World (from a manuscript catalogue, unpublished).

have impeded communication and lead to more frequent re-description of taxa than in the New World, where English was much more dominant (C. O'Toole, pers. com.). Again, while this factor is likely to have contributed to the observed patterns of synonyms, it does not explain why (at a lower rank) so many infrasubspecific names were described exclusively for taxa from the Old World.

Another possible interpretation, which might explain more of the differences in description dates between Figs. 1–3 as well as the differences in the distribution of bumble bee subspecies, synonyms and infrasubspecific names between hemispheres (Fig. 5), is that during the twentieth century, effort for describing the variety of these insects may have become, in effect, re-directed towards finer distinctions and lower nomenclatural ranks within known species. This is perhaps likely as undescribed species became inevitably more difficult to find close to home for the most active taxonomists, who were based in Europe. Three lines of evidence are consistent with this explanation. First, slightly more of the variation in richness of infrasubspecific names among species is accounted for by variation in the date of first description of the species (partial *r*, Table 2), rather than by variation in total range size. This is in contrast to the pattern for synonyms alone (cf. Table 1), although species that are sufficiently widespread in lowland Europe to include Britain within their distributions still tend to have high numbers of both synonyms and infrasubspecific names (Fig. 6, e.g. *B. pascuorum, B. lucorum*). A second intriguing observation is that compared to the number of authors who have published presently accepted species names, only one third the number of authors (20) have published infrasubspecific names, even though there are nearly four times as many infrasubspecific names. Indeed, just three of these authors (Bruno Pittioni, Edgar Krüger and Alexander Skorikov) are responsible for 70% of the infrasubspecific names (all of the species with many infrasubspecific names had been described before these three authors became active in publishing infrasubspecific names between 1910 and 1960, see Fig. 7). Many similar examples are known from work on butterflies (R. I. Vane-Wright, pers. com.), with authors choosing a particular favoured species and describing large numbers of infrasubspecific names (e.g. Bright & Leeds, 1938). The third point is that the three most prolific authors all worked in Europe, and there is a correlation among all 239 bumble bee species between the number of infrasubpecific names and the breadth of the species' distributions just within Europe (measured as the number of occupied 611,000 km² grid cells between Britain and the Urals, but excluding Atlantic islands, North Africa, Turkey and the Caucasus; Spearman $r = 0.67, t_{237} = 13.99, p < 0.001$). Thus, a high proportion of the many infrasubspecific names were published by very few European authors, for previously described species that are also particularly widespread in Europe.

High numbers of synonyms and infrasubspecific names for *B. terrestris* and *B. lucorum* (subgenus *Bombus*) and for *B. humilis* and *B. pascuorum* (subgenus *Thoracobombus*) in Fig. 6 raise the possibility that large numbers of names are associated with particular groups of species, perhaps with particular subgenera. Number of names per species is plotted against range size per species for subgenera in Fig. 8. These properties are correlated (log-transformed data, correlation $r = 0.58, F_{1,36} = 18.16, p < 0.001$), but it is the subgenera with high scores that are more informative. The subgenus *Kallobombus* includes many names, but only a single, very variable species *B. soroeensis*, which is broadly distributed in Europe (see below and Reinig, 1939: fig. 10). The subgenera *Alpinobombus* and *Laesobombus* also have broadly distributed

Table 2 Results of multiple regression of numbers of infrasubspecific names (from a manuscript catalogue, unpublished) on date of first formal description for presently accepted species and range size (number of occupied 611,000 km² grid cells world-wide). Species without infrasubspecific names were excluded from the analysis. Partial r values indicate the correlations with the infrasubspecific names variable after adjusting for the other predictor variable in each case.

$\log_e(\text{infrasubspecifics}+1) = 14.169(\pm 3.638) - 0.007(\pm 0.002).\text{date} + 0.742(\pm 0.212).\log_{10}(\text{range})$			
	multiple $r = 0.66$	$F_{(2,94)} = 36.57$	$p < 0.0001$
	partial r	t_{94}	p
date	−0.364	−3.79	< 0.001
$\log_{10}$(range)	0.340	3.50	< 0.001

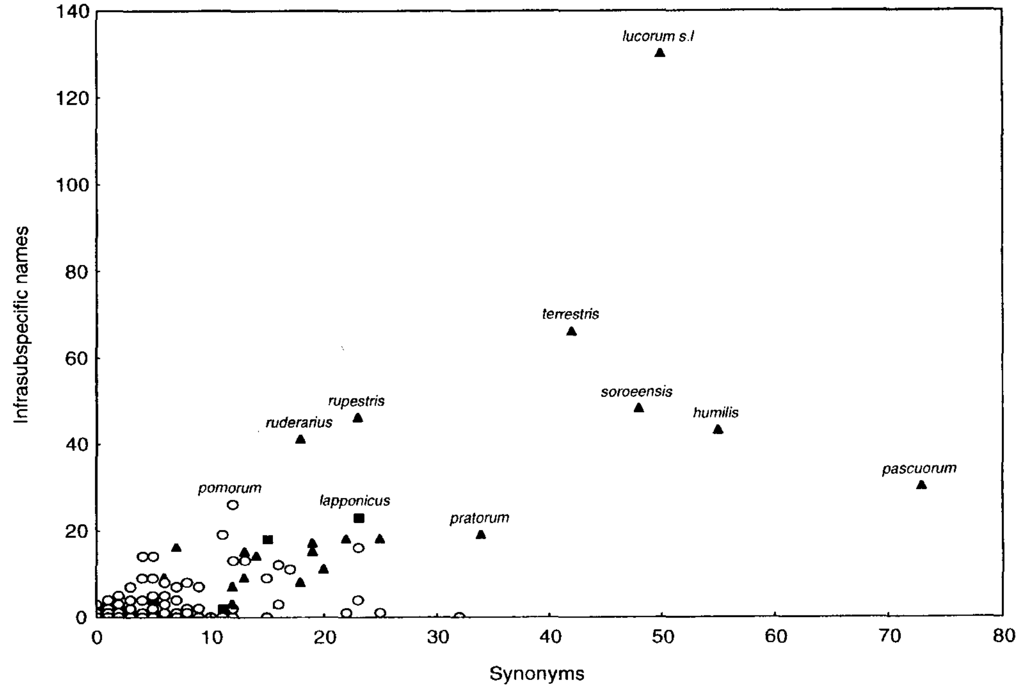

Fig. 6 Scatterplot of 239 presently accepted bumble bee species by numbers of infrasubspecific names and numbers of synonyms/subspecific names (from a manuscript catalogue, unpublished). The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus, B. balteatus, B. polaris* and *B. lapponicus*) as squares, and some widespread European species are labelled individually.

species but relatively few names, perhaps because they are absent or not abundant in those parts of Europe where the authors publishing most bumble bee names have worked, despite several of the species being very variable in colour pattern (e.g. *B. balteatus*). In contrast, the high ratio of names per species for the subgenus *Bombus* shows the keen interest by some European authors such as Krüger (1951, 1954, 1956, 1958) in describing the finer points of variation, not so much within the North American species, but particularly within the widespread European species, *B. terrestris* and *B. lucorum*.

