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# The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini)

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## CONTENTS

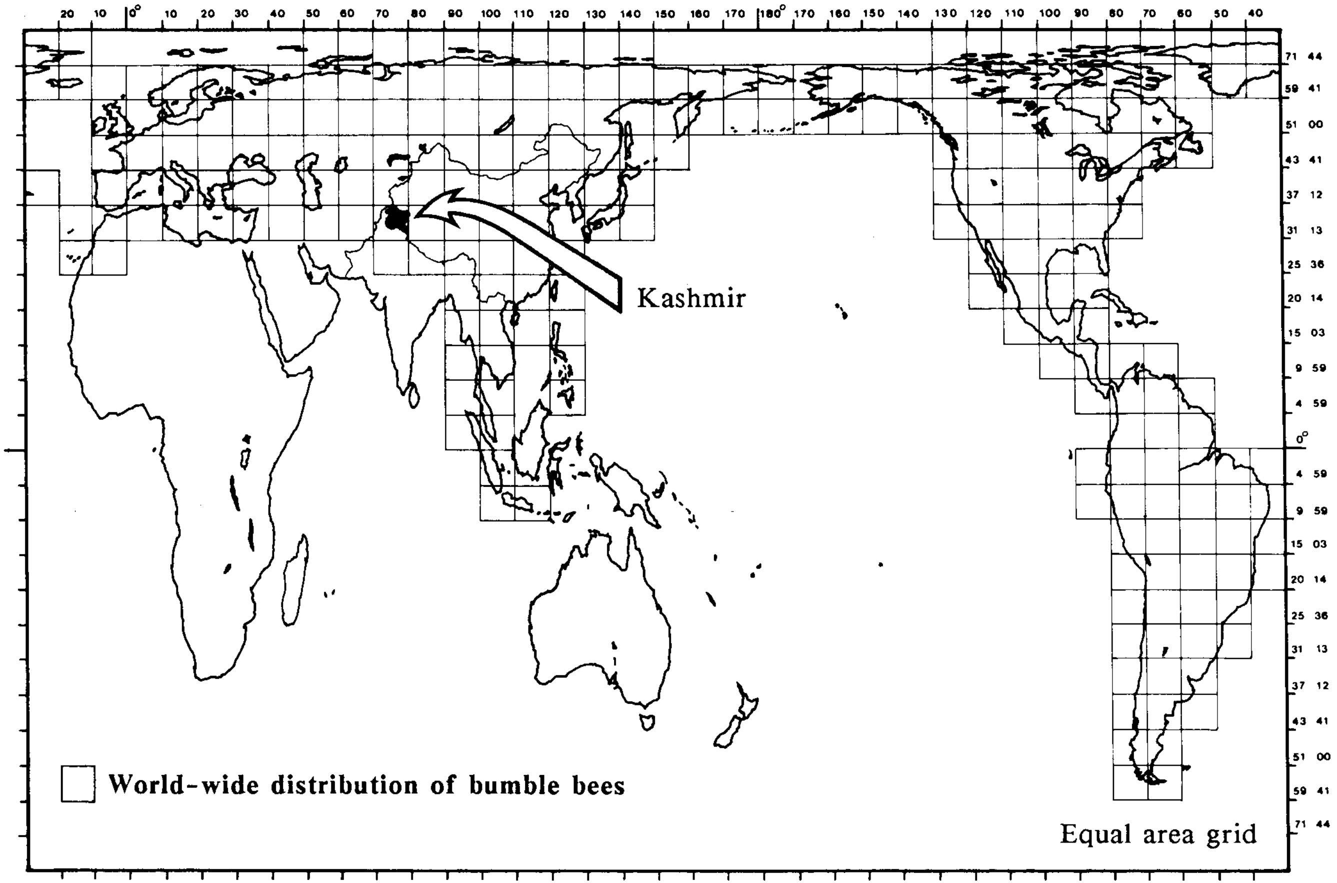
**Synopsis.** Bumble bees are extraordinarily variable in the colour patterns of their pubescence. This has contributed to the lack of agreement among authors concerning the discrimination of species. Material from Kashmir has been listed previously under 80 names, but for the broadest interpretations of these species, more than 500 names have been published for differing individuals from throughout their distributions. In this review, all of the available voucher material from Kashmir (6312 museum specimens from 78 sites) is assigned to just 29 species. The reduction in the number of nominal taxa that are inferred to represent separate species depends on two factors. First, variation is examined among the larger samples of new material. Second, current species concepts require a re-assessment of this evidence for the limits of reproductive cohesion in space and time. A particular study is made of the variation in male mate-searching behaviour and of its relationship to the different kinds of habitat. For *Bombus asiaticus*, patterns of colour variation across the Great Himalaya are compared with those expected from simple genetic models. Type material is examined for 103 of the nominal specific and subspecific taxa. Seventeen lectotypes are designated and 80 new synonyms and provisional new synonyms are established. Keys to the species are accompanied by diagrams of the colour patterns and by distribution maps.

## INTRODUCTION

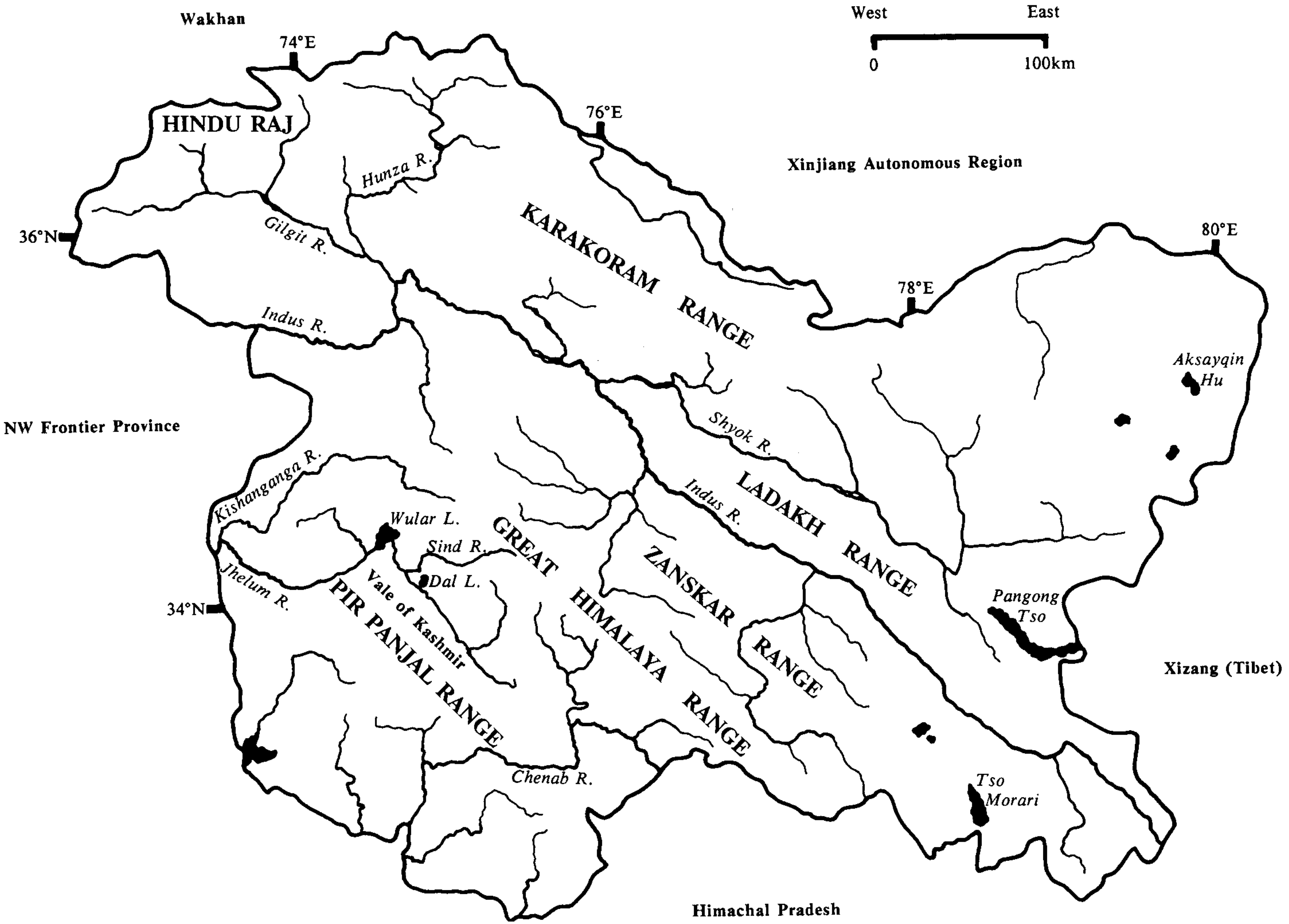
Bumble bees rank among the most abundant and conspicuous of flower visitors in alpine, temperate and arctic environments of the northern continents. In the southern hemisphere they are native only in the East Indies and South America (see Map 1), where most species are associated with the highlands. Adults feed mainly on nectar, which provides energy for flight. The larvae are fed on a mixture of pollen and honey, which provides their requirements for growth. Most species are social (reviews of behaviour by e.g. Alford, 1975; Morse, 1982; Plowright & Laverty, 1984). The colonies consist almost always of a single, mated queen, which lays most of the eggs, and usually of no more than a few hundred, unmated workers. The establishment and development of colonies takes place each summer and may take less than two months (Richards, 1973), culminating with a switch to the production of males and young queens near the end of the season. After mating, young queens normally diapause through the winter, away from the nest, before they attempt to found colonies on their own in the following year. Only a few species from the tropics of South America (Sakagami, 1976) and South East Asia (Michener & Amir, 1977) may have colonies that persist for more than one year. Bumble bees show unusually well-developed endothermy, which can be facultative when foraging (reviewed by Heinrich, 1979). Almost all species are generalists in their choice of food-plants, visiting any remunerative flowers. Their foraging follows a 'scramble' pattern, without either recruitment of nest-mates to good food sources or defence of food sources. These characteristics of bumble bees may account for their abundance in cool environments that have a predictable season of adverse conditions, where flowers are often fairly evenly dispersed. In contrast, the other social, long-proboscis bees (honey bees and stingless bees) have their centres of diversity and abundance in the tropical lowlands.

The bumble bees of Kashmir are of particular interest because this narrow corridor of mountains is almost the only major, modern point of contact between the large and divergent Oriental and Palaearctic bumble bee faunas. These faunas are otherwise separated by deserts in central Asia and in China, except for another corridor of contact near Beijing, which is occupied by relatively few species (Panfilov, 1957). Greater Kashmir encompasses almost the entire mountain system that links the high Tibetan (Xizang-Qinghai) plateau in the east with the Hindu Kush, Pamir and Tien Shan mountain ranges to the west and north. Hence Kashmir covers segments of the Pir Panjal, Great Himalaya, Zanskar, Ladakh, Karakoram and Hindu Raj ranges (Map 2), and includes some of the highest peaks in the world (altitudes range between about 400–8600 m; for an account of the geological structure see Searle *et al.*, 1988). Kashmir is slightly larger in area than the European Alps and lies at the same latitude as Syria, Tunisia and Arizona. Since Indian independence in 1947, the sovereignty of Kashmir has been a matter of dispute and sections are now administered by India (Jammu & Kashmir State), Pakistan (Northern Areas) and China (as part of the Xinjiang Autonomous Region).

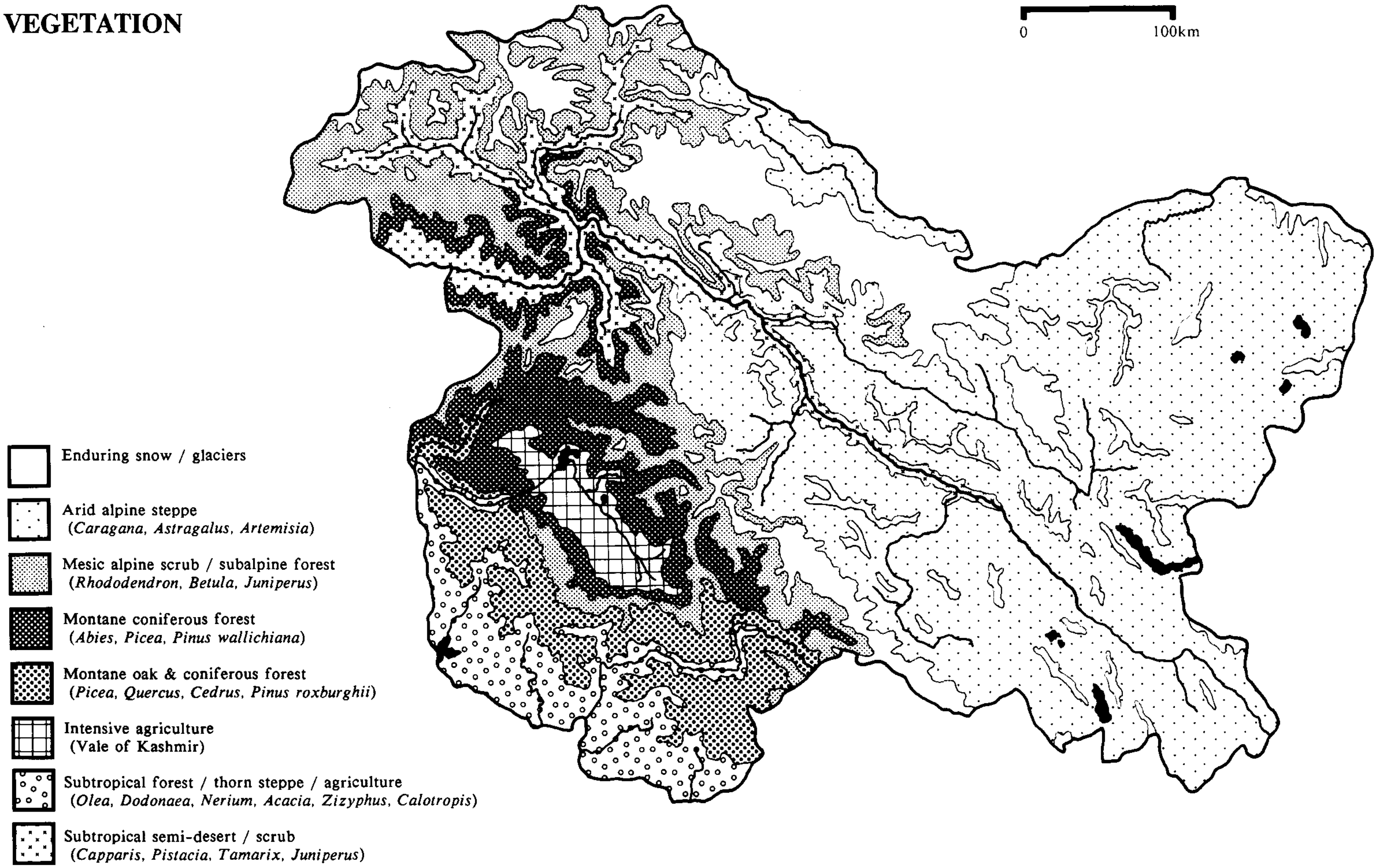
The high relief of Kashmir provides a broad range of habitats for bumble bees. Patterns in the distributions of bumble bees in Europe have been linked with climatic factors (e.g. Pekkarinen *et al.*, 1981). The differing climates of Kashmir can be summarised in three regions (e.g. Gurcharan Singh & Kachroo, 1976). First is the subtropical region of the Jammu foothills, which is subject to the summer monsoon (Fig. 2). Second, beyond the Pir Panjal range, is the more temperate Vale of Kashmir, where most of the rain and snow fall in the winter months (Fig. 1). Third, in the rain shadow of the Great Himalaya, is the arid alpine region of the Zanskar, Ladakh and Karakoram ranges (Figs 3 & 4). But of equal importance to climate, as an influence on whether or not a species of bumble bee could persist at a particular locality, may be the nature of the local vegetation (e.g. Bowers, 1985; Williams, 1988, 1989), even though bumble bees are seldom dependent on particular species of food-plants. Map 3 shows a summary of the vegetation in Kashmir, based on the survey of the Himalaya by Schweinfurth (1957). Not only do the three principal climatic regions within Kashmir differ in their flora, but in combination with the influences of local altitudinal zonation and variation in local exposure (Troll, 1972), this contributes towards a particularly broad range of habitats. In comparison with some parts of the Himalaya, Kashmir retains relatively



**Map 1** Position of Kashmir (in black) in relation to the known, native distribution of all bumble bees, which is shown covered by the grid. This map uses a cylindrical equal-area projection that is orthomorphic at 45° N/S, where bumble bee records are particularly numerous. The grid is calculated from intervals of longitude of 10°. The area covered by the grid in Central and South America may be a slight over-estimate of the distribution of bumble bees there.



