III-IV in workers and males; only tergum III in queens) or white (most of terga IV-VI in queens, terga V-VI in workers, terga V-VII in males), rather than red with white tips. They also resemble some of the *B. himalayanus* (Figs 247–249), *B. novus* males (Figs 260 & 262), *B. lemniscatus* (Figs 325 & 326), *B. lepidus* (Figs 330, 331, 333, 334) and *B. biroi* (Figs 338 & 339) that occur with them. Females of *B. rufofasciatus* can be recognised easily because they have terga V-VI with white hairs rather than with orange-red hairs.

FOOD PLANTS. (Ranunculaceae) *Aconitum laeve* Royle, *A. heterophyllum* Wallich ex Royle, *A. violaceum* Jacquem. ex Stapf; (Balsaminaceae) *Impatiens glandulifera* Royle; (Leguminosae) *Trifolium repens* L., *Lupinus* sp. [introduced]; (Sambucaceae) *Lonicera quinquelocularis* Hardw.; (Compositae) *Cirsium falconeri* (Hook.f.) Petrak, *C. wallichii* DC., *Lactuca lessertiana* (DC.) C. B. Clarke, unidentified dandelion-like composites; (Ericaceae) *Rhododendron anthopogon* D. Don; (Gentianaceae) *Swertia petiolata* D. Don; (Scrophulariaceae) *Scrophularia pauciflora* Benth., *Digitalis lanata* Ehrh. [introduced], *Pedicularis oederi* Vahl, *P. roylei* Maxim., *P. pectinata* Wallich ex Benth., *P. rhinanthoides* Schrenk, *P. punctata* Decne.; (Labiateae) *Phlomis bracteosa* Royle ex Benth., *Nepeta podostachys* Benth., *Prunella vulgaris* L., *Thymus linearis* Benth. ex Benth.

DISTRIBUTION OF THE FAUNA

Distribution with altitude

The slopes of Mt Apharwat in the Pir Panjal range (Map 4 locality 1) show many of the more mesic kinds of habitat in which bumble bees occur in Kashmir. Differences in the distributions of the bumble bee species with altitude can be described from transect walks of the north-eastern flank of Apharwat (see the introduction on mate-searching behaviour of male bumble bees in Kashmir). These transects ran from Tangmarg at 1800 m in the Vale of Kashmir, through Gulmarg at 2700 m, to the peak of Apharwat above at 4143 m (13,592 ft). More than 2000 bumble bees were examined in the field along these transects during July, August and September 1985. Fig. 6 shows the records for each of the social species between the 500 ft contours of the 1 : 63,360 British Survey of India map (Oxford University Library). These patterns of distribution are similar to those found along the same transects in 1980 and 1986, and on other mountains around the Vale of Kashmir in all three years.

Away from the foot of the mountain, the middle of the Vale of Kashmir around Dal Lake (1500 m) is marshy and much of this area is used for the cultivation of rice. No bumble bees were found there. As the land slopes gently towards the mountains, terraces of rice give way on drier ground to apple orchards and higher still, near Tangmarg, to maize. Above Tangmarg, the lower coniferous forest (1900–2700 m) is dominated by *Pinus wallichiana* A.B. Jackson, with *Cedrus deodara* (Roxb. ex D. Don) G. Don near the lower margin. The forest is protected by law, although its lower edge now largely coincides with a pronounced increase in slope just above Tangmarg. The understorey is very disturbed and although few trees are felled, their branches are still collected for firewood. Flowers used by bumble bees are scarce in the lower forest (species listed in Table 5) but are more abundant around buildings and along roadsides. Bumble bee densities are very low, with *B. tunicatus* and *B. trifasciatus* the most abundant species both within the forest and around its lower edge.