Summary of historical and regional trends in describing bumble bees

Based on the evidence of asymptotic tendencies in species-discovery curves, a higher proportion of all

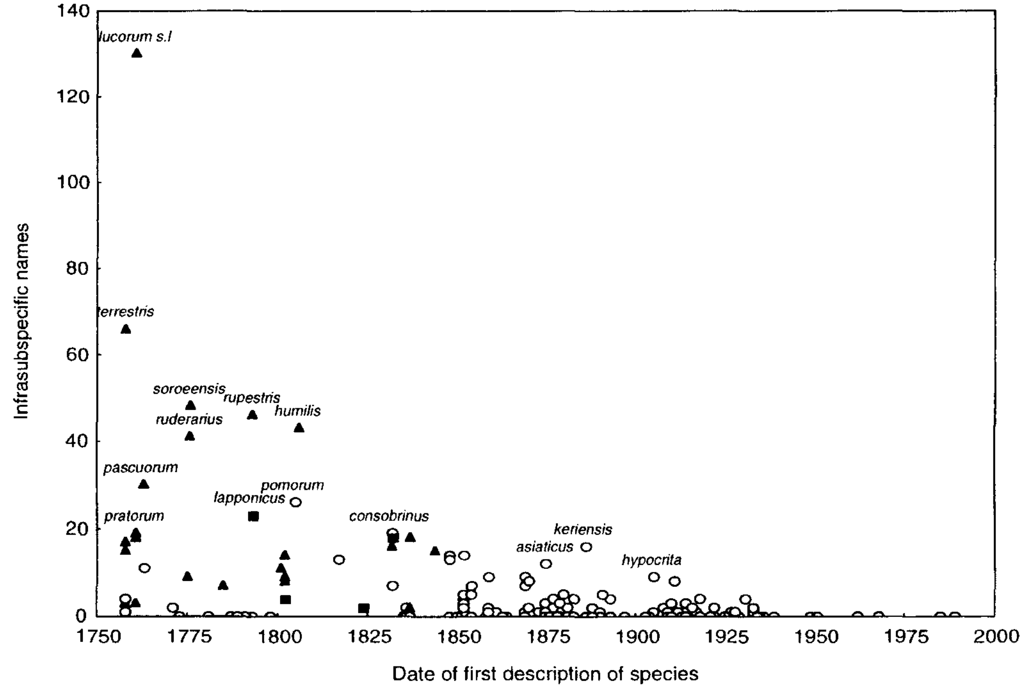

Fig. 7 Scatterplot of 239 presently accepted bumble bee species by numbers of infrasubspecific names (from a manuscript catalogue, unpublished) and date of first formal description of species. The British fauna is distinguished as filled triangles, the nearly circumpolar fauna (*B. hyperboreus, B. balteatus, B. polaris* and *B. lapponicus*) as squares, and some species with more infrasubspecific names are labelled individually.

species appear to be known for bumble bees than for many other groups of organisms. Most of these bumble bee species have been described by authors working in Europe (including European Russia). The species with the largest geographic range sizes, and particularly the European species with the largest ranges, have tended to be described first. The same species have also attracted the highest numbers of synonyms and subspecific names. As a group, bumble bees have an unusually high ratio of synonyms and subspecific names per species, which is otherwise known for some of the groups of larger and more colourful butterflies.

A few European authors were disproportionately prolific between 1910 and 1960 in describing finer variation at infrasubspecific rank, which now accounts for one third of all bumble bee names. Again, this more detailed effort has been largely concentrated on the earlier-described species that are more widespread within Europe (in contrast, New World bumble bees have been ignored at this level), presumably because large samples were more readily accessible to the most active authors. Determining whether this re-direction of activity towards lower nomenclatural ranks was a logical progression in the recognition of useful taxa, a fashion in taxonomic concepts, or in some cases merely a less disruptive channelling of the enthusiasm of some authors to publish more names (the '*mihi* itch'), is beyond the scope of this preliminary review.

All of these patterns in the descriptions of bumble bees must, as yet, be interpreted with caution. Much work still remains to be done on the rates of description of taxa at different nomenclatural ranks (species, subspecies, infrasubspecies), on rates of recognition of synonymy and of changes in rank, and particularly on how this activity is partitioned among different time periods, different geographic regions, different taxonomic subgroups and different authors.

Fundamental to almost all analyses are taxonomic revisions and checklists of bumble bee species. A revised checklist is now overdue, because nearly half (49%) of all names for bumble bees have been published since the last synoptic checklist (Skorikov, 1922*a*).

Development of a revised checklist

To begin to bring a checklist up to date, a draft was made in 1980 and first circulated for comment in 1985 (Williams, 1985*a*). This project was developed during a more detailed study of the west Himalayan fauna (Williams, 1991) and as part of continuing work on the large fauna of China in collaboration with Wang S.-f.

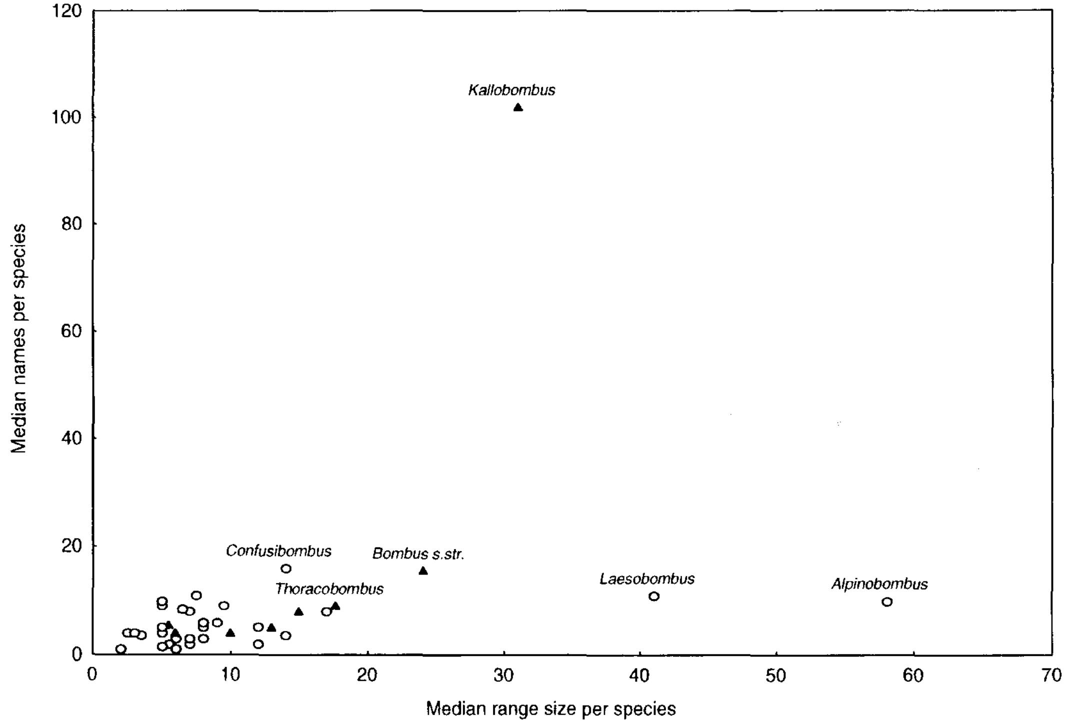

Fig. 8 Scatterplot of 38 bumble bee subgenera by median numbers of all names per species (including synonyms, subspecific and infrasubspecific names; from a manuscript catalogue, unpublished) and median range size per species (number of occupied 611,000 km² grid cells world-wide). The subgenera represented in the British fauna are distinguished as filled triangles and some subgenera are labelled individually.

and Yao J. (unpub.). Some of the broader revisions that have had the greatest influence on this include works by Vogt (1909, 1911), Franklin (1913), Stephen (1957), Milliron (1970*b*, 1971, 1973*a*, *b*), Løken (1973, 1984), Pekkarinen (1979), Reinig (1981), Wang (1982, 1987, 1988), Rasmont (1983, 1988), Thorp *et al.* (1983), Labougle (1990), and especially the publications by Skorikov (1910–1938) and Tkalcŭ (1959–1989). Inevitably, the present checklist cannot be expected to solve all biological and nomenclatural problems, but it is hoped that by identifying some of the major problems it will stimulate further research.