**Map 2** Principal mountain ranges and rivers of Kashmir in the broad sense.



**Map 3** Summary of the vegetation that predominates in the different regions of Kashmir (adapted from Schweinfurth, 1957). Much of the area at lower altitudes (see Map 4) is heavily exploited for agriculture.

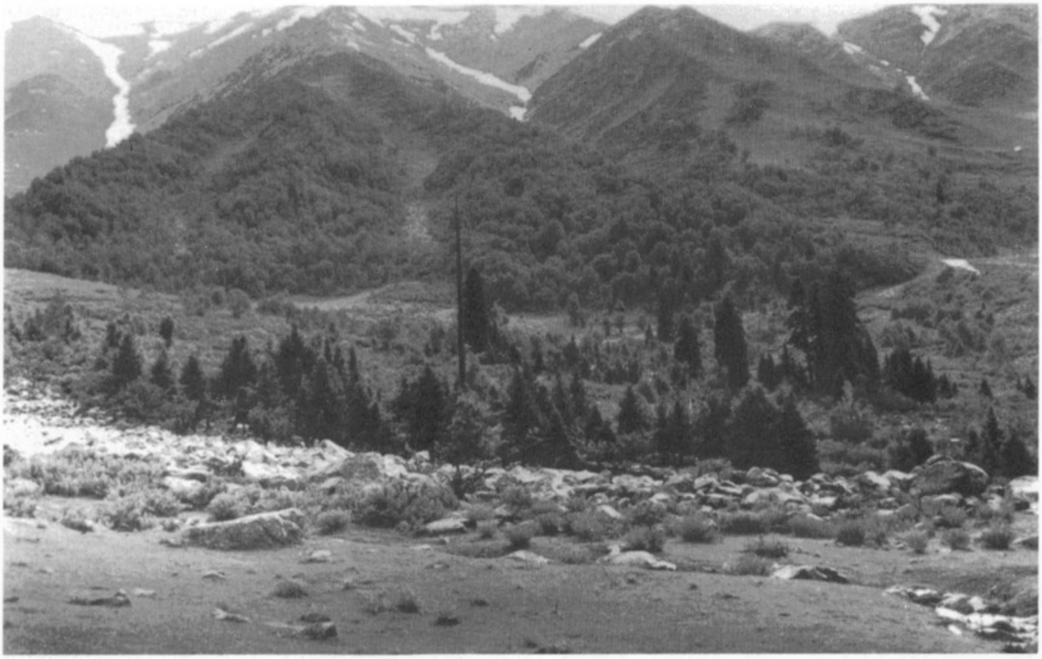


**Fig. 1** Subalpine zone of Mt Apharwat in the Pir Panjal range, viewed from 3000 m towards the peak at 4143 m (Map 4 locality 1: foreground pasture with *Euphorbia wallichiana*; lower slopes dominated by *Betula utilis*, *Salix* sp., *Syringa emodi*, with a few *Abies spectabilis*; middle slopes dominated by *B. utilis*, *Rhododendron campanulatum*; higher slopes dominated by *R. anthopogon*, *Juniperus recurva*). Of 17 species of bumble bees recorded in this immediate area, the most restricted to this zone is *B. biroi*, and the most abundant is *B. rufofasciatus*.

**Fig. 2** Lower montane coniferous forest zone on the Patnitop ridge in the Jammu foothills, viewed from 2000 m towards the plains of India (Map 4 locality 11: Patnitop dominants, *Cedrus deodara* [foreground], *Pinus wallichiana, P. roxburghii*). Of 3 species of bumble bees recorded in this area, the most restricted to this zone is *B. haemorrhoidalis*, and the most abundant is *B. trifasciatus*.

**Fig. 3** High, arid alpine steppe zone at the terminal moraine of Nimaling plain in the Zanskar ranges, viewed from 4800 m across the southern lateral moraine towards a peak (Kang-y-sey) at 6400 m (Map 4 locality 51: foreground, shrubs of *Caragana versicolor*). Of 9 species of bumble bees recorded in this immediate area, the most restricted to this zone are *B. personatus*, *B. oberti* and *B. ladakhensis*, of which the most abundant is *B. oberti*.

**Fig. 4** Subalpine semidesert zone at Lamayuru near the Indus valley, with a view of valley terraces at 3400 m, against a background of mountain ridges at 4000–5000 m (Map 4 locality 42). Of 3 species of bumble bees recorded in this area, the most restricted to this zone, and the most abundant, is *Bombus semenovianus*.

large forests and yet access to some of the varied alpine areas is no longer difficult.

Previous studies of the bumble bees of Kashmir have been based on a total sample of only a couple of hundred specimens. The first important collection of bumble bees from Kashmir was made by Lt.-Col. C. G. Nurse in 1901. A complete inventory of this material was never published, although it provided the specimens that have since been described as the types of many nominal taxa (Friese, 1909, 1918; Richards, 1928*a*, 1928*b*, 1930; Tkalců, 1974*b*). Other collections were mostly small, but particularly important material was obtained by A. Jacobson in Kashmir and Ladakh during 1912 (Skorikov, 1914*a*) and by Col. R. Meinertzhagen in Ladakh during 1925 (Richards, 1928*b*). Skorikov (1933*b*) compiled a preliminary list of the fauna of Kashmir and discussed the fauna of the entire Himalaya, though his work was based on a different concept of the species from that accepted at present. The only recent revision of any part of the large Himalayan fauna is Tkalců's (1974*b*) description of a collection of 73 bumble bees from Nepal. Although there are many elements in common between the faunas of Nepal and Kashmir, 16 species that are known from Kashmir are not represented in this collection. In the same paper Tkalců refers to his '*Monographie der Unterfamilie Bombinae des Himalaya*' as in press. Unfortunately this has never been published, although recently he has described several new taxa from the region (Tkalců, 1989). The only key that has been intended to cover any part of the Himalayan fauna is that published by Bingham (1897). This key artificially subdivides four of the species now recognised from Kashmir, whereas a further 20 species are not included at all.

For this review, much of the older material is reexamined and compared with the larger collections of new material, in order to describe some of the patterns of variation (and the discontinuities in these patterns) among the bumble bees of Kashmir. This evidence, together with information from the habitat associations of the species in Kashmir and information from their broader distributions beyond Kashmir, is used to discuss the likely relationships of ancestry and interbreeding among the nominal taxa.

## MATERIAL EXAMINED AND DEPOSITORIES

Large samples of undescribed material are available from western Kashmir in the collections

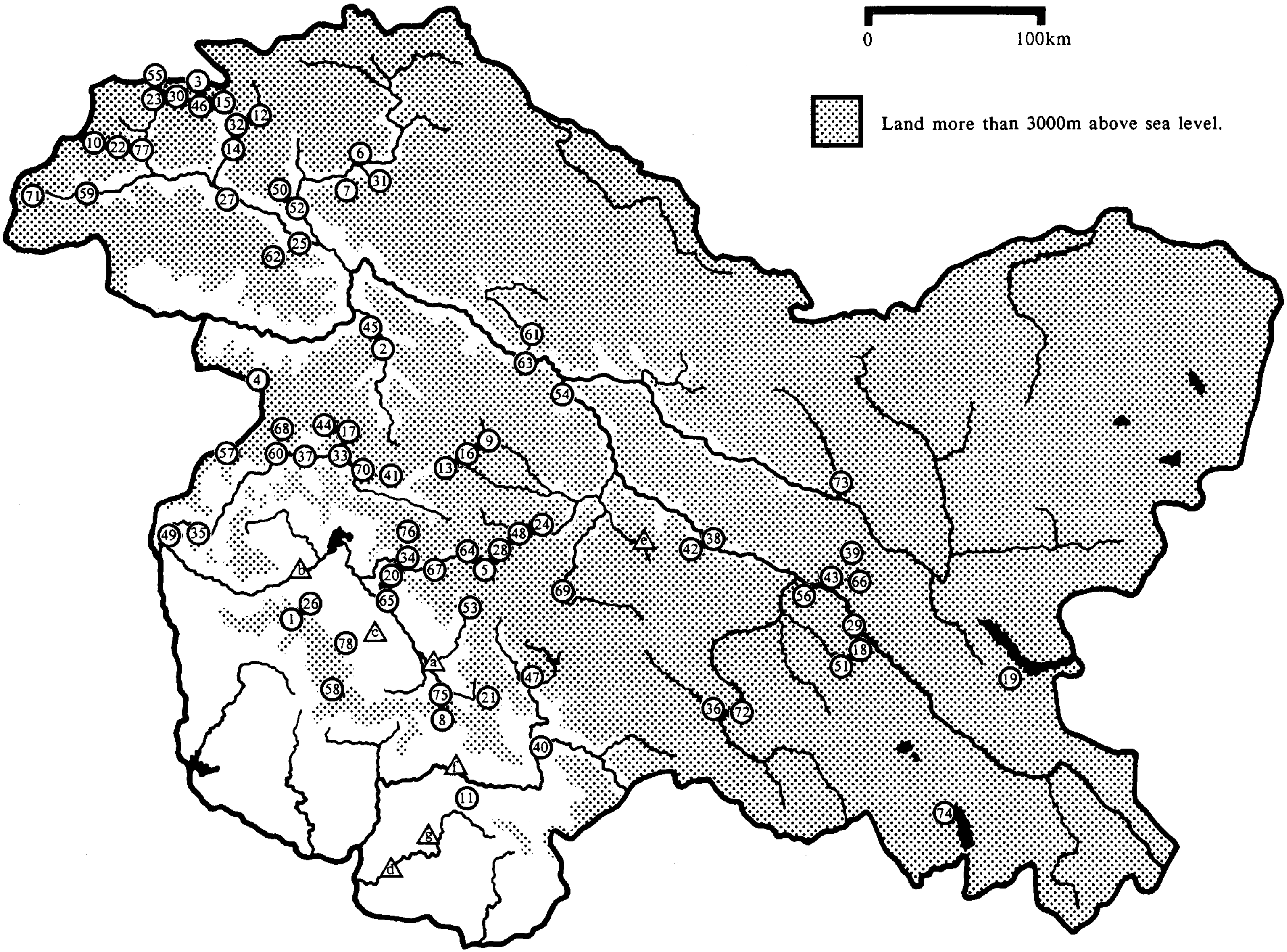
**Table 1** Localities that have been sampled for bumble bees. Sites in close proximity are treated as combined and represented by a single number on Map 4.

Localities from which samples of bumble bees have been examined (numbers in circles on Map 4).

1 (Mt) Apharwat
2 Astor
3 Atro Sar
4 Babusar
5 Baltal
6 Baltit
7 Banidas
8 Banihal
9 Bara Deosai
10 Batakush
11 Batote
12 Bulandi
13 Burzil Chauki
14 Chakorkhand
15 Chhantir Gah
16 Chhota Deosai
17 Chittakatha Sah
18 Chogdo
19 Chushul
20 Dachhigam
21 Daksum
22 Dalti
23 Darkot
24 Dras
Gamelti = Darkot
25 Gilgit
26 Gulmarg
27 Gulmiti
28 Gumri
Harwan = Dachhigam
29 Hemis
30 Holojut
31 Holshal
Hunza = Baltit
32 Imit
33 Janwai
34 Kangan
35 Kanur
36 Karsa
37 Kel
38 Khalsi
39 Khardung La
Khilanmarg = Apharwat
40 Kishtwar
41 Lal Pani
42 Lamayuru
43 Leh
44 Lilam
45 Luskum
46 Mahthantir Gah
Martselang = Chogdo
47 Maru
48 Matayan
49 Muzaffarabad
Nagar = Holshal
50 Naltar
Nigagar = Baltal
51 Nimaling
52 Nomal
Nowgam = Banihal
53 Pahalgam
54 Parkutta
Patnitop = Batote
55 Rawat
56 Rumbak
57 Saif-ul-Maluk Sar
58 Sangisfaid
59 Shamran
60 Shardi
61 Shigar
62 Shinghai Gah
63 Skardu
64 Sonamarg
65 Srinagar
66 Stakmo
67 Sumbal
68 Surgun
69 Suru
Tangmarg = Gulmarg
70 Taobat
71 Teru
Thajiwas = Sonamarg
72 Thonde
73 Tiggur
74 Tso Morari
Tungri = Karsa
75 Verinag
76 Wangat
77 Yasin
78 Yusmarg
Zoji La = Gumri

Localities at which no bumble bees could be found during brief surveys in August–September 1980, 1985 or 1986 (letters in triangles on Map 4).

a Anantnag
b Baramula
c Chrar-i-Sharif
d Jammu
e Mulbekh
f Ramban
g Udhampur



Map 4 Localities from which material has been

made during 1953 and 1954 by F. Schmid (BMNH accession 1962–457; account of the expedition in Schmid, 1958). In addition, I was able to make large, selective collections from southern and eastern Kashmir during 1980, 1985 and 1986. Unfortunately, large areas near the borders, especially to the north and east of the country, are prohibited to foreign visitors, so only a few specimens from older collections are available.