Gulmarg (= 'flower-meadow', 2700 m) occupies a basin on a shoulder of the mountain. This natural, marshy meadow is grazed intensively by cattle, sheep and horses, yet the flowers from which bumble bees feed (Table 5) remain abundant. In the extensive wet areas of the meadow, *Prunella vulgaris* is a major nectar source and *Pedicularis punctata* a major pollen source for much of the summer. Large stands of the thistle *Cirsium falconeri*, which is often over 2 m tall, occur on disturbed slopes around the edges of the meadow. *Impatiens glandulifera* is abundant around water outflows from houses. The density of bumble bees is high (e.g. 89 bees/km, from 2.7 km transect, 14.ix.1986), with *B. asiaticus* and *B. tunicatus* the most abundant species, although there are fewer species than in the other zones (Fig. 6).

The upper coniferous forest is dominated in turn by *Pinus wallichiana* (2700 m), *Picea smithiana* (Wallich) Boiss. (2700–2900 m) and *Abies spectabilis* (D. Don) Mirbel (2900–3000 m). Prominent members of the shrub layer are bushes of *Sambucus wightiana* Wallich ex Wight & Arn. and *Euonymus hamiltonianus* Wallich. Flowers used by bumble bees (Table 5) are few, as in the lower forest. *Digitalis purpurea*, and more commonly *D. lanata*, are naturalised just above Gulmarg. Bumble bee density is low (23 bees/km, from 4.2 km, 14.ix.1986), with *B. pyrosoma* and *B. tunicatus* the most abundant species.

The lower slopes (3000–3200 m) of the sub-alpine

Table 5 Lists of the plants that were visited most frequently by foraging bumble bees on Mt Apharwat during 1985 and 1986 in the different altitudinal zones (LF, lower forest; GM, Gulmarg meadow; UF, upper forest; SA, subalpine; A, alpine; +, visited frequently; *, major food source).

Family	Binomen	Altitudinal zone				
		LF	GM	UF	SA	A
Ranunculaceae	*Aconitum heterophyllum* Wallich ex Royle				+	
	Aconitum hookeri Stapf				*	+
Balsaminaceae	*Impatiens glandulifera* Royle	+	*			
Leguminosae	*Lupinus* sp.		+			
	Trifolium repens L.		+	+		
Caprifoliaceae	*Lonicera quinquelocularis* Hardw.				+	
Compositae	*Cirsium falconeri* (Hook. f.) Petrak		*	+	+	
	Cirsium wallichii DC.	*	+	+		
	Lactuca lessertiana (DC.) C.B. Clarke				+	+
	yellow dandelion-like composites				+	+
Ericaceae	*Rhododendron anthopogon* D. Don				*	
Oleaceae	*Syringa emodi* Wallich ex Royle				+	
Gentianaceae	*Swertia petiolata* D. Don			+	*	*
Scrophulariaceae	*Scrophularia pauciflora* Benth.				+	
	Digitalis purpurea L.		+			
	Digitalis lanata Ehrh.	+	+	*		
	Pedicularis oederi Vahl					+
	Pedicularis roylei Maxim.					+
	Pedicularis pectinata Wallich ex Benth.					+
	Pedicularis punctata Decne.	+	*	+		
Labiateae	*Phlomis bracteosa* Royle ex Benth.				+	
	Stachys sericea Wallich ex Benth.		+			
	Prunella vulgaris L.	+	*	+		
	Thymus linearis Benth. ex Benth.				+	+
	Salvia hians Royle ex Benth.				+	
Polygonaceae	*Bistorta vivipara* (L.) Gray					+

zone (Fig. 1) are dominated by species of *Salix*, *Betula utilis* D. Don and lilac, *Syringa emodi*. Large areas are strewn with boulders. Spaces between the rocks provide nest sites for bumble bees and refuges from grazing for *Scrophularia pauciflora*, which, despite its green flowers, is very attractive to bumble bees. Much of this zone is used as pasture for goats, sheep and cattle, especially in the more gently sloping area, known as Khilanmarg, that is immediately above the forest. Pasture areas have many bushes of *Euphorbia wallichii* Hook. f. and flowers of *Anemone obtusiloba* D. Don. The steeper middle slopes (3200–3400 m) are dominated by *B. utilis* and *Rhododendron campanulatum* D. Don. The upper slopes (3400–3800 m) are dominated by *R. anthopogon*, *Juniperus recurva* Buch.-Ham. ex D. Don and *Bergenia stracheyi* (Hook. f. & Thoms.) Engl. Overall, the subalpine zone has the largest number of bumble bee species (Fig. 6), although their total density (32 bees/km, from 4.2 km, 12.ix.1986) is less than at Gulmarg. The most abundant species throughout the subalpine zone is *B. rufofasciatus*.