Acknowledgements

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TAXONOMY

Bumble bees are a monophyletic group (Williams, 1985*b*, 1995), constituting the tribe Bombini. They may be distinguished from other bees (family Apidae) by the following diagnosis (from Williams, 1991, which includes descriptions of the characters and discussion of homologies):

Bombini have the labrum at least twice as broad as long. The labrum lacks a longitudinal median ridge, although for the females it has a strong transverse basal depression. The clypeus has a transverse subapical depression and the apicolateral corners are curved back towards the occiput. A 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 lobe (= anal lobe). The volsella (= lacinia) of the male genitalia is greatly enlarged and is produced apically beyond the gonostylus (= squama).

Bumble bees are large (body length 7–27 mm) robust insects. Their bodies have a dense covering of variously coloured long plumose hairs, although these are few or absent on some parts of the ventral surface of the gaster, on parts of the propodeum, on parts of of the anterior face of gastral tergum I, and on parts of the head. The sclerites are usually black, or lighter brown on the distal parts of the limbs, but are never marked with bright yellow, red or metallic (= interference) colours. The wings may be transparent (= hyaline) to strongly darkened (= infuscated), but rarely show strongly metallic reflections.

Female bumble bees have 12 antennal 'segments' (= scape, pedicel and 10 flagellomeres) and six visible gastral terga and sterna (abbreviated to TI–VI, SI–VI). Males have 13 antennal 'segments' (= scape, pedicel and 11 flagellomeres) and seven visible gastral terga and sterna (abbreviated to TI–VII, SI–VII).

Where possible, a divisive, 'top-down' approach to the description of bumble bee diversity has been followed, in the sense of concentrating initially on higher-rank relationships and then distinguishing progressively the species groups, species and then variation within species (as opposed to beginning with described infraspecific taxa and searching 'upwards' for close relatives). At the rank of species, this accepts those putative species or species complexes that are supported by consistent evidence for separate status, and which can be reliably identified throughout their range for the purpose of mapping distributions. This kind of broad over-view at least has the potential to apply consistent criteria across all taxa, even though it is appreciated that not all taxa at the rank of species are necessarily of the same kind (Ackery & Vane-Wright, 1984; de Queiroz & Donoghue, 1988). Specialists will need to modify this list as further information becomes available for particular species groups.

Phylogeny, supra-specific taxa and ordering of species

From available cladistic evidence (Williams, 1991, 1995), use of *Psithyrus* as a genus for the social parasites separate from the remainder of the social bumble bees in *Bombus* can no longer be justified, so a single genus *Bombus* is used for all of the species of bumble bees (see the comments under the subgenus *Psithyrus*).

A system of subgenera has become widely used by specialists who wish to label assemblages of the more closely similar species. This system is summarised with subgeneric diagnoses and keys by Richards (1968). For a review of supraspecific classifications of bumble bees, see Ito (1985).

The subgeneric system would be more useful if the names were applied only to strictly monophyletic groups. Unfortunately, Richards's (1968) concepts of the bumble bee subgenera do not always agree well with recent estimates of phylogeny, because some of these assemblages now appear to be paraphyletic (e.g. *Mendacibombus*) or even polyphyletic (e.g. *Sibiricobombus* in the sense of Richards, 1968, includes *Obertobombus*, whereas he placed *B. (Sibiricobombus) flaviventris* in *Subterraneobombus*) (Williams, 1991).

Furthermore, the system of subgenera would probably be more useful if it were simplified (e.g. Menke & Carpenter, 1984; and reply by Williams, 1985c). For example, in the New World, both the monophyletic *fraternus*-group of subgenera and the subgenus *Fervidobombus* are endemic, and these are the only two groups represented south of the Panama isthmus. But whereas *Fervidobombus* has been treated nearly consistently as a single, relatively large subgenus (20 species in this list), the *fraternus*-group (18 species in this list) has regularly been split into as many as nine subgenera.

However, no attempt is made in this checklist to revise radically the subgeneric system, because stability will only be served when a revision can be supported by a comprehensive cladistic analysis. This should include not only a broad sample of species, but also a broad range of morphological and molecular characters. Minor modifications from the subgeneric system described by Richards (1968) are detailed in the list after the subgeneric names.

Full synonymy of supraspecific names is included in this checklist, along with details of type species, because these have been revised since Richards (1968). The given generic combination for subgeneric names is shown. Where a genus-group name was published at the rank of genus and subsequently treated at subgeneric rank, the first such action is listed separately. The two-letter abbreviations for subgeneric names are based on those used by Ito (1985).

Species are listed in an order (Table 3) that represents their phylogenetic relationships (after the sequencing convention of Nelson, 1972) as these are currently understood from cladistic studies of the adult morphology of both sexes (Williams, 1995, and many references therein). Within subgenera, this information is still of a very preliminary nature (e.g. Williams, 1991). Many other estimates of relationship exist and would result in different sequences of species names. An alphabetic index is provided as an aid to finding names in this list.

Table 3 List of names for subgenera of the genus *Bombus*, with numbers of species recognised in this checklist. The subgeneric classification is based on Richards (1968), modified to accommodate recent publications (see text; no attempt is made to revise the subgeneric system, because stability will only be served when a revision can be supported by a comprehensive cladistic analysis). Subgenera are listed in an order that represents their phylogenetic relationships (after the sequencing convention of Nelson, 1972) as these are currently understood from cladistic studies of the adult morphology of both sexes (Williams, 1995).

	Subgenus	Number of species
1	*Mendacibombus*	12
2	*Bombias*	2
3	*Confusibombus*	1
4	*Mucidobombus*	1
5	*Eversmannibombus*	1
6	*Psithyrus*	29
7	*Laesobombus*	1
8	*Orientalibombus*	3
9	*Exilobombus*	1
10	*Thoracobombus*	19
11	*Tricornibombus*	3
12	*Fervidobombus*	20
13	*Senexibombus*	4
14	*Diversobombus*	4
15	*Megabombus*	14
16	*Rhodobombus*	3
17	*Kallobombus*	1
18	*Alpinobombus*	5
19	*Subterraneobombus*	9
20	*Alpigenobombus*	6
21	*Pyrobombus*	43
22	*Festivobombus*	1
23	*Rufipedibombus*	2
24	*Pressibombus*	1
25	*Bombus s.str.*	10
26	*Cullumanobombus*	4
27	*Obertobombus*	2
28	*Melanobombus*	14
29	*Sibiricobombus*	5
30	*Fraternobombus*	1
31	*Crotchiibombus*	1
32	*Robustobombus*	5
33	*Separatobombus*	2
34	*Funebribombus*	2
35	*Brachycephalibombus*	2
36	*Rubicundobombus*	1
37	*Coccineobombus*	2
38	*Dasybombus*	2

Criteria to discriminate species

It is not possible or appropriate to discuss species concepts in detail in this paper (though the selected references provide some introduction; for recent reviews, see Claridge *et al.*, 1997; Mallet, 1997). However, in order to interpret the checklist, where possible it would be useful to make the species-discriminating criteria explicit. It is equally important to convey the present belief that there is no simple solution to the problem, and that no single known approach can resolve all of the cases in a uniform and entirely satisfactory manner.