The sites in Kashmir from which material has been examined are listed in Table 1 and shown on Map 4. Geographical information is taken from the United States Survey of India maps (scale 1 : 250,000) and from The Times atlas of the world (1987). The world-wide distribution of species is also shown by maps (see Map 1). These are compiled with a preference for records from those specimens that I have been able to examine, supplemented by a list of selected references. The source material is summarised briefly in the text either by political region (for the Himalayan/Tibetan mountain system in India and China) or by major mountain system (for the more restricted bumble bee faunas of central Asia), such as the Elburz, Hindu Kush, Pamir, Alai – Tien Shan (in its broadest sense) and Altai mountains. More precise data can be found in the original references. The specimens that have been examined are deposited in collections as shown by the references to the following abbreviations.

| | |
|---|---|
| AB | Dr A. A. Bhat, S.K. University of Agricultural Sciences & Technology, Srinagar, India. |
| BMNH | British Museum (Natural History), London, U.K. |
| BPBM | Bishop Museum, Honolulu, U.S.A. |
| BT | Dr B. Tkalců, Prague, Czechoslovakia. |
| FA | Faculté des Sciences Agronomiques de l'Etat, Gembloux, Belgium. |
| INHS | Illinois Natural History Survey, Champaign, U.S.A. |
| ITZ | Instituut voor Taxonomische Zoölogie, Amsterdam, Netherlands. |
| IZ | Institute of Zoology, Beijing, China. |
| LK | Dr L. S. Kimsey, University of California, Davis, U.S.A. |
| LSL | Linnean Society, London, U.K. |
| MCSN | Museo Civico di Storia Naturale, Genoa, Italy. |
| MI | Dr M. Ito, Hokkaido University, Sapporo, Japan. |
| MNHN | Muséum National d'Histoire Naturelle, Paris, France. |
| MNHU | Museum für Naturkunde an der Humboldt-Universität, Berlin, D.D.R. |
| NM | Naturhistorisches Museum, Vienna, Austria. |
| NMP | Národní Muzeum, Prague, Czechoslovakia. |
| NMS | Natur-Museum Senckenberg, Frankfurt, D.B.R. |
| NR | Dr N. D. Rishi, University of Kashmir, Srinagar, India. |
| PW | Author's collection, London, U.K. |
| RH | Dr R. W. Husband, Adrian College, Adrian, U.S.A. |
| SEMK | Snow Entomological Museum, Lawrence, Kansas, U.S.A. |
| TL | Dr T. M. Laverty, University of Western Ontario, London, Canada. |
| TM | Természettudományi Múzeum, Budapest, Hungary. |
| UM | University Museum, Oxford, U.K. |
| USNM | United States National Museum, Washington D.C., U.S.A. |
| ZI | Zoological Institute, Leningrad, U.S.S.R. |
| ZM | Zoologisk Museum, Copenhagen, Denmark. |
| ZMMU | Zoological Museum of Moscow State University, Moscow, U.S.S.R. |
| ZS | Zoologische Staatssammlung, Munich, D.B.R. |

## DIAGNOSIS OF HIMALAYAN BOMBINI

Among the Apidae, the 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 apico-lateral 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 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).

## CHARACTERS STUDIED

Although this review aims to describe many aspects of variation among the bumble bees of the Kashmir Himalaya, inevitably those characters that vary most among species and least within species receive most attention. Many characters of the females show more pronounced expression and divergence among the queens (which are usually the larger females) than among the workers (smaller females).

The most variable characters of bumble bees are the colours of their pubescence. These are so variable that they can be very misleading if used alone for the identification of species. For instance, it is known that in some areas of Europe and North America the local parts of populations from even very divergent species-groups appear to have converged closely in colour pattern (see the comments on discrimination of species and intraspecific variation, and the discussion of colour patterns of the Kashmir fauna). Differences in the shape and sculpturing of the sclerites have been found to be more reliable indicators of relationship.

On the head, the shape and details of the sculpturing of the LABRUM, CLYPEUS and MALAR AREA (= oculo-malar space) are frequently used as characters (Fig. 14). The superficial structure and sculpturing of the labrum may be particularly complex (Figs 23–30, 220–222). The shape of the malar area can be measured as the ratio of the oculo-malar distance to the breadth of the mandible at its base (Fig. 15). This shape is related to variation in proboscis length (Medler, 1962), which is in turn related to variation in the behaviour governing flower choice, both among and within species (reviewed by e.g. Morse, 1982). However, within at least some of the species with longer proboscides, the shape of the malar area may be subject to allometric effects among individuals of different sizes (e.g. Sakagami, 1972). Furthermore, because the boundaries of the malar area require arbitrary definition, measurements by different authors are not always comparable. Therefore this character is used here only when the differences in shape are relatively large. The MANDIBLES provide many characters including the number and shape of the ridges known as KEELS, between which are grooves, such as the SULCUS OBLIQUUS (Figs 31–38). There is a BASAL TOOTH, variable numbers of subsidiary or INTERCALARY TEETH and often an APICAL TOOTH, which is defined at its base by an anterior notch known as the INCISURA. These characters vary within species as well as among them and are subject to further apparent variation caused by wear. Nonetheless, they can still be useful in some species-groups (e.g. the subgenera *Psithyrus*, *Alpigenobombus*). The shape of ANTENNAL 'SEGMENTS' (= scape, pedicel and flagellomeres), measured as ratios of length to breadth, is also used here, but only when the differences in shape are large (Figs 17–22, see the comments above on the shape of the malar area). The OCELLI vary in size and in position relative to the compound eyes. The separation of the lateral ocellus from the neighbouring margin of the compound eye can be measured in relation to the diameter of the lateral ocellus (Fig. 16). The strongly enlarged ocelli of the females of some species are associated with enlarged compound eyes among the conspecific males, and hence with particular kinds of male mate-searching behaviour (see the comments on mate-searching behaviour of male bumble bees in Kashmir). One of the characters most prone to variation, both within and among species, is the sculpturing of the OCELLO-OCULAR AREAS of the VERTEX (= frontovertex), on the top of the head (Figs 215–219). Just as for variation in the sculpturing of the labrum and clypeus, some of the elements in the patterns of punctures of the ocello-ocular areas are constant among large groups of species, whereas other details are subject to variation among individual bees from the same colony.

On the thorax, the majority of characters are taken from the appendages (Fig. 43). Subtle differences in the shape of the wing venation have occasionally been used (e.g. Milliron, 1971; Plowright & Stephen, 1973), although these are not easy to measure (see the comments above on the malar area). Above the wing bases are a pair of small dome-shaped TEGULAE, which are shown in the colour pattern diagrams. Between the tegulae, on the thoracic dorsum, is the SCUTUM (= mesoscutum), and immediately posterior to it, the SCUTELLUM (= mesoscutellum). These sclerites show some variation in sculpturing (Figs 223 & 224), but are also useful for relating to the distribution of pale or black pubescence. The relative length of the pubescence on various parts of the legs can be used to measure the general length of the pubescence of the body (e.g. by comparison with tibial breadth). The outer surface of the hind TIBIA has large areas without long pubescence for females of most species, although to a lesser extent for females of the subgenera *Psithyrus* and *Mendacibombus* and for males of some other species (Sakagami & Ito, 1981). For these females the bare areas are surrounded by dense fringes of long, stout hairs that function as a CORBICULA for carrying pollen. Variation in the length and extent of this pubescence and in the sculpturing of the bare areas have been used to distinguish taxa (Figs 225 & 226), although there can be considerable differences between queens and workers within the same species (see the comments on *B. simillimus*). Among some species-groups there is a pronounced development of the disto-posterior corners of the hind tibia and of the mid and hind BASITARSI (= first tarsomeres) (Figs 39–42). These can form spinose projections, but differences between closely-related species are seldom discrete. The shape, sculpturing and pubescence of the hind basitarsus are also used (Figs 227–229).

On the abdomen, the most obvious characters are found in the variation of the sculpturing of the sclerites. Bumble bees, like other Apocrita, have a waist between the first two abdominal segments, so that the first abdominal segment (= propodeum) is associated with the thorax, whereas the subsequent segments form a separate unit, the GASTER (= 'metasoma'), which can be moved independently. In this review all references to segment numbers for the dorsal TERGA (= tergites) and ventral STERNA (= sternites) refer to gastral segments, so gastral tergum I is the dorsal sclerite of the second abdominal segment. For the females, variation in sculpturing is often especially clear on gastral tergum VI (= epipygium or pygidium) and sternum VI (= hypopygium), which may also show single or double KEELS (= ridges) (Figs 206–211), or even a rounded boss, as well as variation in the shape of the apex (Figs 212–214, 230, 231). There is some variation in the structures associated with the female STING (= modified ovipositor), especially in the shape of the 'inner projections from the sting sheath' (Richards, 1927*b*, 1968; see also Kopelke, 1982). However, many of the 'sting sheath' characters are parts of the folds that lie between the rami of the left and right valvulae (see Williams, 1985: fig. 5) and these folds are usually only weakly sclerotised. Consequently they do not always preserve well in dried specimens and may become distorted, so these characters are not used here. In contrast, the male GENITALIA (= genital capsule) do preserve well because they are strongly sclerotised and so require no treatment other than a straightforward extraction from the gaster with a pin. The male genitalia consist of a pair of gonoforceps for clasping the female and an intromittant organ (Figs 44 & 45). During pairing, the female is locked with her sting assembly pulled posteriorly and dorsally away from the male (Williams, 1985: fig. 5) by at least three points of contact: (1) the VOLSELLAE (= laciniae, but see the discussion below) press the sting base from above and (2) the GONOSTYLI (= squamae) hold the rami of the female valvulae with an opposing action from below, so that the sting base is gripped; at the same time, (3) the apex of the female's sternum VI is gripped between the male's parapenial processes of the GONOCOXITES (= stipes) and the base of the SPATHA, ensuring that the sting assembly is clamped in a protruded position, which gives access to the female gonopore for the male intromittant organ. Kopelke (1982) describes how the PENIS VALES (= sagittae) anchor among the weakly sclerotised folds that lie between the rami of the valvulae of the female sting base. Many of these structures of the male genitalia show complex elaborations that are particularly valuable taxonomic characters (Figs 46–205, see the comments on relationships among species by ancestry). For the males, gastral sternum VIII and sternum IX (= subgenital plate) are found below the genital capsule and are normally retracted above sternum VII. Variation in their shape and pubescence has been described by many authors. This variation may also be great even within species and it is often accompanied by a pronounced overlap in variation among related species. Consequently these characters are not used here.

There has been some disagreement as to the homology of the 'lacinia' of male bumble bee genitalia, concerning whether it is derived from part of the volsella or from part of the gonostylus (e.g. Snodgrass, 1941; Smith, 1970). As yet no study of ontogeny has been sufficiently detailed to establish its homology conclusively, so the interpretation depends on comparative studies of the morphology of adults. Zander (1900) did study the ontogeny of male bumble bee genitalia and concluded that a small scale ('Schuppe') on the inner ventral surface of the gonocoxite is of volsellar origin because it is in the expected position and becomes strongly chitinised early in development. However, he made no detailed observations on the derivation of the larger ventral structure known as the 'lacinia'. Later Smith (1970) concluded from their topological similarity that the ventral scale is derived from the digitus of the ancestral volsella, but that the larger ventral structure known as the 'lacinia' is derived from the cuspis of the ancestral volsella. Snodgrass (1941) had argued that Zander's scale is the only expression of the volsella and that the large ventral 'lacinia' is derived from the ventral lobe of the gonostylus. He supported this argument with the observation that the 'lacinia' is connected with the dorsal gonostylus for part of its length by a membrane. However, against this argument it must be noted firstly that some bees, including centrines such as *Epicharis rustica* (Olivier) and euglossines such as *Eufriesea pulchra* (Smith), clearly show both major lobes of the gonostylus as well as a third large ventral sclerite in a similar position to the base of the 'lacinia' of bumble bees, below the inner ventral margin of the gonocoxite (see Fig. 5). Therefore this 'lacinia' cannot be the ventral lobe of the gonostylus, although it is in a reasonable position to be part of the volsella and appears to be distinct from Zander's scale. Secondly, among these bees with a bilobed gonostylus, the two lobes are clearly strongly fused near their bases, which is not known between the gonostylus and the 'lacinia' for any bumble bees, which have only the weakly sclerotised membrane noted by Snodgrass. Traces of the two lobes of the gonostylus may be retained among bumble bees as the distal lobe and the interio-ventral process, although these are reduced among species of the subgenus *Mendacibombus* and among many euglossine bees. Thus in the absence of a more detailed ontogenetic study, the weight of evidence supports the argument that a volsellar derivation for the 'lacinia' is most likely.

## RELATIONSHIPS AMONG SPECIES BY ANCESTRY

The bumble bees, including the 'cuckoo' bumble bees, form an easily recognised and monophyletic (sensu Hennig, 1981) group of about 240 species (present estimate). Their closest relatives are believed to be the South American orchid bees, the Euglossini (Winston & Michener, 1977; Kimsey, 1984), which have been used in the cladistic analyses for out-group comparisons. Opinions differ concerning the relationships among the many described species-groups of bumble bees, so that many specialists working with bumble bees currently follow their own individual supraspecific classifications.

The present ideas of relationship among species of bumble bees are revised and developed from those proposed in a preliminary cladistic analysis of the functional characters of the male genitalia (Williams, 1985). In practice, most authors since Schmiedeknecht (1882) and Radoszkowski (1884) have used differences in characters of the male genitalia to recognise species-groups among bumble bees. Richards (1968) reviewed the variation in morphology among these established groups and provided diagnoses that also include other characters from both sexes. More recently, Ito (1983, 1985) compared similarities between the male genitalia of species in these groups in a detailed phenetic study.

Some criticism has been made of the classification of bumble bees primarily by characters of the male genitalia because it relies on such a restricted character set. But the characters of the male genitalia that function in clamping the male to the female for copulation (see the comments on characters studied) are especially suitable for use in classification not only because they present many different character states but also because there appears to be a particularly high congruence in the patterns of these character states among taxa (Williams, 1981, 1985). The evolutionary interpretation of the high congruence in the patterns of character states of bumble bee genitalia is that there is relatively little homoplasy among these characters. The classification of flowering plants has long been based on characters of their genitalia for similar reasons.

Evolutionary explanations for why male genitalia are often so strongly differentiated among species have included those that depend on a principal role for the genitalia as a species-isolating mechanism (the lock-and-key hypothesis, reviewed by Shapiro & Porter, 1989), or as a mechanism for female arousal (the stimulation hypothesis, see Eberhard, 1985), or as an impregnable holdfast mechanism (see below). From a study of bumble bee morphology, Richards (1927*a*, 1927*b*) concluded that at least in their case mechanical incompatibility is unlikely to have evolved as an isolating mechanism (see also the comments on the biological species and the Recognition Concept). At that time Richards had apparently not actually observed how the genitalia fit together during pairing between bumble bees, because he referred to Boulangé (1924) for a description of a pinned pair of *B. hortorum* (L.): '[p. 290] ... les branches du forceps sont vigoureusement appliquées par leurs extré – [p. 291] mités sur les parties latérales du VII$^{e}$ sternite de la femelle (c'est-à-dire le dernier visible en surface).'. This led Richards (1927*b*: 262) to conclude that '... the stipes, volsella and squama, that is the most complex part of the genitalia, do not enter the abdomen of the female at all ...'. In contrast to this, present evidence confirms that for bumble bees the apices of the volsellae and gonostyli (= squamae) do grip tightly around the female sting base in the manner shown for *B. (Melanobombus) lapidarius* (see Kopelke, 1982: figs 1–3;

Williams, 1985: fig. 5), even among apparently rather divergent species (e.g. from direct examination of live paired *B. (Bombus) lucorum*, *B. (Sibiricobombus) asiaticus*, *B. (Melanobombus) rufofasciatus* and from a freshly-killed pair of *B. (Fervidobombus) niger* Franklin [= *B. atratus* Franklin, a name preoccupied by *B. mucidus* var. *atratus* Friese]). In fact, whether these claspers grip sternum VI or the sting base has little effect on the substance of Richards's arguments against the lock-and-key hypothesis, namely that the supposed 'lock' structures of the females are relatively undifferentiated among species and that inter-specific pairing is probably rarely attempted in any case. Eberhard (1985) believed that similar comments by Richards (1927*a*) showed that the male genitalia of bumble bees could not function as 'holdfast devices', although I have seen two pairs in museum collections that were still locked together firmly by their genitalia.

Eberhard (1985) suggested that an alternative explanation for the elaborate structure of male genitalia is that they function as female stimulaters, which have diverged as a result of inter-sexual selection by female choice. Of course this idea does not depend on an absence of the holdfast function, but it does require that a female should be able to discern differences in stimulation by males with subtly different genital morphology. However, at present there is little evidence from bumble bees either for the existence of the sensilla that would be required in those heavily sclerotised areas of the sting base that are clasped by the males, or for the definite rejection of some males in preference to others by females.