The alpine zone (3800–4143 m) is marked by an absence of the low bushes of *R. anthopogon* and by the presence, at least in exposed areas, of a silver-grey mat vegetation with *Anaphalis triplinervis* (Sims) C.B. Clarke and species of *Leontopodium* (Edelweiss). *Bistorta vivipara* is conspicuous, but the major food-plants for bumble bees are species of *Pedicularis*, *Swertia petiolata* etc. (Table 5). The most abundant bumble bee species are *B. rufofasciatus* and *B. kashmirensis* (density of all bumble bees 31 bees/km, from 2.3 km, 12.ix.1986). These two species are closely similar in colour pattern and general appearance, but all of the individuals with this colour pattern that were caught visiting flowers of Compositae were of *B. rufofasciatus*, whereas those visiting *Aconitum hookeri* were all of *B. kashmirensis*.

The overall pattern in the distribution of the species' foraging activities with altitude on Mt Apharwat (Fig. 6) is very similar to that found on other mountains around the Vale of Kashmir (e.g. near Pahalgam and near Daksum). The overlaps in the species' altitudinal ranges on these mountains were more extensive than those measured along the floor of the Sind valley (Fig. 12). For instance, species such as *B. trifasciatus* and *B. tunicatus* are restricted to the lower end of the Sind valley (e.g. Kangan, 1900 m) and other species such as *B. rufofasciatus* and *B. keriensis* are restricted to the upper end (e.g. Sonamarg, 2700 m), although they have all been collected from the same meadow on Apharwat (2700 m). The Sind river runs from deep in the Great Himalaya to the Vale of Kashmir, so the slope of the valley floor is far less steep than the north-eastern flank of Mt Apharwat. It is more likely that individuals could wander or commute to forage outside their optimal altitudinal zones on Apharwat, simply because the zones are so much closer together horizontally. *B. simillimus* was common in the lower Sind valley (e.g. at Kangan, 1900 m) but was not found on Apharwat during 1980 or 1985. Three workers of this species were found at 3000 m on Apharwat in 1986.

In general, the distributions of bumble bee species are most likely to be governed by the combined effects of climate and of local levels of food resources (discussed in Williams, 1988, 1989). The environment in Kashmir is particularly complex, because the regional climate may be greatly modified locally by the effects of altitude and exposure (e.g. Troll, 1972). This is likely to have three principal direct effects on bumble bees. First, lower average temperatures at higher altitudes may increase thermoregulatory expenditure of energy by bumble bees, especially for queens, which must incubate their first brood alone in the spring. Second, a shorter annual season of temperatures above freezing point in the high mountains constrains the time available for colony development. However, daytime temperatures even in the alpine zone of Kashmir may be higher and more favourable than further north (e.g. in the Alps), although the day lengths are shorter in Kashmir. But third, at lower altitudes, bumble bees may actually suffer from heat stress. For instance, foraging activity by bumble bees (chiefly *B. trifasciatus* and *B. haemorrhoidalis*) at Patnitop (2000 m) in the Jammu foothills ceased during the warmest part of the day, between 10 a.m. and 5 p.m. (6–8.ix.1986), when the patches of *Impatiens glandulifera* and *Pteracanthus urticifolius* from which they were foraging were no longer in the shadows of the forest trees. The bumble bees could not be found visiting any other flowers elsewhere during these periods. A less pronounced trend towards bimodality in diurnal foraging patterns is well known for some temperate bumble bees (e.g. Heinrich, 1979; Willmer, 1983) and is also reported for the large carpenter bees of the genus *Xylocopa* at a subtropical lowland site (Abrol, 1987). In both of those situations, foraging activity by the bees was inversely related to air temperature and intensity of direct solar radiation, but was positively associated with nectar availability. At Patnitop, small and medium-sized anthophorine bees continued to forage from the same flowers throughout the day, so presumably at least some nectar was still available. A restriction of diurnal foraging periods for bumble bees is likely to reduce the daily rate of food supply to colonies and so slow their development within the limited foraging season. This has at least the potential to limit a species' distribution at the southern edge of its range.