Species concepts (ideas or general notions of the class of objects) and species diagnoses (operational determinations of individual objects) are contentious and probably unresolvable issues. Therefore there is arguably no single 'true' list of species, only more or less valid interpretations from different viewpoints.

Unresolveable conflicts may arise from opposing views of the nature of species. Species have been regarded either as typological classes, with membership to be defined by some shared essence (reviewed by Templeton, 1981), or as individuals, to be discovered (Ghiselin, 1975). There are also conflicting opinions concerning criteria (characteristics or standards by which an object may be judged) for recognising species, based in part on differing emphasis on pattern or process (de Queiroz & Donoghue, 1988).

Species may be considered not to differ from taxa at other ranks (e.g. genera, subspecies) in any qualitative way. There may be quantitative differences in the numbers of character differences that distinguish them in comparison with taxa of lower rank. For example, according to Mallet (1995:294), Darwin (1859) held this view. The problem with quantitative criteria (whether applied to genetic or phenotypic characters) is there is no reason to believe that any choice of threshold in the degree of difference used to recognise taxa at the rank of species is anything other than essentially arbitrary and thus idiosyncratic to particular authors.

In another view, species may be considered to differ qualitatively from taxa at other ranks. It is widely accepted, though often implicitly, that taxa at the rank of species should be recognised so as to mark the boundary between, on the one hand, reticulate relations (for sexually reproducing organisms), and on the other, more consistently divergent genealogical relations. One problem is that this distinction may require predictions as to whether or not currently distinct groups of individuals are likely to show reticulate relationships again in the future.

Interbreeding and the associated genetic recombination is an important part of Dobzhansky's (1937) 'modern synthesis' of Mendelian genetics with Darwin's natural selection theory for evolution. Emphasising interbreeding as a criterion for recognising species characterised what Mayr (1940, 1963) called the 'biological' species concept. These ideas have been modified in the recognition concept of species (Paterson, 1985). One problem with interbreeding or mate recognition as criteria for recognising species is that direct and reliable evidence is rarely available and the results of tests under artificial conditions cannot necessarily be generalised (Splitter, 1982). Another is that the capacity for interbreeding is an ancestral condition (i.e. not an homology) and so cannot provide support for recognising taxa in the phylogenetic sense (Rosen, 1979).

In practice, all that is usually available to discriminate species as 'different' is evidence from character differences and their patterns of concordance among individuals. The phylogenetic species concept (Cracraft, 1989) is popular because it also embodies the notion that species mark the boundary between different patterns of relationship among individuals and yet it does not rely on inference of interbreeding. The problem is that discovery of phylogenetic species as minimum cladistically-diagnosable (discrete) groups of individuals requires that these groups uniquely share homologies (synapomorphies), which may not always be the case (Ackery & Vane-Wright, 1984; Frost & Kluge, 1994).

Mallet (1995) has argued for minimising the number of assumptions built into species concepts. He suggests that two nominal taxa should be considered conspecific until it can be demonstrated that data for multiple characters distinguish consistent subgroups of individuals with few or no intermediates (the character-cluster concept of species). Although he was arguing against the use of the widely-held biological species concept, he recognised that his prescription differs little from recent common practice. The problem with the cluster concept is how to decide on a threshold for permissable numbers of intermediate individuals between taxa for them still to be considered separate species.

Ultimately, species may be seen as useful conventions to aid in the communication of information gathered about the individuals that are their parts. It may be argued that the most important initial goal is to describe the nature of the variation in each particular case and to avoid presenting only theory-laden (and constrained) interpretations. In this way, basic information on variation will remain available for re-interpretation as theory changes.

For the sake of illustration, four principal classes of problems in geographical variation may be distinguished within the spectrum of kinds of relationships, with the following examples:

Broad co-occurrence of differing individuals

Skorikov (1931) and Reinig (1935) recognised that throughout much of the range of *B. keriensis*, both yellow-banded and cream- or white-banded individuals with indistinguishable morphology co-occur (Fig. 9). From available evidence, it is possible that *B. niveatus / vorticosus* may show a similar pattern of yellow/white variation, as may *B. impetuosus/potanini*, although with differing degrees of geographical variation in colour-form frequency (see the comments on these species). Consequently, taxa in these pairs are also treated as conspecific for the present (it is possible that in some cases such colour differences may be controlled by alleles at a single locus, see Owen & Plowright, 1980, on *B. melanopygus*; and Williams, 1991, on *B. asiaticus*; or by small numbers of loci, see Plowright & Owen, 1980, on *B. rufocinctus*). In contrast, although the yellow-banded *B. shaposhnikovi* and the white-banded *B. handlirschianus* also show a broadly-overlapping pattern of distribution, the one white-banded male that I have seen is distinct from the yellow-banded males in the morphology of its genitalia (Williams, 1991).

Broad clinal variation

Many species show broad trends in variation across continents, most obviously in colour pattern (e.g. *B. cingulatus*, Fig. 10; and the *trifasciatus*-group, Fig. 13, which may be combined with locally convergent colour variation, e.g. within the *haemorrhoidalis*-group, *breviceps*-group and *rotundiceps*-group, see Sakagami & Yoshikawa, 1961; Tkalcü, 1968*b*, 1989). In North America, several pairs of nominal taxa were described originally from individual type-specimens with differing colour patterns from eastern and western regions respectively (e.g. *B. auricomus/nevadensis*, *B. fervidus / californicus*, *B. pensylvanicus / sonorus*, *B. terricola / occidentalis*). These taxon pairs have long caused difficulties, for example with Franklin (1913:239) commenting on a list including these taxa and others that are now considered conspecific that 'it must be entirely a matter of personal opinion whether they should be given full species rank or be considered as only subspecies' (although, intriguingly, *B. auricomus/nevadensis* were not included in Franklin's list). In at least some of these cases, many individuals with what appears to be a continuum of intermediate colour patterns are now known from broad intervening areas, so that threshold criteria for distinguishing these taxa appear to be essentially arbitrary (e.g. making decisions based on whether a particular tergum has the pubescence entirely yellow, rather than having a few black hairs present). In consequence, taxa in these taxon pairs are treated here as conspecific and maps are compiled for the more clearly recognisable, more inclusive taxa (but see the comments on *B. auricomus / nevadensis*).