Another likely evolutionary explanation of the great range of morphology of the male genitalia of bumble bees is that they function primarily as impregnable holdfast devices, which have diverged as a result of intra-sexual competitive selection among males (Richards, 1927*a*; Williams, 1985). In Kashmir, male bumble bees were seen to attempt to catch and mount the females in order to clasp them with their genitalia, without any obvious courtship (for further details see the comments on mate-searching behaviour of male bumble bees in Kashmir). Any radical changes in the functional characters of the male clasping mechanism might only be inherited in the unlikely event that they appeared at the same time as the necessary reciprocal changes in the anatomy of the female. Consequently characters of the male claspers might be more conservative than characters that do not have to fit the female securely in order to prevent any interruption of copulation. Yet the competition from other males of the same species to dislodge a paired male for access to the same female might still favour any slight elaborations of structure if this would increase that male's chances of hanging on to reproduce. Competition among males can be intense (e.g. Free, 1971; Lloyd, 1981; pers. obs.), probably because a male bumble bee's principal influence on its reproductive success, other than through the quality of its ejaculate or possibly through the removal of competitor's sperm, is likely to be by maximising the number of matings that it can achieve. This may account in part for why bumble bee mating systems are usually variations of scramble competition polygyny (see the comments on male mate-searching behaviour).

## Genera of Bombini

Many of the inferences of relationship among bumble bees from the preliminary cladistic analysis of characters of the male genitalia remain very tentative (Williams, 1985), especially those for some of the most morphologically divergent species (e.g. the North American *B. nevadensis* Cresson, see the comments on the Kashmir species of *Mendacibombus*). Nevertheless, further evidence from characters of the females (Ito & Sakagami, 1985) and from enzyme mobilities under electrophoresis (Pamilo *et al.*, 1987) supports the conclusion that the socially parasitic or 'cuckoo' bumble bees (*Psithyrus*) constitute a monophyletic group. It also appeared from the results of the preliminary cladistic analysis that *Mendacibombus* could be the monophyletic sister-group to all other bumble bees. This group in turn appeared to consist of two monophyletic sister-groups, the social parasites (*Psithyrus*) and all remaining bumble bees. Consequently the use of three genera was recommended: *Mendacibombus, Psithyrus* and *Bombus*.

Now that it has been possible to examine the male genitalia of most of the described species, the present interpretation is that *Mendacibombus* is probably paraphyletic with respect to all other bumble bees (Fig. 5, *Psithyrus* + *Bombus* represented by *B. exil*, see the comments on the Kashmir species of *Mendacibombus* and *B. (Psithyrus) bohemicus*). So recognising *Mendacibombus* as a genus for these peculiar, high mountain bees is unsatisfactory because it is no longer well supported by evidence of monophyly. But then the traditional concept of the genus *Bombus* that includes *Mendacibombus* as a subgenus, but not *Psithyrus*, is also apparently paraphyletic and so recognisable only by phenetic similarity.

A pragmatic solution is to return to an emphasis of the more widely- shared characters and of the

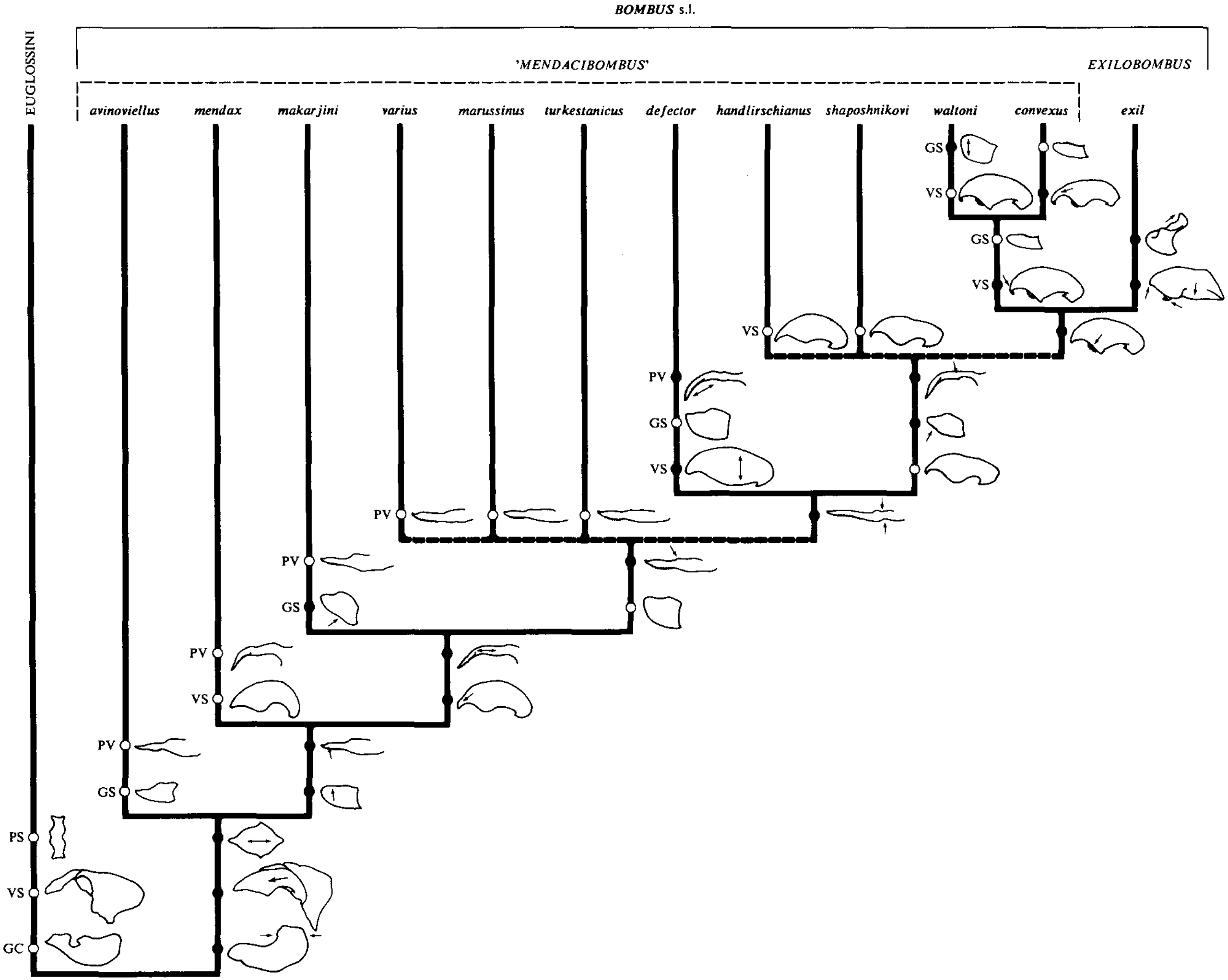


**Fig. 5** Cladogram based on characters of the male genitalia for most species of the subgenus *Mendacibombus*, with *B. (Exilobombus) exil* representing all other bumble bees, including the species of *Psithyrus*. The name *varius* is a junior secondary homonym in the genus *Bombus* s.l. This taxon is likely to be conspecific with *B. himalayanus*, the males of which have not been examined (see the comments on *B. himalayanus*). Light circles show plesiomorphic states and dark circles show the appearance of apomorphic states. Character changes are shown by arrows (see Figs 44 & 45): PS, spatha of penis from the dorsal aspect; PV, right penis valve from the outer lateral aspect or dorso-

more distant affinities for the generic concept, with the result that one genus, *Bombus*, is recognised for all bumble bees, including *Psithyrus*. Of course the use of *Bombus* for all of these species does bring certain names originally ascribed to the genus *Psithyrus* into secondary homonymy with names in the genus *Bombus*. It also requires that qualifications concerning the socially parasitic species will have to be made more often to any generalisations about the species of *Bombus*. But despite this break with the most widely-established bi-generic tradition, the use of one genus for all bumble bees has the advantage that it recognises a group for which the evidence of monophyly is 'particularly strong, so that the nomenclature is most likely to remain stable. This single genus is also very easy for non-specialists to recognise.

Within the genus *Bombus*, the established subgeneric names (e.g. Richards, 1968) may be found convenient by some specialists who wish to label those assemblages of species that are more closely similar to one another. Unfortunately, Richards's usage of subgeneric names does not always communicate ideas of relationship well, because some of these assemblages now appear to be paraphyletic (e.g. *Mendacibombus*) or even polyphyletic (e.g. *Sibiricobombus*, see the comments on *B. asiaticus* and *B. oberti*). Of course subgeneric names can simply be treated as synonyms of *Bombus* Latreille and ignored by those who prefer to do so. But when a comprehensive cladistic revision is available, then perhaps the nomenclature of the more reliably monophyletic species-groups could be revised, if the system is still found to be useful.

In this review, the bumble bee species of Kashmir are listed in a sequence that is chosen to reflect their relationships (after the sequencing convention of Nelson, 1972) as these are currently envisaged.

## DISCRIMINATION OF SPECIES AND INTRASPECIFIC VARIATION

Early work on the taxonomy of Asian bumble bees showed little consistency in the delimitation of the taxa named as 'species' in some species-groups. In part this has been due to the changing nature of the species category as applied to living organisms. The species concept adopted for this review is briefly summarised here so that it is explicit.

A particularly visible part of the problem of discriminating species of bumble bees is that some of their populations are now known to include individuals with very different colour patterns. This was not always appreciated when only small samples were available from widely-scattered localities. Conspicuous colour patterns are likely to be advantageous because they advertise a warning to potential predators against the painful sting that female bumble bees can inflict. Consequently, the theory of Müllerian mimicry may explain not only the regional convergences in colour pattern among unrelated species, but also how parts of the same species may have diverged in colour pattern in different regions of its distribution (see the comments on characters not related to male mate-searching and the discussion of the colour patterns of the Kashmir fauna). It is perhaps precisely because bumble bees are such large and colourful insects that, like butterflies, they have been widely collected and have received so much attention in the literature. The considerable effort that has been invested in the description of subtleties of colour variation among some bumble bees has left an unfortunate nomenclatural burden of over 3000 formal names (i.e. about 12 names per species).

A large part of the more general problem in the application of the category 'species' to living organisms arises from confusion of the different kinds and degrees of relationship among populations (reviewed by e.g. Queiroz & Donoghue, 1988). Sexually reproducing organisms have been envisaged as living in populations that are united by interbreeding, so that in the long term relationships within the population tend to be reticulate. This provides the possibility of some evolutionary cohesion through gene flow, even though without concerted contraction and expansion of populations, random 'diffusion' of genes may not be sufficient to curb divergence (Barton, 1988). In contrast, relationships among populations are envisaged as tending to be more consistently divergent. In the short term, parts of a population may show restricted interbreeding with neighbouring parts of the population and may even show genetic and apomorphic divergence from them. Only with the benefit of hindsight is it possible to know whether divergence will be maintained or whether it will subsequently be dissipated in the broader population, should interbreeding become reinstated when the parts of the population meet. At one extreme, each of these parts of a population that may be more or less reproductively distinct in the short term could be regarded as a terminal element and given a name. But it can be seen that there is a broad range of possible relationships among these parts of the population, which may involve various degrees of inter-breeding both past and present, in differing combinations with various degrees of genetic and apomorphic divergence. Consequently, no absolute criterion can be devised that can universally define the species category.

Faced with the apparent impossibility of finding a universal solution to the 'species problem', it is still clearly desirable to try to minimise the confusion in the application of the species category. For the practice of discriminating species in this review, I have attempted to explore the application of species-defining criteria that place a greater emphasis on the potential for interbreeding (see the following section) than on general apomorphic divergence. General apomorphic divergence may have the appeal that it can be considered to have resulted in an observable pattern of monophyletic taxa, the discovery of which may be independent of any ideas of the process that caused it, which may not be discoverable. However, this rejection of process robs the 'morpho-species' category of any particular theory-based significance and so allows it to be defined only by a choice of some degree of apomorphic divergence that, in consequence, must be essentially arbitrary. Hence the cladistic method is not appropriate for the discovery of biological species. In contrast, the interbreeding criterion should be most closely associated with the process of gene flow within populations over the long term, which is believed to be one of the processes that can maintain some evolutionary cohesion (see Templeton, 1989). Of course there are also considerable problems with applying the interbreeding criterion, which are discussed in the next section. In practice, the application of the interbreeding criterion to many cases requires a similar degree of subjective judgement to that required by the use of the general apomorphic divergence criterion. Often the only available evidence for interbreeding is very indirect and must still be inferred from patterns of variation in characters of morphology or of molecules.

## The 'biological' species and the Recognition Concept

Early authors may have regarded species as convenient classes for the typological description of a particular level of variation, but since Darwin (1859), the evolutionary significance of biological species has been stressed. This biological concept defines species of sexually reproducing organisms by a lack of interbreeding between populations, where these overlap. One of the problems with the biological species concept is that it does not solve the problem of interpretation for populations that do not overlap at present (reviewed by e.g. Splitter, 1982), because in its simple form it does not show how to obtain direct and representative evidence of the 'potential' for interbreeding between individuals that do not meet under natural conditions.

Dobzhansky (1937) suggested that isolating mechanisms have been selected for because they perform the function of preventing interbreeding between species. Isolating mechanisms were said to have the advantage of protecting their 'more harmonious' gene assemblages from disruptive recombination. But since isolating mechanisms might be selected for only when populations with such gene assemblages overlap, Dobzhansky's Isolation Concept provides little help in the assessment of the potential for interbreeding among non-overlapping (allopatric) populations.

Paterson (1980, 1985) criticised Dobzhansky's Isolation Concept of the species in response to difficulties with the population genetics of the selection of isolating mechanisms. Paterson's Recognition Concept defines a species by the common 'specific-mate recognition systems' that are shared by individuals in the population. From this viewpoint, individuals of different species are not expected to interbreed because they do not recognise one another as potential mates (thus 'postmating isolating mechanisms' [Mayr, 1963] are, strictly speaking, incidental to delimiting species). Paterson stressed that the breakdown in recognition at speciation might occur in allopatric populations, but only indirectly, as a consequence of other evolutionary divergences and not by reinforcement of hybrid disadvantage (i.e. 'premating isolating mechanisms' [Mayr, 1963] evolved as effects, and were not selected *for* their isolating function). Evidence of this particular kind of divergence in allopatry might help in the assessment of the potential for interbreeding among non-overlapping populations.

Paterson's Recognition Concept is not entirely satisfactory in that any allopatric populations with effective postmating isolation but no premating isolation would apparently be included in the same species. If these populations subsequently made contact, there would then be a selective advantage for reinforcement by premating isolation, as envisaged in the Isolation Concept.

Ultimately it is likely that both kinds of speciation process have occurred, so that a major contribution of the Recognition Concept may be its emphasis on the role of premating barriers or specific-mate recognition systems. Changes in these specific-mate recognition systems could evolve rapidly by sexual selection (see West-Eberhard, 1983) in allopatry, despite stabilising selection. Furthermore, neither stabilising selection nor sexual selection necessarily imply uniform selection pressures across a geographically extensive population and so they do not preclude the possibility of clinal variation in the recognition system (see Verrell, 1988). But if the characters that are crucial to specific-mate recognition were known to differ among individuals of at least some of the problematic disjunct populations, then the Recognition Concept might provide better grounds for discounting a potential for interbreeding and gene flow in these cases (e.g. Vrba, 1985).