In common with many other organisms, bumble bees tend to occur at higher altitudes in Kashmir than they do further north, but in zones with similar climate. *B. lucorum* is most abundant on Mt Apharwat around the upper edge of the montane forest zone (c. 3000 m) and is recorded from 2100–4600 m at other sites in Kashmir. Further north in the Alps, it is common on the forested middle slopes (1300–2600 m recorded by Pittioni, 1937). In cool temperate Britain, this species is common in virtually all of the available altitudinal zones down to sea level (0–1200 m).

Climate may also affect bumble bees indirectly through its effects on food resources. The lower parts of the valleys in Kashmir often appear to receive less rain or snow in summer than the mountain ridges. In some of the drier areas the availability of bumble bee food-plants in late summer may be very restricted and bumble bees are sometimes either absent or present at only very low density (e.g. at Baramula and Anantnag in the Vale of Kashmir). Food sources are also scant in the shade of the evergreen, coniferous forests on the hillsides. But higher in the mesic subalpine zone, the density of nectar-rich food-plants is often high and their diversity may be at its highest. In the alpine zone, the frequent freezing and overcast conditions throughout the summer are likely to reduce plant productivity and hence resources for bumble bees. The favourable balance of these climatic and food resource factors in the subalpine zone may help to account for its large number of species of bumble bees (Fig. 6).

Although the meadow at Gulmarg has much the highest density of bumble bees on Mt Apharwat,