Narrow hybrid zones

In some cases, otherwise discrete colour forms with closely similar morphology meet in narrow zones (of the order of a few km in breadth), where there may be evidence of intermediate or genetically recombinant individuals. In Europe this is best known for *B. ruderatus / argillaceus* (Fig. 11; Scholl, Obrecht & Zimmermann, 1992), and in Asia it has been suggested

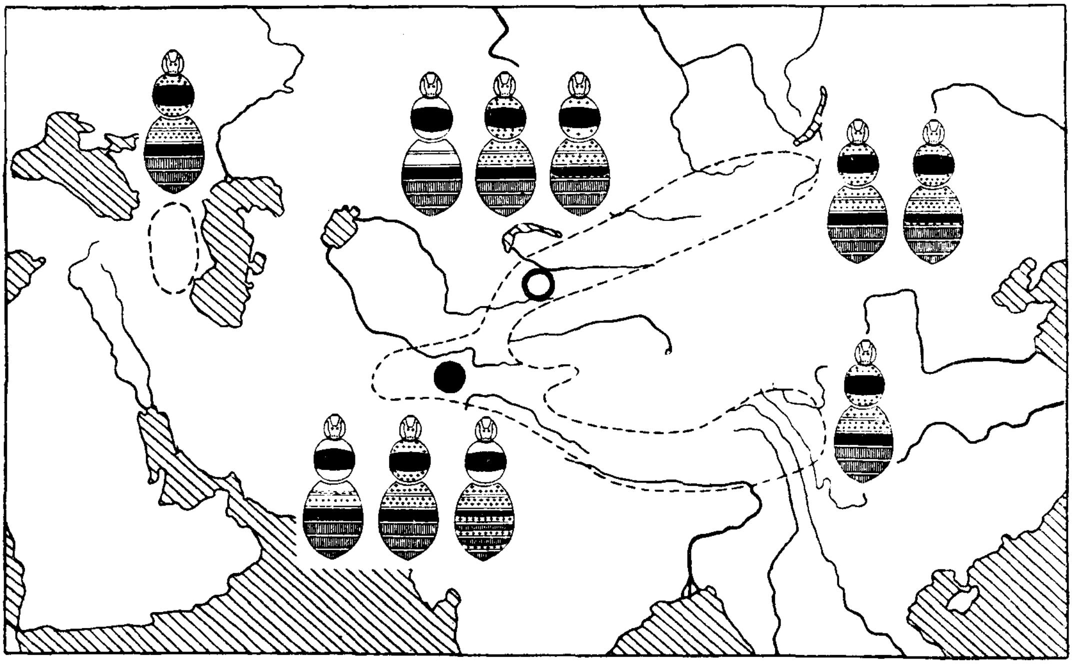


Fig. 9 Approximate distribution range (area within the dotted line) and principal colour variation for *B. keriensis* from Reinig (1939: fig. 23). Many more records are available now, but the pattern remains similar, with broad overlap of yellow- and white-banded individuals in Mongolia, Tien Shan, Pamir and western Himalaya. Yellow and cream pubescence is shown on the bees by crosses; red pubescence by vertical hatching.

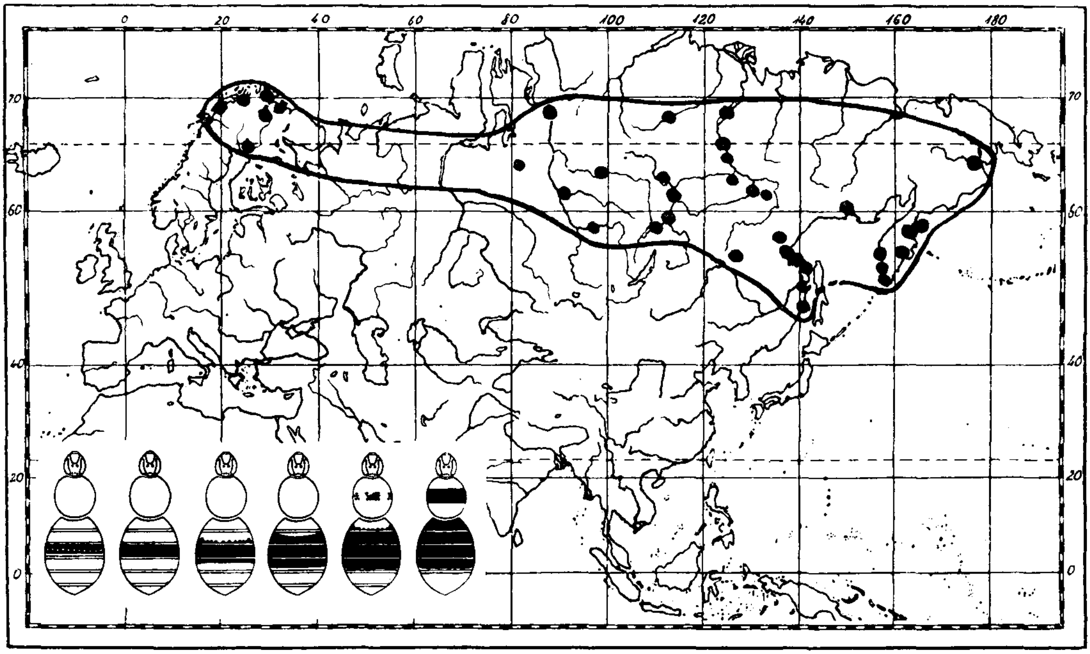


Fig. 10 Distribution records (spots), approximate range (area within the line) and principal colour variation for *B. cingulatus* in the northern Palaearctic Region from Reinig (1939: fig. 7). The lightest individuals occur in the east (Kamchatka) and the darkest individuals (with the black thoracic band) occur in the west, with intermediate individuals in intervening areas.

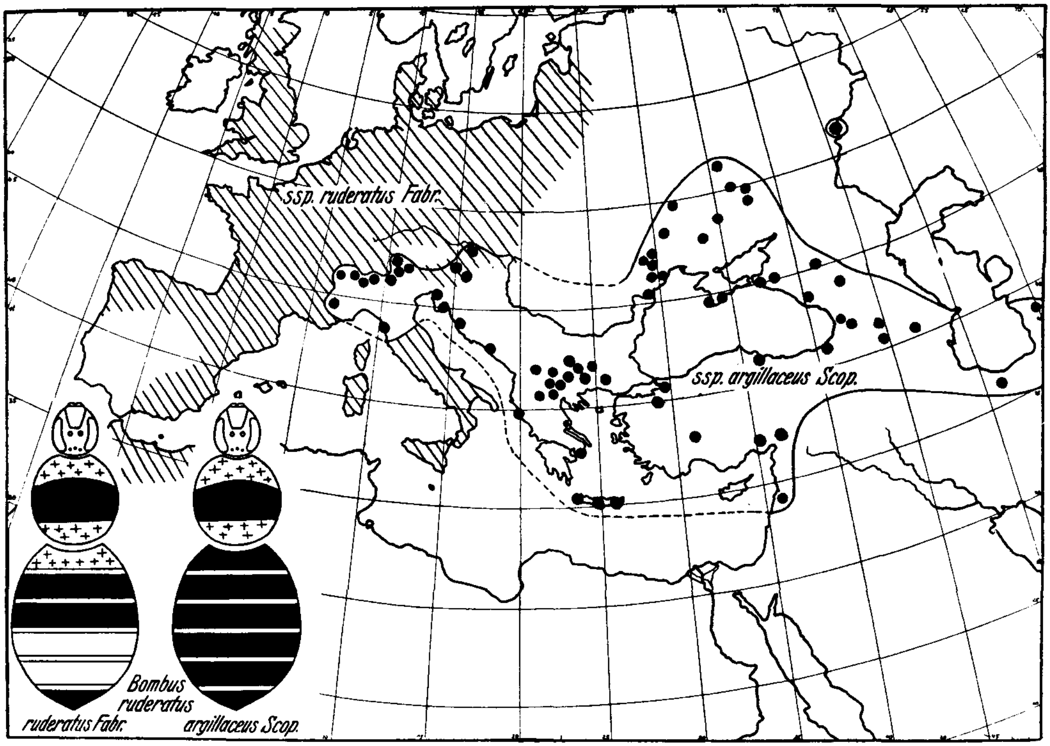


Fig. 11 Distribution records (spots), approximate range (area within the cross-hatching, left, and line, right) and principal colour variation between queens of *B. ruderatus* and *B. argillaceus* in Europe from Reinig (1939: fig. 7). These taxa were regarded as subspecies by Reinig, but have recently been treated as separate species. Although there is evidence of a hybrid zone between some areas of parapatry, the hybrid individuals are very rare (Scholl, Obrecht & Zimmermann, 1992). Yellow pubescence is shown on the bees by crosses.