In principle, the most widely-applicable morphological criterion for the discrimination of species might therefore be found where there are differences in the characters that function in specific-mate recognition. However, the Recognition Concept of species does not require individuals of separate species necessarily to differ at all in morphology (or in ecology, see Hengeveld, 1988) and the search for key characters for the discrimination of species has indeed been unsuccessful (reviewed by Templeton, 1981). This search can be traced to the classical concept of species as typological classes, whose members should share some particular similarity or 'essence'. More recently species have been viewed as individuals (Ghiselin, 1975), characterised instead by their internal organisation, within the population (Hull, 1980). This organisation could be provided by their shared specific-mate recognition systems and potential for interbreeding. Yet from a cladistic viewpoint, free interbreeding within a population is a shared ancestral characteristic and so does not define a taxon (Rosen, 1979). Cladists would therefore be obliged to recognise some paraphyletic terminal elements, because interbreeding populations are not always distinguished by the possession of convenient apomorphies by all individuals (e.g. Ackery & Vane-Wright, 1984; Queiroz & Donoghue, 1988). If apomorphic characters were always to become fixed throughout a population as a necessary part of the process of speciation, then these character states might fulfil the role of an essence. In contrast, character states correlated with specific-mate recognition systems are not essences because they may only be expected to evolve as secondary consequences of reproductive processes and they may occur in just one of the sexes. So these characters can provide no more than a guide for the inference of the potential for interbreeding among individuals as parts of the same species in certain cases.

## Mate-searching behaviour of male bumble bees in Kashmir

The mate-searching behaviour of male bumble bees represents some of the first stages in the specific-mate recognition systems of these insects (cf. Paterson, 1985: fig. 2). In Kashmir, differences in male mate-searching behaviour among some closely-related species are associated with differences in some of their morphological character states, such as eye size and shape, antennal length and thoracic shape. Two contrasting examples are summarised briefly here (see the comments on the inference of allopatric, conspecific taxa & on allopatric, separate species). By analogy, these differences might provide a particularly strong form of morphological evidence from which to discriminate certain other likely species, even among preserved specimens in collections.

The use of characters related to specific-mate recognition systems for discriminating species still requires support from the study of the subsequent stages in the operation of these systems. Key components in this may involve certain volatile or contact pheromones. The head-gland secretions of males of European 'patrolling' species are believed to act as female arrestants (Svensson, 1979) and some of these secretions have been characterised (e.g. Bergström *et al.*, 1981). This has not been undertaken for female head-gland secretions, which may be just as important in the subsequent stage of specific-mate recognition by males (see Free, 1971; van Honk *et al.*, 1978). Some method to assay for behavioural discrimination between secretions of different composition by the organisms themselves in the field is now needed.

In 1985 I recorded the distribution of mate-searching activity in time and space from transect counts of numbers of male bumble bees around Gulmarg. Distribution with respect to altitude is described from altitudinal transects of the Pir Panjal range (the mountains on which Gulmarg is situated), between Tangmarg at 1800 m in the Vale of Kashmir, and the peak of Mt Apharwat above at 4143 m (13,592 ft) (total number of bumble bees identified > 2000, see Fig. 6). The habitat is described in more detail, together with the altitudinal distribution of foraging females, in the discussion of distribution with altitude. Spatial and temporal pattern in the distributions of mate-searching males can also be described at the smaller scale of a 30 m-high hill at Gulmarg, from vertical and horizontal transects (Figs 7 & 8).

I also recorded the activities of males that had

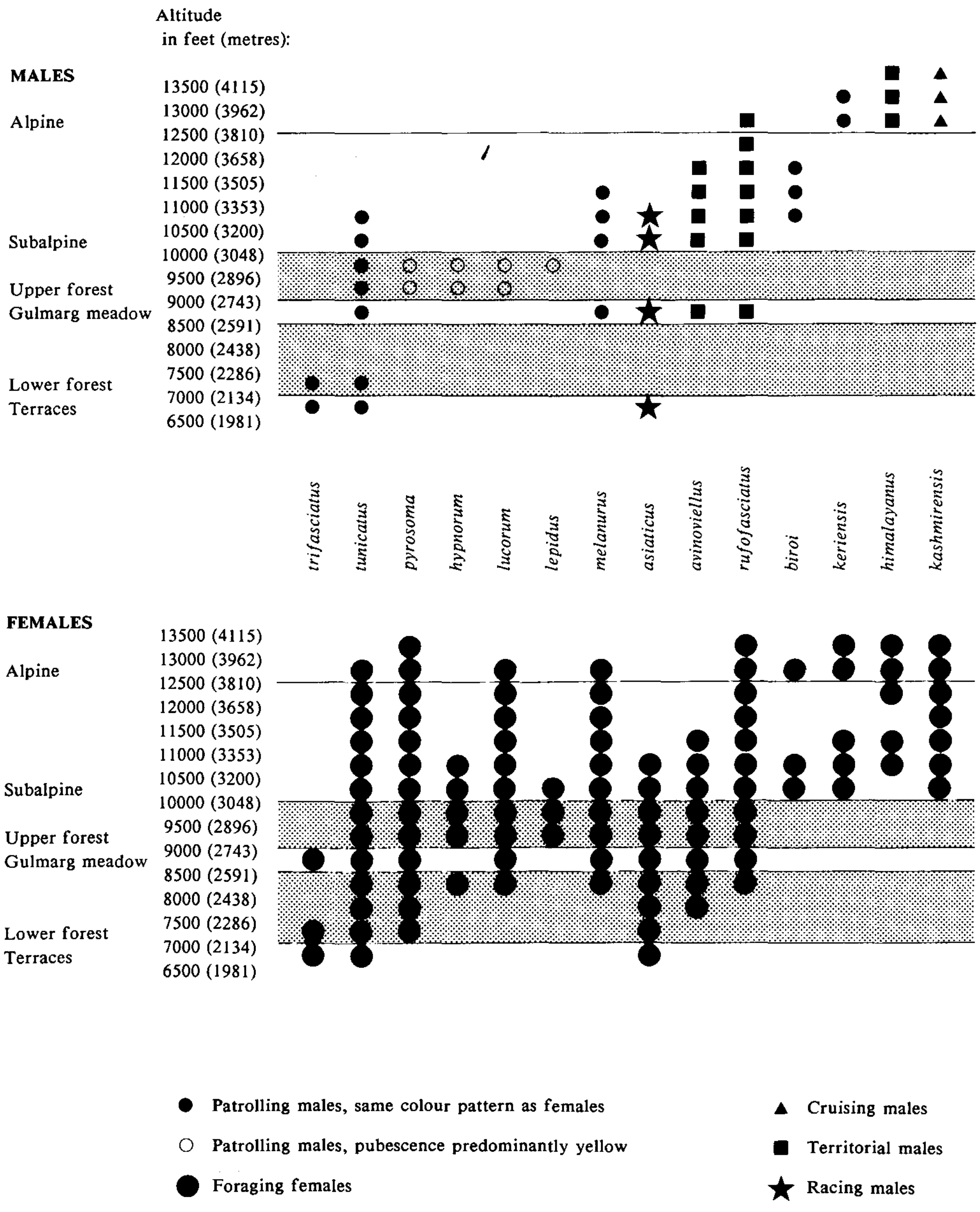
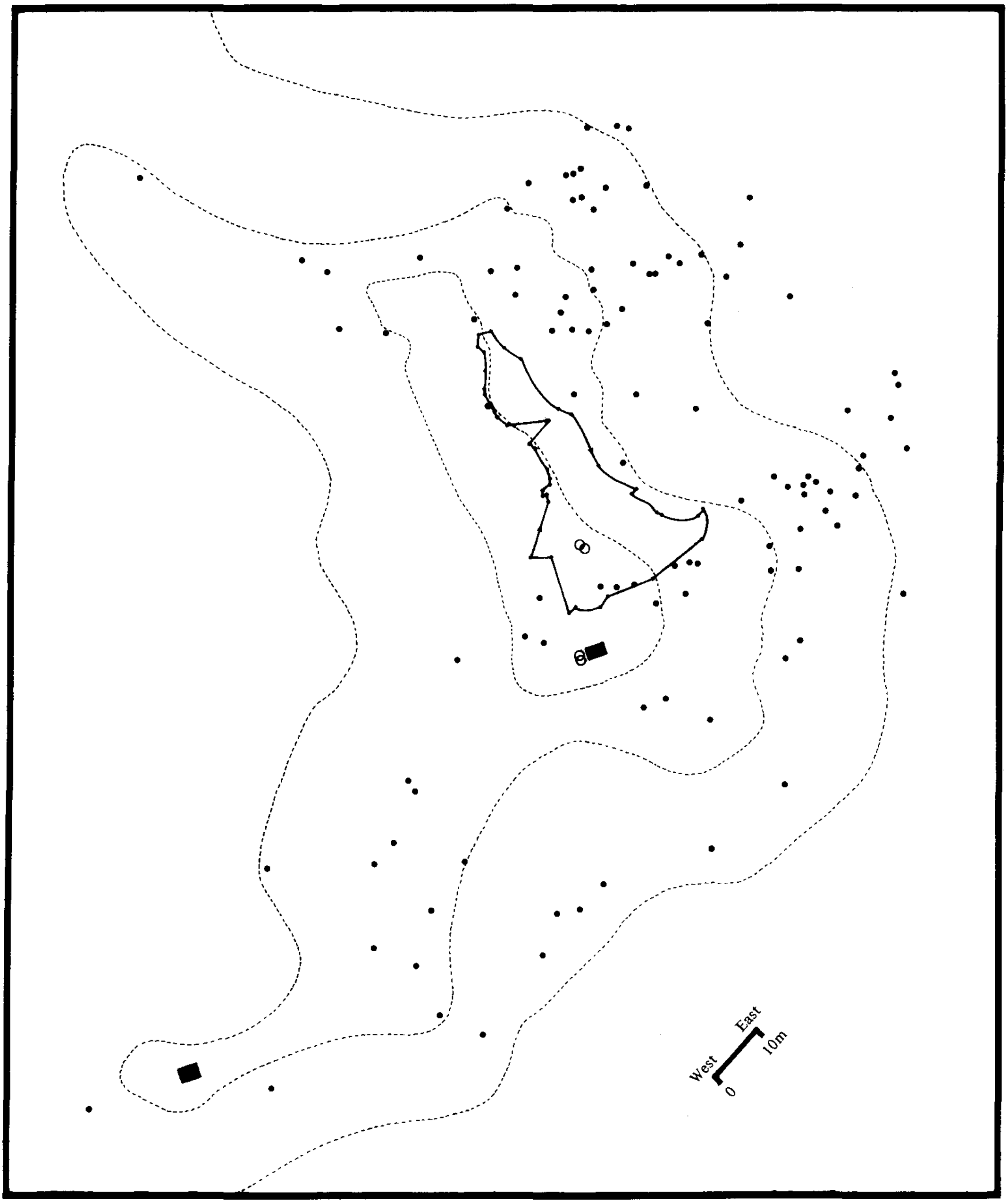


**Fig. 6** Distribution of mate-searching males (above) and foraging females (below) of the social bumble bees (i.e. excluding species of the subgenus *Psithyrus*) with altitude on Mt Apharwat in the Pir Panjal Range around Gulmarg. Altitudes are estimated from the 500 ft contours of the 1 : 63,360 British Survey of India Map (Oxford University Library). Records are combined from transects made during July, August and September 1985. For a description of the vegetation in each habitat zone, see the discussion of distribution of the fauna with altitude.

been individually labelled, using the plastic tags that were developed for use with queen honey bees (52 male bumble bees were labelled in the vicinity of the 30 m hill in 1985; 108 males labelled in the same area in 1986). Numbered tags are ideal for the many perching males, which can be approached for their tags to be read, but plain discs of different colours are all that can be seen on patrolling bees, which spend most of their time in rapid flight. Labelling individuals did not obviously affect them adversely. For instance, one *B. tunicatus* male had resumed patrolling within 10 minutes of being released. Activities of males were recorded in part to compare their time



⁘ Perches of **racing** *B. asiaticus* males (29.viii.1986).

⊗ Contested perch area of two **territorial** *B. rufofasciatus* males (20.viii.1985).

☐ Circuit of places approached by a **patrolling** *B. tunicatus* male (14.viii.1985).

**Fig. 7** Sketch map of the 30 m hill on Gulmarg meadow, showing the distribution of mate-searching activity by individually-labelled males of three species of bumble bees. Dotted lines show contours at 10 m intervals, black rectangles show the positions of two huts.

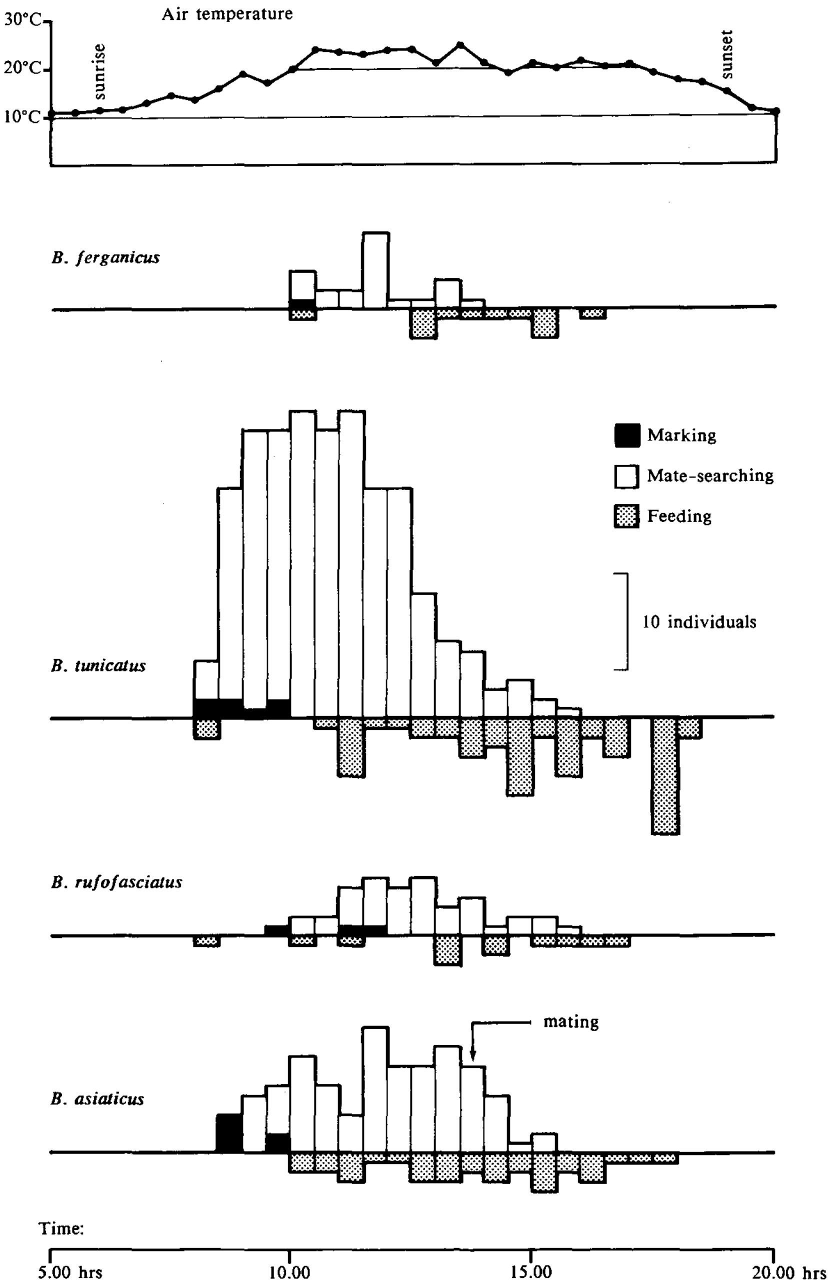


**Fig. 8** Distribution of activity by males of four species of bumble bees between dawn and dusk on the 30 m hill in Gulmarg meadow. Counts were made every 30 mins during 19.viii.1985, along a transect of 450 paces around the 30 m contour at the top of the hill (see Fig. 7).

budgets, but also to record the nature and outcome of interactions between males. This included mapping the circuits followed on the 30 m hill by males of each of three species (*B. ferganicus*, *B. melanurus* and *B. tunicatus*), and mapping the perch positions of other species (*B. avinoviellus*, *B. rufofasciatus* and *B. asiaticus*). The reactions of males of all species to moving objects of different sizes were observed and tested. Young queens of *B. asiaticus* were tethered with lengths of thin black cotton at different places on the 30 m hill and the reactions of perching males were noted.