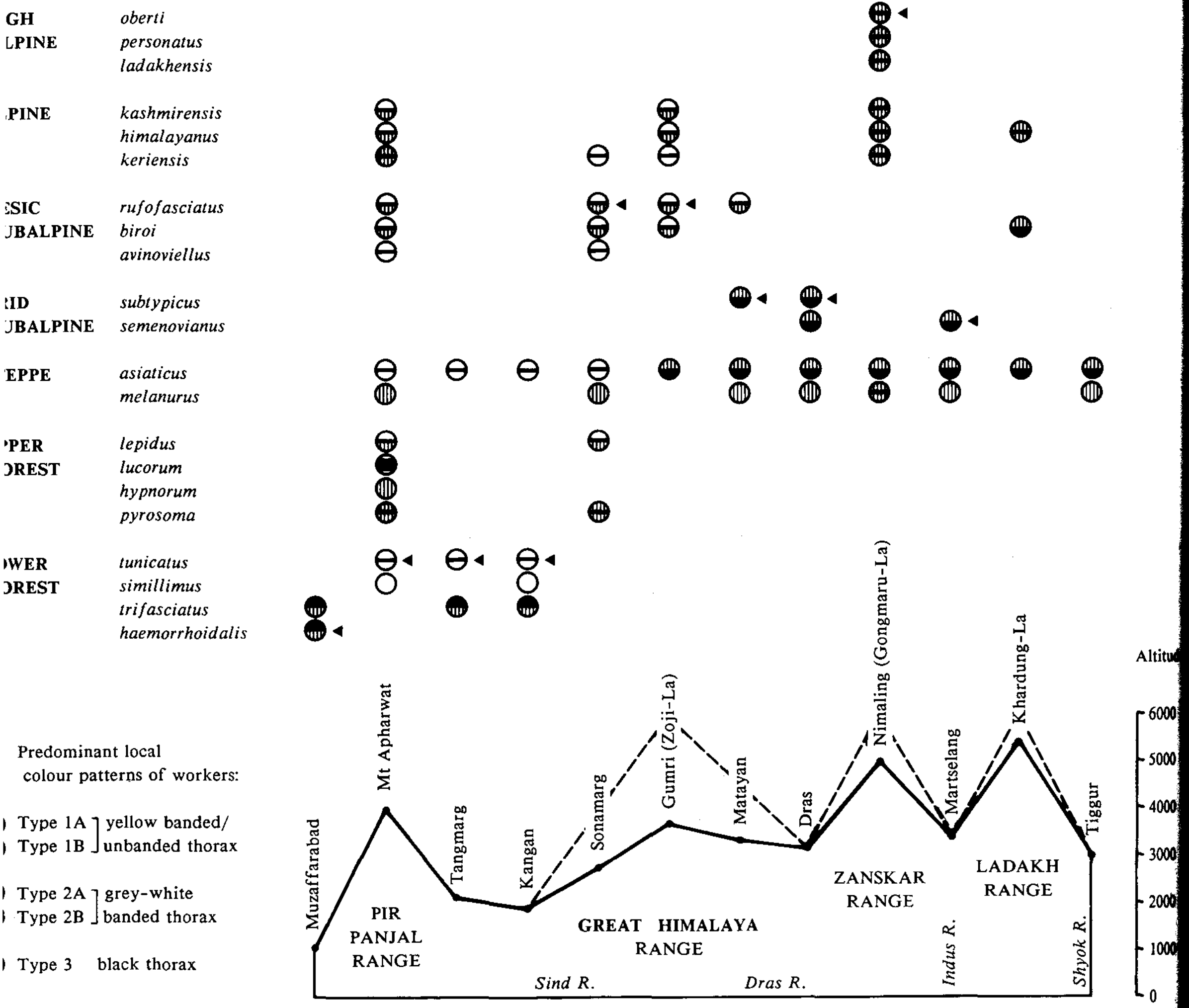

Fig. 12 Distribution of the social species of bumble bees (i.e. excluding species of the subgenus *Psithyrus*) and their local colour patterns across the Himalaya. Only the locally predominant patterns among the workers are represented. Triangles show the most abundant species at each locality. *B. lemniscatus* is not included for lack of information.

it has rather few species (Fig. 6). This may be partly because the abundance of food-plants is particularly uneven, although the relationship between diversity of food-plants and diversity of bees may not be straightforward (Williams, 1989). *Pedicularis punctata* and *Prunella vulgaris* are by far the most abundant of the food-plants used by bumble bees in the meadow. The meadow is often extensively flooded and some areas around streams are permanently marshy, although these plants are apparently tolerant of water-logged soil. Most of the more abundant species of bumble bees in the meadow, such as *B. tunicatus* and *B. pyrosoma*, are also among the most common species in the forest. Nests of both species have been found in the forest, but not in the meadow, so it may be that many of their foragers commute from nests in the forest to the richer resources in the meadow. *B. asiaticus* is unusual because it is both abundant on Gulmarg meadow and generally associated with open habitats.

The locality at the highest altitude in Kashmir from which I have collected a large sample of bumble bees is on Nimaling plain (4800 m). This is a high glacial valley, surrounded by large areas of arid alpine steppe that have very few if any bumble bees. Visits for 13 days in July 1980 and for three days in September 1986 found nine species of bumble bees (including the social parasite *B. (Psithyrus) branickii*) visiting the flowers of only a single plant species, *Caragana versicolor*. This plant forms low, thorny bushes on the old lateral and terminal moraines (Fig. 3), from which the glacier snout has retreated up the valley by about 10 km to the south-east. If the foragers do all genuinely use what appears to be a single food-resource, and there were no other obvious potential food-plants to be seen, then this situation deserves further study. It would follow from the application of competition-based ideas of 'community structure' to these bumble bees (e.g. Inouye, 1977) either that the flowers of *Caragana* are very variable in the accessibility of their rewards to the different bumble bee species, or that other factors are preventing the local assemblage of bumble bee species from reaching equilibrium by the local extinction of most of the species (cf. Williams, 1989).