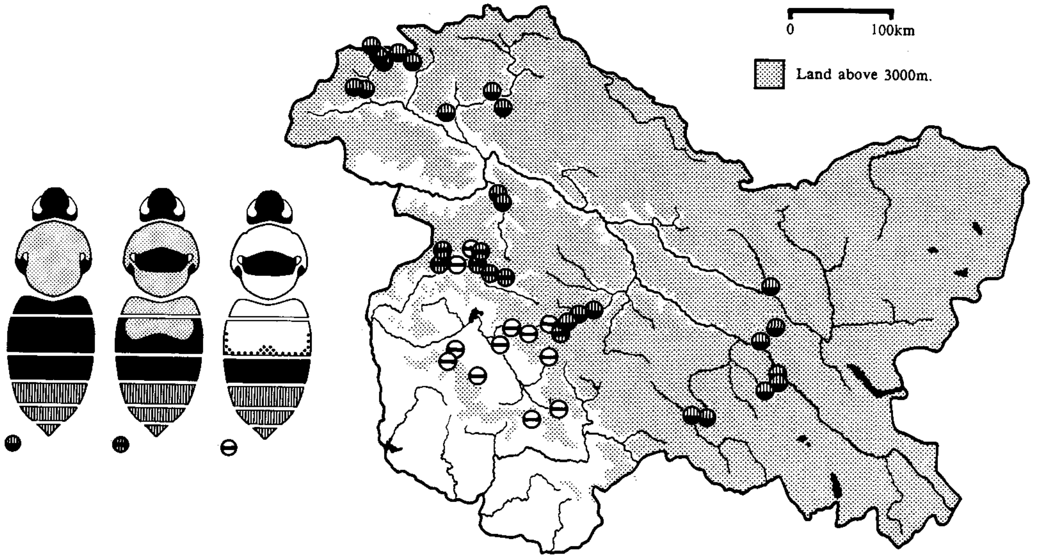


Fig. 12 Distribution records (spots) and principal colour variation for *B. asiaticus* in Kashmir from Williams (1991: map 48). There is evidence of a hybrid zone between some areas of parapatry, such as some high passes along the divide of the Great Himalaya Range, where there are abundant hybrid individuals. The spot symbols show the locally most abundant colour pattern. Yellow pubescence is shown on the bees by fine stippling; red pubescence by vertical hatching.

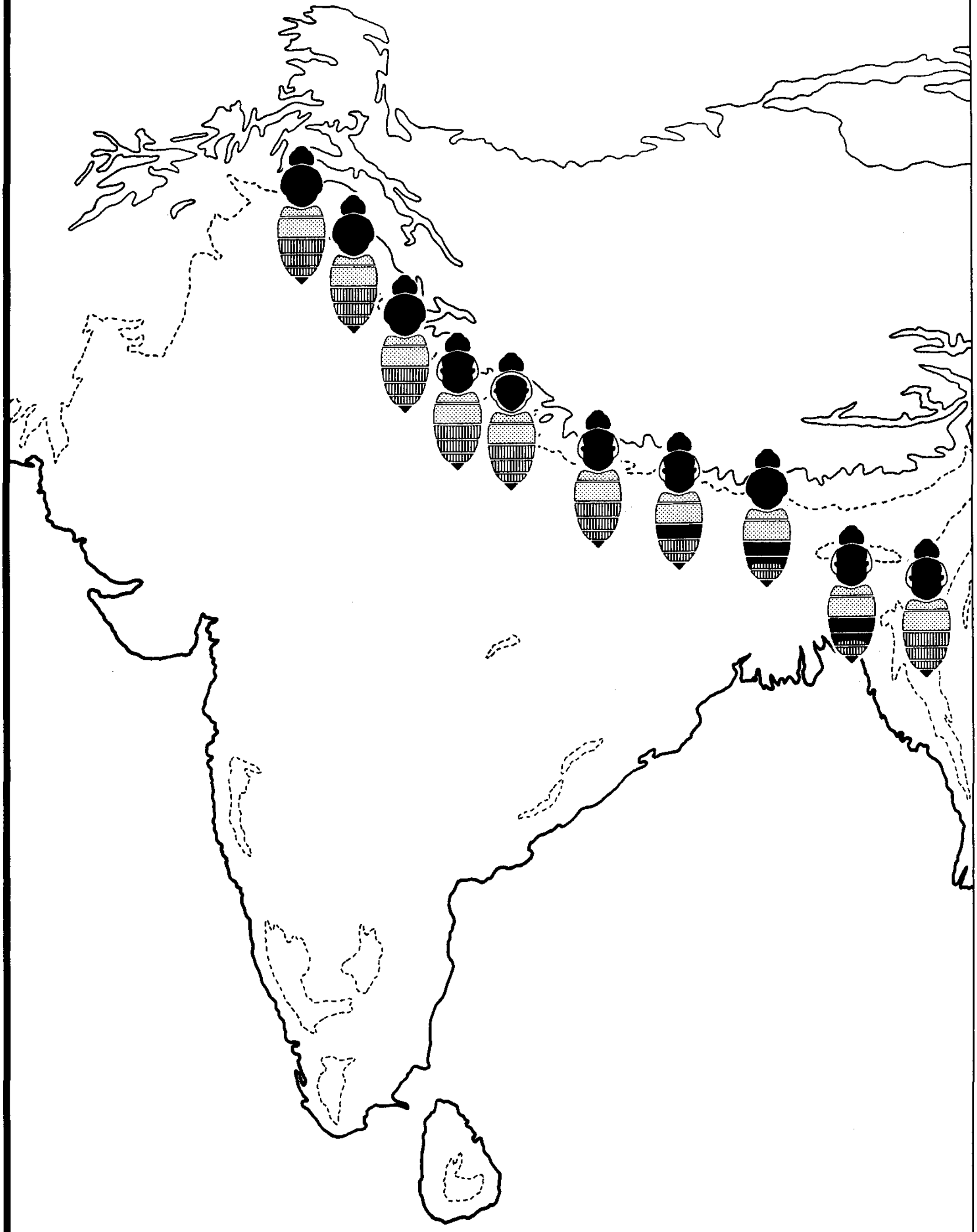
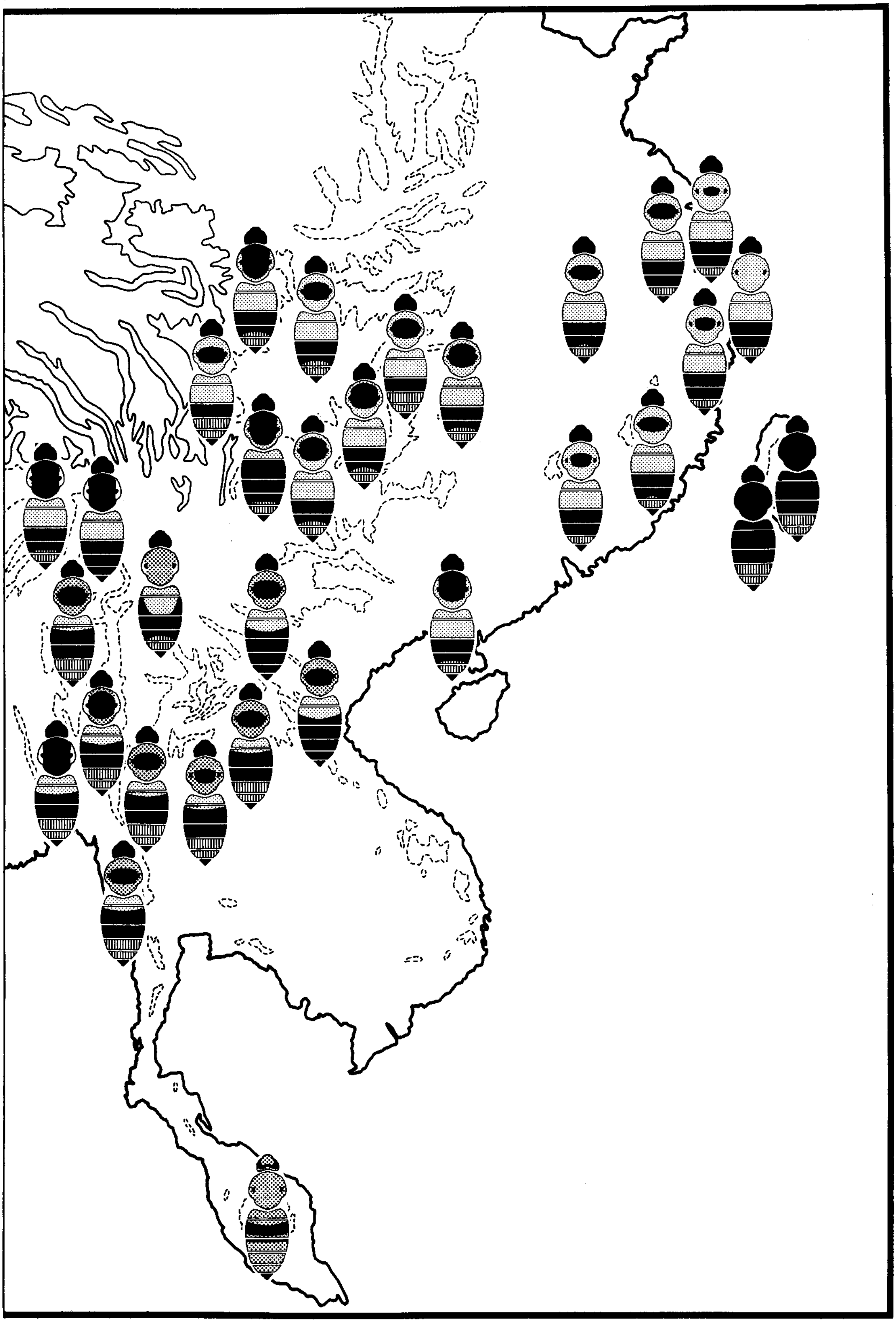