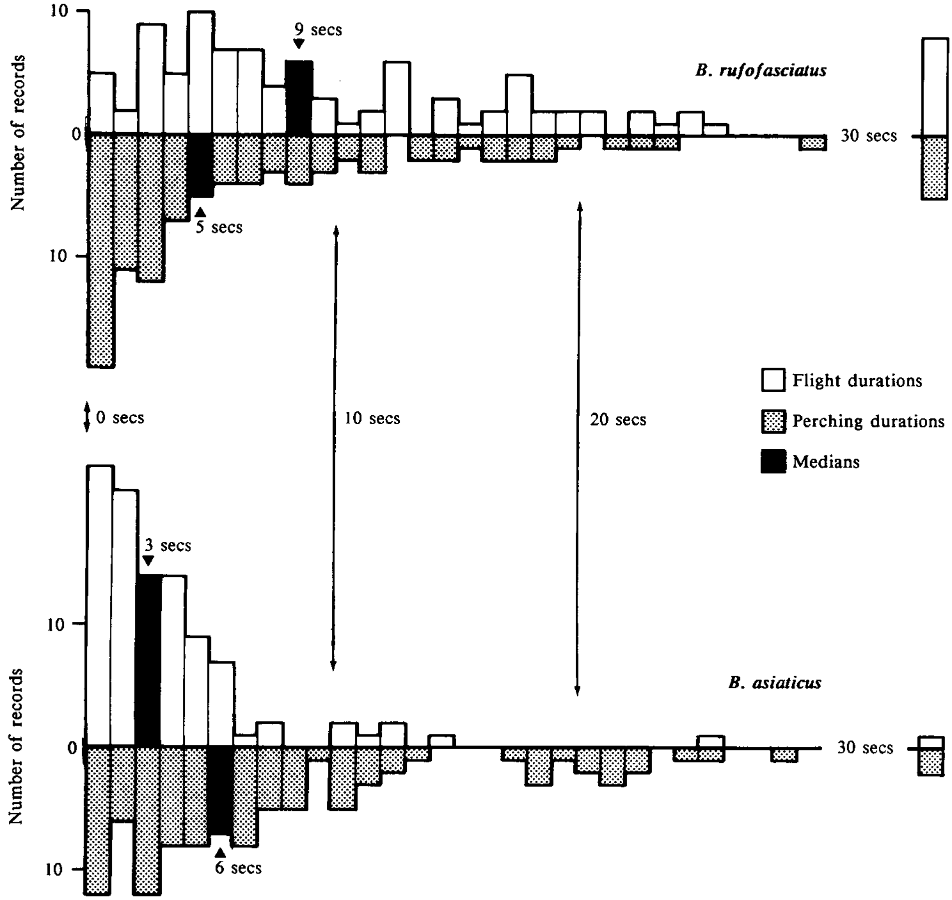


**Fig. 9** Duration of consecutive flight and perching periods for mate-searching males of *B. rufofasciatus* (above) and *B. asiaticus* (below). For each species, records of 20 consecutive flight and perching periods were made from each of five males on the 30 m hill in Gulmarg meadow, during 11–12.viii.1985.

Four kinds of male mate-searching behaviour were observed during 1985. These are referred to here as 'patrolling', 'racing', true 'territorial' and 'cruising'. The territorial behaviour can be considered as an example of what has been termed pure dominance or lek polygyny, whereas the other three categories of behaviour represent divergent forms of scramble competition polygyny (see Thornhill & Alcock, 1983).

(A) **PATROLLING** behaviour has been described previously from British bumble bees and from most other European species (e.g. Darwin, see Freeman, 1968; Awram, 1970; Schremmer, 1972; Alford, 1975; Svensson, 1979). These males appear to mark objects early each day with an oral secretion, which presumably contains a pheromone. The objects are numerous, spaced by any distance from a few centimetres to some tens of metres, and chosen so that they can be patrolled as 'approached places' on a circuit flown regularly by the male. It has been suggested that receptive females are arrested at these pheromone 'traps' and that mating takes place when the male returns on his next patrol of the circuit (see Svensson, 1979). Examples of species whose males perform patrolling behaviour in Kashmir are *B. pyrosoma* and *B. tunicatus* (e.g. records from the 30 m hill, see Fig. 7). These males did not interact with one another directly nor did they respond to moving objects by pursuit, either near or between approached places.

(B) **RACING** behaviour differs from patrolling in that each male perches in one small area and will then pursue potential mates from this look-out position, but without competing with other males for preferred perches.

Racing behaviour is described here from *B. asiaticus*. These males perched on rocks, cowpats, leaves or fragments of wood (a maximum of 107 males were recorded at their perches on the 30 m hill on any one day, 29.viii.1986, Fig. 7). The perches were not associated with flowers (i.e. food resources) or nests (no nests of any species were found on the 30 m hill in either 1985 or 1986). Males would leave their perches in darting flights in pursuit of rapidly moving objects, which included conspecific queens and other males in flight, birds flying overhead and even stones thrown past the perch. Males rarely performed any slow inspection flights around perches (as shown by the short durations of flights by *B. asiaticus* males in Fig. 9). Successful pursuit flights with conspecific queens ended with the male bringing the queen to the ground, where he grappled with her, and attempted to mount her and clasp her sting base with his genitalia. There was no obvious courtship. When a queen was tethered, males approached rapidly and hovered for a few seconds, antennae almost in contact, before attempting to clasp her. Once a male had succeeded in clasping an untethered queen with his genitalia, she ceased pushing at him with her legs and the pair immediately flew from the area in tandem.

When a pursuit flight with a conspecific male resulted in an approach within a few centimetres, they diverged without clashing and returned to their perches without displacement of either male. Males were rarely found to have damaged limbs (2/108 labelled males, 1986, 30 m hill). Individual males returned to the same perches on many days (the maximum period spanned 27 days, 2–29.viii. 1986, male red-83, 30 m hill) and other males rarely usurped these perches after they had become vacant (occupancy is known to have changed for 5/170 perches 2.viii–11.ix.1986, 30 m hill, though only 108 males were individually labelled). Marking of perches with oral secretions was observed only occasionally, and only immediately after males arrived at their perches in the morning.

Some of these males were found to spend the night torpid in tight clusters of up to 10 individuals, deep among the short plant stems and roots on the middle slopes of the 30 m hill. Some individuals (e.g. male red-18, 1986) switched between clusters on successive nights, although this could have been the result of disturbance.

(C) **TERRITORIAL** behaviour differs from patrolling in that each male perches in one small area and will then pursue potential mates from this look-out position, but unlike racing behaviour, the males do compete for preferred perches.

Territorial behaviour is described here from *B. rufofasciatus* (e.g. on the 30 m hill, see Fig. 7). These males perched and pursued moving objects much as racing males did, but they also responded to conspecific males on their perches as well as in the air, and clashed audibly with them during extended chasing flights (Fig. 9). This may have contributed to the higher incidence of damage to appendages among these males (5/20 males labelled on the 30 m hill, 1985, had lost at least half of one antenna or leg) and did result in displacement from perches. For instance, on 18.viii.1985 male green-7 was perched above the entrance to a 3 m-long, 1 m-deep gully at the edge of the flat-topped 30 m hill. It left this perch to engage yellow-7 as it entered the gully, but after the ensuing chase, only yellow-7 returned to the gully, where it then perched within 10 cm of where green-7 had been. Later the same day green-7 returned, chased and replaced yellow-7 in this gully (occupancy changed at least 14 times for 9 perches 9–20.viii.1985, with or without contest, and 10 of these changes were for this gully). Yellow-7 then moved to a less frequently occupied perch area that was 10 m away on the side of the hill. These perches were not associated with nests or with concentrations of resources, but nevertheless continued to be highly preferred despite a high turnover in individual males (only 9 perch areas, each 2–4 m in diameter, could be found on the entire 30 m hill, but 20 males were labelled in these areas between 9–20.viii.1985). Males of *B. rufofasciatus* marked their perches with oral secretions much more frequently than did males of *B. asiaticus*.

The frequent inspection tours of *B. rufofasciatus* males around perch areas, such as the gully at the top of the 30 m hill, have a characteristic slow, stalling flight, with a low, interrupted buzz. Pursuit flights, like those of *B. asiaticus*, are much faster than the flight of females and have a higher-pitched buzz.

(D) **CRUISING** behaviour differs from patrolling in that each male uses one small area as a look-out position from which to pursue potential mates. Unlike racing behaviour, the males hover almost stationary in the air rather than perch, and unlike territorial behaviour the males do not compete for preferred positions.

Cruising behaviour was not seen on the 30 m hill and is described from observations of *B. kashmirensis* from just a few days (most on 23.viii.1985) near the peak of Mt Apharwat. These males maintained a very slow, almost hovering flight about 1 m above the ground, but each was confined within an area only 3–4 m across. From these aerial positions they pursued moving objects, much as racing and territorial

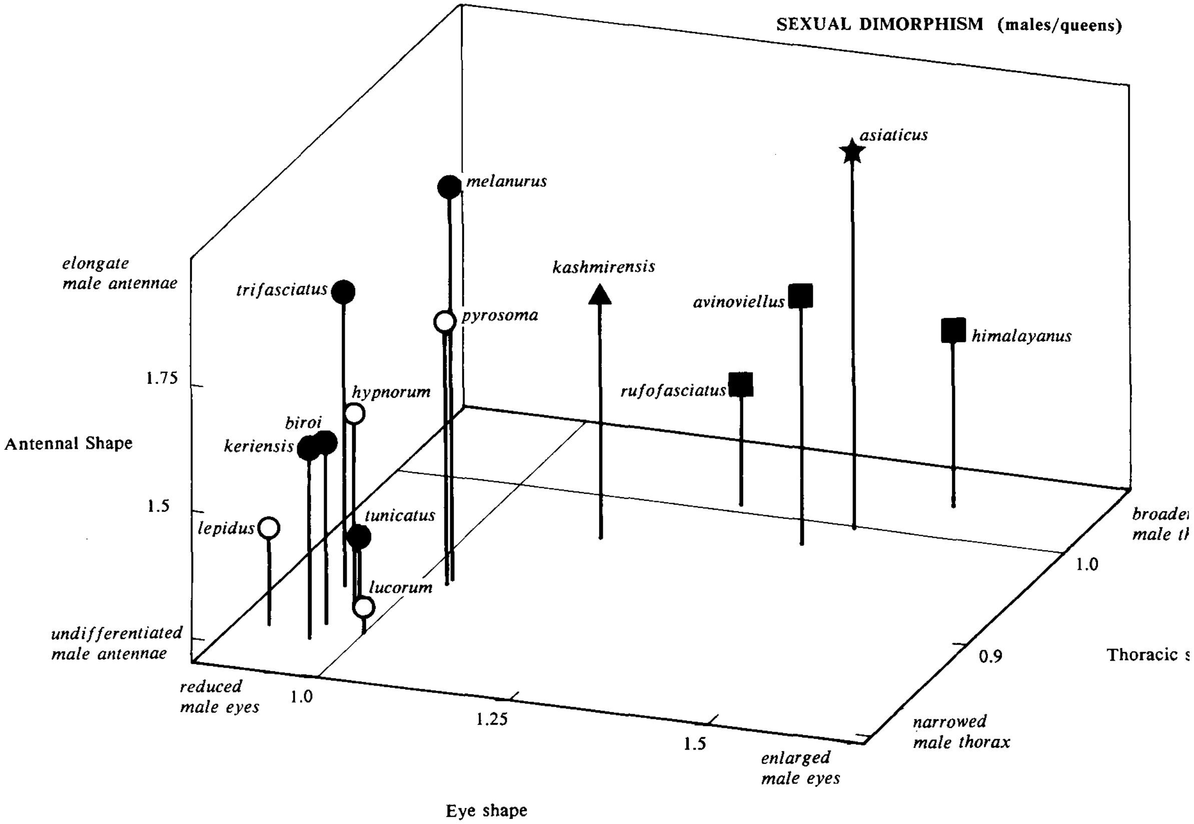


**Fig. 10** Sexual dimorphism in some characters that may be related to male mate-searching behaviour among the social species of bumble bees (i.e. excluding species of the subgenus *Psithyrus*) of Mt Apharwat in the Pir Panjal Range. Shape dimorphism is measured as the ratio of mean shape of males/mean shape of queens, so values of 1.0 show no dimorphism in shape between males and queens. Eye shape is measured as the ratio of the maximum right compound eye length/minimum dorsal inter-compound eye distance; antennal shape is measured as right flagellum length/right scape length; and thoracic shape is measured as distance between and including tegulae/right radial cell length. Sample sizes (males/queens): *B. avinoviellus* (10/10), *B. himalayanus* (10/3), *B. trifasciatus* (8/5), *B. melanurus* (10/10), *B. kashmirensis* (10/10), *B. hypnorum* (10/4), *B. lepidus* (2/6), *B. biroi* (6/5), *B. tunicatus* (10/10), *B. lucorum* (8/3), *B. asiaticus* (10/10), *B. keriensis* (4/8), *B. pyrosoma* (10/10), *B. rufofasciatus* (10/10). Symbols show the different kinds of male mate-searching behaviour and colour pattern dimorphism (see Fig. 6, strong divergence in male colour pattern from worker colour pattern is only apparent among patrolling species): filled circles – patrolling males with similar colour pattern to females; open circles – patrolling males with pubescence predominantly yellow; star – racing males; squares – territorial males; triangle – cruising males.

males did on the 30 m hill. Cruising males also interacted in flight, but no clashes with violent physical contact were detected, no males were found to have damaged limbs (0/12 of the males collected) and no displacement of males was seen. Marking of vegetation with oral secretions within the cruised area was seen.

Patrolling behaviour is well known for bumble bees, but the other three categories are distinguished here for the first time. Males of a few species from central Europe and from North America have also been seen to return to perches between intermittent pursuit flights (e.g. Schremmer, 1972; Haas, 1976; Alcock & Alcock, 1983). Pairs of males of some of these species were seen to engage in protracted interactions, at least occasionally, so their behaviour may correspond to the territorial behaviour described here (e.g. Schremmer, 1972; Alcock & Alcock, 1983).

Sexual dimorphism in relative eye size, antennal length, wing shape and thorax shape is least strongly developed in patrolling ('marathon') species and more pronounced among the other 'perch and sprint' categories (e.g. review by Schremmer, 1972), especially for the racing species (Fig. 10). The species that patrol exclusively in the upper forest show pronounced sexual dimorphism in colour with similar, almost uniformly bright yellow males (see the discussion of colour patterns of the Kashmir fauna).