Fig. 13 Distribution records and principal colour variation within the *trifasciatus*-group in Asia (updated from Williams, 1991: fig. 11). The individuals may all be considered parts of a single species, *B. trifasciatus*, depending on which species-defining criterion is accepted. The dashed line shows the 1000 m contour above sea level and the solid line shows the 4000 m contour. Yellow pubescence is shown on the bees by fine stippling, orange pubescence by coarse stippling, red pubescence by vertical hatching.



for *B. asiaticus / longiceps* (Fig. 12; Williams, 1991). Other possible examples include *B. lapponicus / monticola* in Europe and *B. pyrosoma / friseanus / miniatus* in China. In the case of *B. asiaticus / longiceps*, I have treated them as conspecific, because intermediate individuals greatly outnumber 'typical' individuals at some localities. For the other cases, I have followed earlier treatments of these taxa as separate species, because intermediate individuals are rare or not well known (although this may be a consequence of poor sampling in some inaccessible areas).

Disjunct peripheral populations

Some peripheral populations on offshore islands or habitat islands (e.g. mountains) show some divergence in colour pattern with little morphological divergence. European examples include *B. terrestris / canariensis* and *B. hortorum / reinigiellus*. Asian examples include *B. schrencki / honshuensis*, *B. trifasciatus / maxwelli* (Fig. 13, Peninsular Malaysia), *B. trifasciatus / wilemani* (Fig. 13, Taiwan), *B. breviceps / angustus*, *B. parthenius / sonani*, *B. flavescens / rufoflavus* and *B. flavescens / baguionensis*. For the application of the biological species concept, in these cases there is no 'natural' meeting of individuals between the taxon pairs and so no admissible evidence on interbreeding (Splitter, 1982). For the application of Mallet's (1995) cluster concept, quantitative analysis of patterns of variation is urgently needed. Where this information is absent, I agree with his prescription of treating taxa in these taxon pairs as provisionally conspecific. *Bombus honshuensis* and *B. schrencki* are mapped separately here because, from published accounts and a small sample of material examined, their colour differences appear to coincide with stronger and more consistent morphological distinctions.

It is hoped that further information may help to clarify these cases. In the interests of pluralism, I aim to report not only a preferred interpretation in the comments on each species, but also at least the more widely-held alternative interpretations.

Sub-specific taxa

For this checklist the interest is primarily in problems of recognition and nomenclature for taxa at the rank of species. Subspecific names refer to parts of species, and so for present purposes these can be treated as synonyms of specific names (e.g. Schwarz *et al.*, 1996). This is not to say that subspecific taxa should not be recognised if they are considered useful, and of course other biologists may add subspecies to this list (cf. Rasmont *et al.*, 1995).

NOMENCLATURE

Nomenclature should be seen as the servant of biology: its purpose is to provide labels that enable biologists to communicate information about organisms with minimal confusion concerning the organisms to which they refer. Accounts of the history of nomenclature for many groups of organisms (e.g. on British bumble bees: Alford, 1975; Prŷs-Jones & Corbet, 1987:82) show that this is not a trivial matter and that rules are necessary.

Treatment of names follows the *International Code of Zoological Nomenclature* (*International Commission on Zoological Nomenclature* [ICZN], 1985). The Principle of Priority is generally adhered to, although regard is given to the stated purpose of priority (ICZN, 1985: Article 23b): namely that it should be used to promote stability and is not intended to be used to upset a long-accepted name in its accustomed meaning (Article 79c) through the introduction of an unused name that is its senior synonym. Similar action is also suggested where cases of homonymy affect current usage, although this action cannot be taken when it is felt desirable to maintain availability of a senior homonym. My suggestions for applications to ICZN for conservation of names in current use are indicated by stars (✪).

Typographical conventions

Bombus b-us	valid name in the species group,
c-us	available name in the species group, including synonyms of a valid species name,
?*d-us*	available name in the species group, a provisional synonym of a valid species name,
[*e-us*]	unavailable name, informally associated with a valid species name,
f-us examined	type material for species-group name *f-us* examined (in whole or in part),
●	comments on status of species,
○	comments on application of names,
✪	suggestion for application to ICZN.
?*Bombus g-us*	valid name in the species group, for a taxon that is recognised provisionally as a separate species from *B. b-us*.

A question mark (?) before a valid name shows that, while it refers to a taxon that is considered likely to be a separate species, it may be conspecific with the preceding taxon in the list (i.e. while *Bombus g-us* may be conspecific with *Bombus b-us*, *Bombus d-us* is much more likely to be conspecific with *Bombus b-us*).

Names in the more detailed references are followed by names of authors, date of first publication (within the meaning of ICZN, 1985), and page reference. Wherever possible, the true first date of publication is given in preference to any purported date of publication when these differ. If a name were published originally in a different generic combination, then the original genus is shown in brackets. If the name had been published originally with a different termination, or with capital initial letters, diacritic marks etc., then the original form is shown without the mandatory changes (with the exception that small capital letters are reduced to lower case).

Selection of synonyms

This checklist is based on a much longer catalogue of over 2800 names. As a checklist, it is not required to include the full list of synonyms, so synonyms are selected for this list primarily where they help to clarify the identity and scope of the species (including the subspecies included by some authors), particularly with reference to those names in most common use in the literature of the last 25 years. Misidentifications are not included with the lists of synonyms and are discussed only when necessary to clarify the application of problematic names.

Applications to ICZN

Flexibility in interpretation of the status of taxa is possible where the evidence to distinguish among interpretations is absent, inconclusive, or may permit different interpretations under different species concepts. Otherwise flexibility in the application of names depends on whether systematists are eager to apply to the International Commission on Zoological Nomenclature to use its Plenary Power in order to conserve a preferred usage of names (e.g. Løken *et al.*, 1994; ICZN, 1996).

I propose that this could be achieved in a single application to include all names for which action is currently known to be required (*atratus, balteatus, distinguendus, flavifrons, humilis, hyperboreus, mesomelas, mixtus, norvegicus, polaris, pyrenaeus, soroeensis* and *variabilis*). Comments on this proposal would be welcomed.

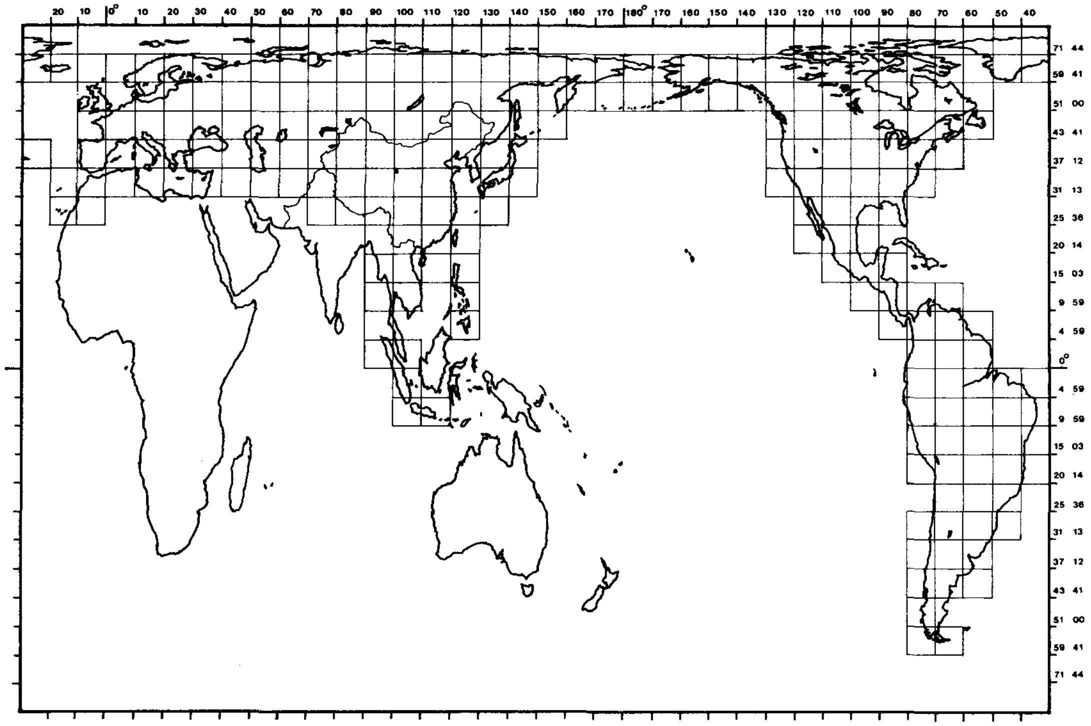
DISTRIBUTION MAPS

This checklist was compiled in conjunction with distribution data in support of biogeographic studies. Maps of world-wide distribution at a coarse grain size were designed for use in comparisons of regional bumble bee faunas (e.g. Williams, 1989, 1991, 1993, 1995, 1996*a, b*; Williams & Seddon, 1993; Williams & Humphries, 1996).

Aside from any difficulties in identifying species or localities, comparisons among faunas are complicated by two principal factors: first, by differences in sampling effort (as illustrated by 'species-accumulation curves', e.g. Colwell & Coddington, 1994); and second, by differences in the extent of sampling areas ('species-area effects', e.g. Connor & McCoy, 1979). Fortunately for the first problem, the attractiveness of bumble bees to collectors has ensured that they have been relatively intensively sampled, so that most faunas are relatively well known. But in order to reduce this problem further, rather than extrapolate local richness and lose information on individual species, the expected distributions of some species are interpolated on the basis of knowledge of their habitat associations (see the legend to Fig. 14). To reduce the second problem of species-area effects, equal-area grid cells were established using a cylindrical, equal-area projection of the world, marked at intervals of 10° of longitude and calculated intervals of latitude (Fig. 14). However, this does not ensure equal land areas among grid cells, or equal areas of habitat suitable for bumble bees.

Because the intention is to study biogeographic patterns, maps are required to show all historical records, including data from areas where species may now be extinct. On the other hand, data exclude fossil taxa (reviewed by Zeuner & Manning, 1976) and documented introductions (e.g. Oliff, 1895; Frison, 1925*b*; Gurr, 1957; Prŷs-Jones *et al.*, 1981; Arretz & Macfarlane, 1982; Cardale, 1993).

The maps for every species are not included with this checklist because many data are still being collected, although for each subgenus a preliminary map of species richness is included as a general guide (or for monotypic subgenera, a map of records for the single species is included). The numerical values for the grey-scale classes differ between maps and are not shown. This is because I have adopted an alternative approach of using equal frequency classes, which have the advantage that each grey-scale class remains consistent in its relative richness among all maps (e.g. dark grey always shows the richest one fifth of occupied cells excluding the maximum etc.). The sources of the distribution data have not been included because this will be included in a later atlas.



Key to map symbols:

Maps for single species

- ● specimens examined,
- ◉ precise literature records (e.g. 'Dungeness TR01, UK'),
- ◍ vague locality data (e.g. 'Florida'),
- ○ interpolations of expected distribution (following common practice for range-filling maps; the rules adopted here are to fill cells between occupied cells when filled cells are known to have had a high proportion of suitable habitat within recorded history; these records amount to < 10% of all gridcell records at this scale, Williams, 1993).

Maps for multiple species

maximum species counts are shown in black, otherwise counts are divided into five grey-scale classes of approximately equal size by numbers of grid cells.

Fig. 14 Map of the world (excluding Antarctica) using a cylindrical equal-area projection that is orthomorphic (minimum shape distortion) at 46° North and South (where bumble bee records are particularly plentiful). Intervals of 10° longitude (top of map) are used to calculate intervals of latitude (right of map) that provide equal-area grid cells of c. 611,000 km². The portion of the grid shown covers the known, native distribution of bumble bees. Map symbols are shown above for (a) plotting individual species, for which different spots distinguish different data categories (Map 3); or (b) for plotting coincidence maps for multiple species, using a grey scale for variation in species richness (Map 1).