## Relationship between male mate-searching behaviour and habitat structure

It seemed likely from a comparison of the male mate-searching behaviour among the bumble bees observed during 1985 that each of the four categories could have advantages for increasing a male's number of matings. But which of these kinds of behaviour is most advantageous to an individual male for maximising his mating success is likely to depend on the particular conditions of density and dispersion in the distributions of receptive females. This scheme is summarised in Table 2. Each species' characteristic density and dispersion of receptive females is expected to reflect the particular responses by its individuals to the different kinds of habitat in the mountains:

**Table 2** Summary of the likely characteristics of the distributions of receptive female bumble bees on Mt Apharwat (altitudes 2700–4143 m), for the most abundant species in the four principal kinds of habitats (1985 survey). These different distributions may each favour one of the four groups of male mate-searching behaviour (in bold).

| | | Dispersion | |
|---|---|---|---|
| | | high<br>(even) | low<br>(clumped) |
| Density | high | meadow<br>**RACING**<br>e.g. *B. asiaticus* | high alpine<br>**CRUISING**<br>e.g. *B. kashmirensis* |
| | low | forest<br>**PATROLLING**<br>e.g. *B. pyrosoma* | subalpine<br>**TERRITORIAL**<br>e.g. *B. rufofasciatus* |

(A) **PATROLLING**. Males of all species found around Gulmarg to be mate- searching only within the forest (1900–3000 m) (e.g. *B. pyrosoma*), and males of the species most widespread among the different kinds of habitat (e.g. *B. tunicatus*), were patrolling in search of mates (Fig. 6). The densities of all bumble bees are expected to be especially low in the coniferous forest, where floral resources are scant (see the discussion of distribution with altitude). Dense forest has a complex physical structure, which reduces the visibility of potential mates and obscures any long range visual cues that might be used by individuals to aggregate for pairing. A web of pheromone traps, formed by the approached places that these males patrol, should be especially well suited for collecting mates at low, relatively uniform densities. Patrolling behaviour is also likely to work especially well in open habitats where young queens are present at low density and may not be predictably aggregated (e.g. arctic environments).

(B) **RACING**. Resources in the large meadow of Gulmarg are apparently much richer, because it appears to have the highest density of bumble bees among all of the areas surveyed on Mt Apharwat (see the discussion of distribution with altitude). For species specialising in this open habitat, patrolling behaviour might be expected to break down at high density if some males were to exploit the pheromone 'traps' at approached places by perching there and waiting for the more frequent females to arrive. At high density, males that persisted in patrolling would be wasting much of their time in flight between traps (when patrolling males may not be responsive to receptive females, see Free, 1971), without increasing their chances of finding a receptive female.

Racing *B. asiaticus* were present at more uniformly high densities than patrolling species, in some open, grassy areas below the forest (1800–1900 m), in parts of the meadow at Gulmarg (2650–2700 m) and just above the upper edge of the forest (3000–3100 m, Fig. 6). Males appeared to be less aggregated than those of the cruising or territorial species, which are associated with the higher relief, alpine habitats. This presumably reflects either a more even distribution of receptive females, or the unpredictable spatial pattern of this distribution in the meadow. Transect counts show a tendency for males to concentrate on steep ridges (vertical transects 16 & 23.viii. 1985: 53/86 males in steepest middle half of slope, 7.5–22.5 m up the 30 m hill; horizontal transect 18.viii.1985: 23/26 males on ridges rather than gullies) of south and east-facing slopes (i.e. facing the sun in the morning, see Fig. 7), but perch sites were still relatively widely and evenly spread. The mate-searching activities of *B. asiaticus* males were also spread over a longer period of weeks than those of the territorial or cruising species in subalpine and alpine habitats. This may reflect the longer season during which floral resources are available to fuel colony development and the rearing of young queens at the lower altitude of Gulmarg.

(C) **TERRITORIAL**. Above the forest, in the subalpine zone, the season of profitable foraging is shorter, the levels of resources may be lower than in the forest meadows, and so the bumble bee density is expected to be lower (see the discussion of distribution with altitude). The open subalpine zone covers a large area on Mt Apharwat, although it also provides abundant topological cues that could be exploited to facilitate the meeting of the sexes even if they are present at low density, for instance by local 'hilltopping' (hilltopping could arise through the evolution of female choice, see Kirkpatrick, 1982).

The most abundant species above the forest is *B. rufofasciatus*. Males were indeed seen to be very closely aggregated in small groups on the tops of shoulders protruding from the subalpine slopes of Apharwat (3000–3800 m) and, more rarely, in the alpine zone (c. 3900 m) and on top of the 30 m hill in the meadow at Gulmarg (2700 m, two perch areas shown in Fig. 7). At any one time these males were few in number, but were all closely associated with even fewer perch areas. So although perch areas were widely spaced, they each had up to seven males flying around them. If this does reflect the pattern in the distribution of receptive females, then territorial defence is likely to be more advantageous for these males than for species at higher densities, because it could win exclusive access to females at an especially attractive site, while the probability of missing a female during a male-male chase would be lower.

(D) **CRUISING**. Habitat conditions in the alpine zone resemble those in the subalpine, but are even more extreme in features such as the short foraging season (see the discussion of distribution with altitude). However, this open habitat has the ultimate topological cues for potential mates at low density to meet by hilltopping – the mountain peaks.

The most abundant high alpine specialist is *B. kashmirensis*. Workers forage throughout most of the alpine and subalpine zones (3000–4000 m, Fig. 6), but cruising males were found to be aggregated exclusively in the high alpine zone (4000–4100 m), in the lee of the peak of Mt Apharwat (4143 m). Moreover, males were seen on just a few of the days during which this area was visited, although in larger aggregations than the males of *B. rufofasciatus*, so that mate-searching activity may be highly concentrated in time as well as in space. Both factors could contribute greatly to enhance the encounter rate or effective local density of mates. If the female arrival rate were sufficiently high, then territorial chases between males might result in more females being missed, or lost to 'sneaky' males, than would be lost to tolerated competitors. The hovering flight of cruising males may be one way of gaining an advantage over perching competitors, both by saving time on take-off in pursuit of a potential mate and possibly by increasing the field of view. Thus it may be that, whereas racing males tolerate one another's proximity because no one perch site is predictably much more attractive to females than any other, a male cruising over a particularly attractive site tolerates the proximity of another male because displacing the competitor might cost more in lost opportunities than could be gained through attempts at sole possession.

The characteristics of density and dispersion in the distributions of receptive female bumble bees could not be measured directly. Young queens are not often seen before winter. More particularly, bumble bees have rarely been found *in copula*, despite their abundance. Preliminary searches had shown that male marking activity is greatest in the early morning, so I had expected that searching at this time might yield more observations of pairing. In fact this was seen only four times, all in the afternoon (e.g. Fig. 8). An explanation for the rarity with which bumble bees are seen paired, despite the length of time for which females remain clasped by the males (usually in excess of 20 minutes, pers. obs.), may lie with the observation that paired females and males flew in tandem from the areas where males were mate-searching as soon as the males had clasped the females, which took just a few seconds. This scattering to inconspicuous places may help to avoid competitive interference from other males of the same species. Unfortunately it also precludes the use of any observations of paired bumble bees as a measure of the distribution of receptive females.

Less direct methods may nonetheless reveal the distribution of receptive females. It can be assumed that it would be to the advantage of each individual male if the male were to invest its mate-searching efforts in time and space in a pattern that closely resembles the predictable component in the distribution of receptive females. Therefore the density and dispersion of mate-searching males should reflect the pattern for receptive females.

Estimates of density and dispersion of mate-searching males were made from transect counts in each of the principal habitats at Gulmarg during the summer of 1986 (Tables 3 & 4). Only 54 mate-searching males of *B. pyrosoma, B. asiaticus, B. rufofasciatus* and *B. kashmirensis* were recorded during this transect census. The spring thaw had been unusually late and the summer was cold and wet. The peak of mate-searching activity by males of the alpine and subalpine bumble bee species

**Table 3** Estimates of mean/variance ratio in the number of mate-searching males among 160 m segments of transect on Mt Apharwat as a measure of male dispersion (12 & 14.ix.1986). The figures were calculated for each of the most abundant species only within its associated habitat (see Table 2).

| Dispersion | | | |
|---|---|---|---|
| high (even) | | low (clumped) | |
| *B. asiaticus* | 0.51 | *B. kashmirensis* | 0.21 |
| *B. pyrosoma* | 0.61 | *B. rufofasciatus* | 0.14 |

**Table 4** Estimates of mean number of mate-searching males counted along each 1 km of transect on Mt Apharwat as a measure of male density (12 & 14.ix.1986). The figures were calculated for each of the most abundant species only within its associated habitat (see Table 2).

| | | | | | |
|---|---|---|---|---|---|
| Density | high | *B. asiaticus* | 8.8 | *B. kashmirensis* | 4.4 |
| | low | *B. pyrosoma* | 3.1 | *B. rufofasciatus* | 1.7 |

was about 20 days later in 1986 than it had been in 1985 and their density also appeared to be lower in 1986 (e.g. males of *B. rufofasciatus* were found on the 30 m hill at Gulmarg during 1985 but not during 1986). Further counts were prevented by the first heavy fall of snow, which blanketed the subalpine and alpine zones the morning after the first complete transect census.

Despite the small size of the sample in 1986, the figures in Tables 3 & 4 do appear to corroborate the expected characteristics of the common bumble bee distributions as postulated in Table 2, at least insofar as the figures in adjacent cells of the tables differ in the expected directions. Of course this result is only an apparent correlation based on observations of the bumble bees on one mountain and does not constitute a test of the relationship.

The behaviour of one group of *B. rufofasciatus* males on a high, steep-sided shoulder of Mt Apharwat (c. 3700 m, 23.viii.85) provides stronger support for the importance of distribution, although it is still only circumstantial evidence. In this situation their behaviour was apparently not territorial but resembled the cruising of *B. kashmirensis*. Conforming with the pattern in Table 2, these *B. rufofasciatus* males had formed a large group of unusually high density (estimated to be 50–100 males). However, it must be noted that individuals of most species are apparently not this flexible in their behaviour. For instance, *B. asiaticus* males were never found patrolling, even where they were present at low density. No males of patrolling species were found racing, either at localities with unusually high density or otherwise.

If differences in habitat structure between separated (allopatric, peripatric or parapatric) parts of an ancestral population may affect the balance of advantage among the different kinds of mate-searching behaviour, then the mate-searching behaviour of the descendent populations could diverge very rapidly by sexual selection. This may be particularly likely to affect the specific-mate recognition system and could result in speciation (see Rice, 1987, for a similar model for sympatric speciation).

## Inference of allopatric, conspecific taxa

Several nominal taxa that are closely similar in morphology show pronounced variation in the colour pattern of the pubescence among adjacent regions. One example is provided by individuals with the two principal colour patterns that are ascribed to *B. asiaticus* in Kashmir (see the comments on *B. asiaticus*). Individuals with both the unbanded yellow pattern (e.g. Figs 371–376) and the banded grey-white pattern (e.g. Figs 386, 387, 389–391) of *B. asiaticus* occupy similar open meadow or steppe habitats on either side of the Great Himalaya range (Map 48). The mate-searching behaviour of the males in the two regions could not be distinguished and consists of the racing behaviour that is unique to these nominal taxa among the bumble bees of Kashmir. This close similarity in mate-searching behaviour is reflected in the similarity of the associated morphological characters of the males, such as their much larger eyes and longer antennae in relation to those of the females (Fig. 10). Supporting evidence for interbreeding between individuals with the different principal colour patterns is provided by specimens with intermediate colour patterns (Figs 377–382) from a few localities in high valleys of the Great Himalaya. The frequencies of the different states for two of the three variable colour characters examined from these localities is consistent with simple models of population genetics (see the discussion of variation of *B. asiaticus* in Kashmir). So as parts of what appears to be a single, interbreeding population, these nominal taxa are considered to be parts of a single species.

## Inference of allopatric, separate species

Discontinuous geographical variation has also been found in the morphological characters that are associated with the different kinds of male mate-searching behaviour, between what are in other respects very similar nominal taxa. *B. wurflenii* is widespread in Europe among the upper forests of mountains, where the males, which patrol their scent-traps within the forests in search of mates (pers. obs., Austrian Alps), have eyes similar in size to those of the females. The morphologically similar *B. kashmirensis* is widespread in the Himalaya and eastern Tibet (Map 31) among the open alpine zones. The principal difference from *B. wurflenii* is that the males of *B. kashmirensis* possess slightly-enlarged eyes relative to the females (Fig. 10). On Mt Apharwat in Kashmir at least, these males apparently aggregate in the neighbourhood of mountain peaks, where they 'cruise' in search of females by sight. If this behaviour is representative and constant, then individuals of the two taxa would be unlikely to interbreed even if they were to occur on the same mountain, because they appear to search for mates in different ways and in different kinds of habitat. They may therefore have diverged in at least the first stages of their specific-mate recognition systems and so can be considered to be separate species (see the comments on *B. kashmirensis*, and on another group of more or less parapatric sister-species, *B. simillimus*, *B. pyrosoma* and *B. rufofasciatus*).

## Characters of species not related to male mate-searching behaviour

Unfortunately the mate-searching behaviour component of the specific-mate recognition system only differs sufficiently among species for divergence in associated morphological characters to be apparent in a few cases. So, of necessity, discrimination of most species still depends on the interpretation of even less direct evidence of interbreeding. This is usually inferred from a diagnosis by a combination of other morphological characters. Specimens are now available from many more localities in Kashmir so that a more comprehensive examination of the variation in these characters among individuals can be made.

At the beginning of this study, cladistic methods were used to divide material in collections into what are likely to be monophyletic taxa by character state patterns of the male genitalia. Material was further sorted by sample sites. Patterns of variation in a broad range of characters were then examined for description, both within and among these groups of individuals.

For the discrimination of species, particular attention was paid to any strictly coincident discontinuities in the patterns of character variation among individuals, irrespective of whether they occur between the supposedly monophyletic taxa or within them. These coincident discontinuities may provide evidence for barriers to interbreeding between populations and so may show the presence of separate species, which need not correspond to monophyletic taxa.

On the other hand, where individuals were found that show intermediate or mixtures of character states between the otherwise differentiated taxa, this is interpreted as evidence in favour of the occurrence of hybridisation between them, as parts of a single population and a single species. For instance, in Europe wide variation is known to occur between parapatric parts of the population of *B. soroeensis* (Fabricius). Individuals of this species from much of Russia, Scandinavia, Britain and Spain are banded yellow bumble bees with white 'tails'. Individuals from central and south-eastern Europe are unbanded, red-'tailed' bees. But individuals from the intervening areas in both France and eastern Europe show a continuous range of variation in both characters between the two, more widespread, colour patterns (Reinig, 1939: fig. 10). In some areas, individuals with both principal colour patterns may even be reared from the same nest, apparently as the offspring of the same queen (Vogt, 1909). Therefore individuals with either of these two colour patterns have been considered to be interbreeding as parts of the more or less continuous population of a single species.

Zones of hybridisation between nominal taxa can be very narrow, with steep clines in character frequencies (see e.g. Mallet, 1986; Hewitt, 1988). For instance, localised steep clines in hybrid zones are well known for groups of colour pattern characters within populations of certain European bumble bees (e.g. Reinig, 1970). Yet as long as some evolutionary cohesion could be maintained by the passage of some alleles across a hybrid zone through interbreeding, then the parts of the population could be considered to be parts of a single species. Among Sino-Himalayan bumble bees, some of the most difficult decisions concerning conspecific status involve bees from the montane forests (e.g. see the comments on *B. lepidus*, *B. pyrosoma*). These forests are confined to a long, narrow ribbon around the southern and eastern edges of the great Tibetan massif. In this situation, any hybrid zones across this ribbon are likely to be much shorter than those described for *B. soroeensis* in Europe and so more difficult to locate and study adequately.

If some of the provisional decisions reached in this review in cases where the available information remains inconclusive seem unduly biassed in the direction of 'lumping', it is because the burden of proof of a divisive speciation event within an ancestral population is considered to rest with the 'splitter'. It has been argued that evidence from subtle differences between two individuals is not sufficient. For example, it can be seen that the people from the different parts of Europe, of Asia, or even from different areas within Kashmir, also vary in shape and hair colour, and yet from their breeding behaviour they would all be placed in one biological species.

But irrespective of the decisions reached here, as much of the available information as time has allowed is presented in the comments on the variation within Kashmir and in the figures and maps, so that readers with a different concept of the nature of species should be able to make their own decisions regarding this fauna.

### The description of intraspecific variation

Many examples of character variation among samples of a single species can be related to where the samples were collected within the species' distribution. Often this geographic variation in single characters can be regarded as belonging to a continuum between extreme states, so that defining two or more discrete states would require threshold criteria that must be essentially arbitrary. Furthermore, where comparisons are drawn between two or more characters, these may show geographically incongruent patterns of variation, so that most combinations of states can be found somewhere within the species' distribution. Therefore, because variation of characters among individuals does not always delimit discrete sub-units within populations (Wilson & Brown, 1953; but see Mallet, 1986; Barton, 1988), previously described nominal taxa of subspecific rank are not attributed here with formal names. This removes any requirement for a general subspecies concept that would otherwise necessitate imposing more assumptions about the genetic structure of populations. The significance of intraspecific variation is better judged separately for the different cases that are presented by each species.

In the place of the earlier systems of subspecific and infrasubspecific nomenclature, in this review the most obvious character states are referred to using shorthand descriptions. An example is an 'unbanded (= no band of black pubescence between the wing bases) yellow (= colour of the pale pubescence, excluding any red hairs on the apical terga) queen (= large female) of *Bombus asiaticus*'. This terminology may appear less elegant, but it has the advantage that it is easily modified to give a more precise description of the recognised attributes of a particular individual.

Intraspecific variation of selected characters is described separately for each species as it is represented in the samples available, together with the frequencies of the various states in these samples. These frequencies may have been biassed at some sites by selective collecting, at least for the later samples (1985, 1986). But for the maps of the geographical distribution of variation in the bees' colour patterns, it is necessary for clarity of presentation to resort to a more typological approach, referring instead to the predominant local phenotype among the workers (see the figures accompanying the maps). This emphasis is placed on the workers because they are usually the most abundant sex and caste to be seen by collectors. Species' distributions within Kashmir are shown by spot maps rather than by grid maps, because sampling effort could not be even nearly uniform across the country (Map 4; see the comments on material examined and depositories).

## NOMENCLATURAL SUMMARY

Where possible type specimens have been examined in order to assign specific nomenclature more precisely. References in the text to 'Art. n' allude to the numbered articles of the *International Code of Zoological Nomenclature* (ICZN, 1985).

Synonyms are listed here only in cases where I have examined the types or specifically discussed their identity. Names of taxa whose status as part of the same species is in particular doubt are cited as provisional synonyms. Unavailable names are cited in brackets. Nomenclatural details for taxa in the genus group are not repeated in this section.

***BOMBUS*** Latreille 1802*a*
- ***avinoviellus*** (Skorikov, 1914*a*)
  - *callophenax* Cockerell, 1917 **syn. n.**
  - [*subtunicatus* Richards, 1930, infrasubspecific]
- ***himalayanus*** (Skorikov, 1914*a*)
  - *varius* (Skorikov, 1914*a*) (provisional synonym)
- ***marussinus*** Skorikov, 1910*a*
  - *afghanus* Reinig, 1940 **syn. n.**
- ***bohemicus*** Seidl, 1837
  - *nemorum* (Fabricius, 1775)
- ***novus*** (Frison, 1933) **comb. n.**
  - *nepalensis* (Tkalců, 1974*b*) (provisional synonym)
- ***branickii*** (Radoszkowski, 1893) **comb. n.**
  - *eriophoroides* (Reinig, 1930)
  - *elisabethae* (Reinig, 1940)
- ***ferganicus*** (Radoszkowski, 1893) **comb. n.**
  - *indicus* (Richards, 1929*a*)
- ***morawitzianus*** (Popov, 1931) **comb. n.**
  - *redikorzevi* (Popov, 1931)

**skorikovi** (Popov, 1927*b*) **comb. n.**
[*mesoxanthus* (Richards, 1928*c*) infrasubspecific]
*gansuensis* (Popov, 1931)
**trifasciatus** Smith, 1852*a*
*montivagus* Smith, 1878*b* **syn. n.**
*secundus* Dalla Torre, 1890 **syn. n.**
*ningpoensis* Friese, 1909
*wilemani* Cockerell, 1911 (provisional synonym)
*albopleuralis* Friese, 1916 **syn. n.**
*maxwelli* Pendlebury, 1923 (provisional synonym)
*mimeticus* Richards, 1931 **syn. n.**
*albolateralis* Richards, 1931 **syn. n.**
*gantokiensis* Richards, 1931 **syn. n.**
*turneri* Richards, 1931 **syn. n.**
*insidiosus* Richards, 1931 **syn. n.**
*geminatus* Richards, 1931 **syn. n.**
*magrettianus* Richards, 1931 **syn. n.**
*minshanicus* Bischoff, 1936 **syn. n.**
*quasibreviceps* (Tkalců, 1968*b*) **syn. n.**
*atropygus* (Tkalců, 1989) **syn. n.**
**haemorrhoidalis** Smith, 1852*a*
*orientalis* Smith, 1854 **syn. n.**
*buccinatoris* Smith, 1879 **syn. n.**
*assamensis* Bingham, 1897 **syn. n.**
*montivolans* Richards, 1929*b* **syn. n.**
*khasianus* Richards, 1929*b* **syn. n.**
*semibreviceps* (Tkalců, 1968*b*) **syn. n.**
*semicoloricontrarius* (Tkalců, 1968*b*) **syn. n.**
*cinnameus* (Tkalců, 1989) **syn. n.**
**melanurus** Lepeletier, 1836
*tschitscherini* Radoszkowski, 1862 **syn. n.**
*difficillimus* Skorikov, 1912*b* (provisional synonym)
*subdistinctus* Richards, 1928*b* **syn. n.**
*griseofasciatus* Reinig, 1930 (provisional synonym)
*maidli* Pittioni, 1939*b* **syn. n.**
**personatus** Smith, 1879
*roborowskyi* Morawitz, 1886 **syn. n.**
**kashmirensis** Friese, 1909
*stramineus* Friese, 1909
*tetrachromus* Cockerell, 1909
*pulcherrimus* (Skorikov, 1914*a*)
*meinertzhageni* Richards, 1928*b*
[*albohirtus* Richards, 1930, infrasubspecific]
*beresovskii* (Skorikov, 1933*b*) **syn. n.**
**hypnorum** (Linnaeus, 1758)
*bryorum* Richards, 1930 **syn. n.**
*fletcheri* Richards, 1934 **syn. n.**
**subtypicus** (Skorikov, 1914*c*) **comb. n.**
*leucopygus* Morawitz *in* Fedtschenko, 1875
*leucurus* Bischoff & Hedicke, 1931
*kohistanensis* (Tkalců, 1989) **syn. n.**
**lemniscatus** Skorikov, 1912*b*
*flavopilosus* Friese, 1918 **syn. n.**
*peralpinus* Richards, 1930
**lepidus** Skorikov, 1912*b*
*genitalis* Friese, 1913 **syn. n.**
*tetrachromus* Friese, 1918 **syn. n.**
*yuennanicola* Bischoff, 1936 (provisional synonym)
*hilaris* (Tkalců, 1989) **syn. n.**
**biroi** Vogt, 1911
*flavobistriatus* Vogt, 1911 **syn. n.**
[*flavostriatus* Vogt, 1911, infrasubspecific]
[*flavofasciatus* Vogt, 1911, infrasubspecific]
*nursei* Friese, 1918 **syn. n.**
*abbotti* Cockerell, 1922
*agnatus* Skorikov, 1933*b* (provisional synonym)
*kotzschi* Reinig, 1940 (provisional synonym)
**tunicatus** Smith, 1852*a*
*gilgitensis* Cockerell, 1905 **syn. n.**
*simlaensis* Friese, 1909
*fulvocinctus* Friese, 1909
**lucorum** (Linnaeus, 1761)
*cryptarum* (Fabricius, 1775) (provisional synonym)
*modestus* Cresson, 1863
*moderatus* Cresson, 1863
*magnus* Vogt, 1911 (provisional synonym)
*jacobsoni* Skorikov, 1912*b* **syn. n.**
*lucocryptarum* Ball, 1914 (provisional synonym)
*longipennis* Friese, 1918 **syn. n.**
*alaiensis* Reinig, 1930 **syn. n.**
*mongolicus* Krüger, 1954 **syn. n.**
*reinigi* Tkalců, 1974*b* **syn. n.**
**asiaticus** Morawitz *in* Fedtschenko, 1875
*longiceps* Smith, 1878*a*
*regeli* Morawitz, 1880
*miniatocaudatus* Vogt, 1911
[*fuscocaudatus* Vogt, 1911, infrasubspecific]
[*albocaudatus* Vogt, 1911, infrasubspecific]
[*tenuifasciatus* Vogt, 1911, infrasubspecific]
*falsificus* Richards, 1930 **syn. n.**
*flavodorsalis* (Skorikov, 1933*b*)
*oshanini* (Skorikov, 1933*b*)
**oberti** Morawitz, 1883
*semenovi* Morawitz, 1886 **syn. n.**
*duanjiaoris* Wang, 1982 **syn. n.**
**ladakhensis** Richards, 1928*b*
*phariensis* Richards, 1930 **syn. n.**
*variopictus* Skorikov, 1933*b* **syn. n.**
*bianchii* Skorikov, 1933*b*
*reticulatus* Bischoff, 1936 **syn. n.**
**semenovianus** (Skorikov, 1914*a*)
*problematicus* Bischoff, 1935
**keriensis** Morawitz, 1886
*separandus* Vogt, 1909 **syn. n.**
*kohli* Vogt, 1909 **syn. n.**
*postzonatus* Vogt, 1909 **syn. n.**
*kozlovi* Skorikov, 1910*b* **syn. n.**
*incertoides* Vogt, 1911 **syn. n.**
*tenellus* Friese, 1913 **syn. n.**
*meridialis* (Skorikov, 1914*a*) **syn. n.**
*alpivagus* Richards, 1930 **syn. n.**
*karakorumensis* (Tkalců, 1989) **syn. n.**
**simillimus** Smith, 1852*b*
*grossiventris* Friese, 1931 **syn. n.**
*oculatus* (Frison, 1933) **syn. n.**
*tonsus* (Skorikov, 1933*b*) **syn. n.**
*haemorrhous* Richards, 1934 **syn. n.**
**pyrosoma** Morawitz, 1890
*flavothoracicus* Bingham, 1897 (provisional synonym)
*miniatus* Bingham, 1897 (provisional synonym)

[*canosocollaris* Skorikov, 1912*b*, infrasubspecific]
*friseanus* Skorikov, 1933*a* **syn. n.**
*formosellus* (Frison, 1934) (provisional synonym)
*hoenei* Bischoff, 1936 **syn. n.**
[*flavocorbicularis* Tkalců, 1961, infrasubspecific]
*wutaishanensis* (Tkalců, 1968*a*) **syn. n.**
***rufofasciatus*** Smith, 1852*b*
*prshewalskyi* Morawitz, 1880
*rufocinctus* Morawitz, 1880
*chinensis* Dalla Torre, 1890
*championi* Richards, 1928*a* **syn. n.**
[*rufior* Richards, 1928*b*, infrasubspecific]
[*intermedius* Richards, 1930, infrasubspecific]
*waterstoni* Richards, 1934

## TAXONOMY OF THE KASHMIR BOMBINI

### BOMBINI Michener

Bombini Michener, 1944: 290. Type genus: *Bombus* Latreille, 1802*a*: 437.

In this review, formal descriptions of bumble bees are not repeated because the literature already contains many descriptions of particular individuals. Instead I describe just a few characters that may be useful to distinguish species. Tentative interpretations of some of these character-state patterns are included for the continuing discussion of relationships among species.

In the keys, those characters that have been found more reliably diagnostic have generally been placed nearer the beginning of each couplet. Characters of the genitalia are used frequently in the key to males (see Figs 44 & 45), so male specimens should be prepared for examination by extraction of their genital capsules. Colour patterns of the pubescence are used in the final stages of the keys for the determination of species within a species-group, where the range of variation does not overlap among these species within Kashmir. But after a reference collection has been prepared for a particular locality using the keys, it may often be possible to identify the majority of further specimens accurately by direct comparison, using only selected details of their colour patterns. Diagrams of the colour patterns are provided here to illustrate some of the variation (Figs 232–439). These diagrams should be coloured by hand to render them more immediately intelligible (see Fig. 258 for a colour key). Inevitably these diagrams are a compromise between portraying the general appearance of an insect and accurately showing the position of every coloured hair. For instance, the presence of a minority of black hairs among pale pubescence could not be shown without reducing the general resemblance of the diagram to the insect. Consequently these diagrams provide only a guide that should not be used without the keys.

Records of food-plants are included from notes made in the field during 1980, 1985 and 1986. These plant species were identified by reference to Polunin & Stainton (1984). The lists are by no means exhaustive, but they do include at least some of the preferred species.

### Key to species (females: queens and workers)

1 Outer surface of hind tibia flat or partially concave, without long hairs on posterior part of lower or distal half of outer surface (corbicula), but with a comb of stout spines (rastellum) along inner distal margin (Figs 225 & 226); gastral sternum VI without ventrolateral keels; clypeus strongly protuberant, with lateral margins curved back towards occiput (Fig. 15) .......................................... 2

– Outer surface of hind tibia convex, with moderate to long hairs throughout, but without a comb of stout spines along inner distal margin; gastral sternum VI with a pair of ventro-lateral keels (Figs 206–211); clypeus nearly uniformly flat, only apico-lateral corners curved back strongly towards occiput ..... 5

2 Outer (corbicular) surface of hind tibia usually smooth and shining or only weakly sculptured (reticulate coriaceous), without any long stout hairs arising from posterior part of outer surface below upper or proximal quarter (Fig. 226); proximoposterior corner of hind basitarsus strongly and acutely produced, projection longer than its own basal breadth (Figs 41 & 42); labrum with basal transverse depression extending apically as a deep median furrow between pronounced lateral tubercles, displacing ridge between them to form a lamella that overhangs apical margin (Figs 25 & 26) .................. 10

– Outer (corbicular) surface of hind tibia coarsely sculptured (imbricate), appearing very rough, with widely-spaced long stout hairs or bristles arising from near middle of outer surface throughout upper or proximal half (Fig. 225); proximo-posterior corner of hind basitarsus rounded, projection no longer than its own basal breadth (Fig. 43); labrum with a narrow transverse basal depression, leaving a straight transverse ridge joining weak lateral tubercles, so that there is no median furrow and no apical lamella (Figs 23, 220–222) .......................... 3

3 (Subgenus *Mendacibombus*.) Ridge between labral tubercles is, at its mid point, narrower than basal depression (Figs 23 & 220), with few punctures and shining; wings clouded with brown (moderately infuscated) ....................... ***avinoviellus***

– Ridge between labral tubercles is, at its mid point, broader than basal depression, with few or many