Fig. 6 shows the narrower range of altitudes and habitats in which the males search for mates on Mt Apharwat, in comparison with the range of habitats in which the females forage. The possible relationship between the different kinds of male mate-searching behaviour and the different kinds of habitat is summarised in the introduction.

Distribution across the Himalaya

The distribution of bumble bees across the Kashmir Himalaya can be described from the samples collected at selected sites in the Pir Panjal, Great Himalaya, Zanskar and Ladakh ranges during August and September 1986. These data are supplemented with records from specimens collected at Nimaling in 1980 and with others examined in collections from Muzaffarabad (BMNH), from the Khardung-La above Leh (FA, ZI) and from Tiggur near the Nubra/Shyok confluence (BMNH). Together this covers a horizontal distance of about 430 km from west to east, at about 34° latitude. Fig. 12 shows the distributions of the bumble bee species in these samples and their locally predominant colour patterns.

The most widespread species in Kashmir are the steppe species *B. melanurus* and *B. asiaticus*. *B. asiaticus* shows a major change in colour pattern between Nigagar and Gumri in the Great Himalaya range, with some intermediate individuals present at Nigagar (see the discussion of variation of *B. asiaticus* in Kashmir). The alpine element in the fauna is also widespread between the Vale of Kashmir and Zanskar. Like *B. asiaticus*, *B. kashmirensis* and *B. himalayanus* show a pronounced change in colour pattern, but in this case the major transition in the thoracic pattern is to the east of Gumri (and to the west of Nimaling).

The principal boundary in the composition of the fauna is associated with the Great Himalaya range. This region of transition was studied in more detail between 9–11.viii.1986 in samples from Sonamarg, Nigagar, Baltal, Gumri, Matayan and Dras (a gradient-directed transect, see Map 4 & Table 1). The forest element is represented at Sonamarg, Nigagar and Baltal but, like the forest, it is absent to the north-east, beyond the Zoji-La (La = pass). There is also a large change in the subalpine element across the Great Himalaya. Of the subalpine species found on Mt Apharwat, *B. rufofasciatus* reaches across the Great Himalaya as far as Matayan, although *B. biroi* may be more widely distributed in Zanskar and Ladakh (Map 42). At Matayan, *B. rufofasciatus* occurs together with *B. subtypicus*, although *B. rufofasciatus* is no longer the most abundant species, as it is in the subalpine zones around the Vale of Kashmir. The three high alpine species found at Nimaling are distributed widely across the Tibetan massif but are apparently absent from the mountains around the Vale of Kashmir. This abrupt discontinuity in the faunal composition reflects the transition in climate and vegetation from the more mesic, wooded environment of the Vale of Kashmir to the arid (= xeric), steppe environment of the high Tibetan massif (Map 3). The environmental differences between these two regions in Kashmir are more extreme than those across the eastern Himalaya (Chang, 1981), where the Tibetan plateau is generally lower, more humid and dissected by wooded valleys. This is reflected in the distribution of bumble bees such as *B. rufofasciatus*, which penetrates much more deeply into Tibet in the east (Wang, 1982; BMNH).

A second boundary in the composition of the fauna is located on the outer slopes of the Pir Panjal range. The low altitude fauna has not been studied thoroughly here, largely for reasons of inaccessibility (see the comments on material examined). It is dominated by a lower montane forest element (*B. haemorrhoidalis* and *B. trifasciatus*). This includes many more species in the more humid foothills of the central and eastern Himalaya, where the effects of the monsoon are more pronounced.

From the limited amount of material available (BMNH, NMS, PW), the general pattern in the distribution of bumble bees across the Himalaya of Kashmir is similar to that found across the Himalaya of western Nepal (Table 6). The major difference is that the same arid subalpine element is not known to be represented in Nepal or in the adjacent parts of Tibet. The Kashmir-western Nepal region of the Himalaya spans about 1000 km, but shares a broadly similar patterñof climate and vegetation (see the maps in Schweinfurth, 1957). The pattern of vegetation formations is highly convoluted locally because it

Table 6 Distribution of the social bumble bees of Kashmir (i.e. excluding species of the subgenus *Psithyrus*) outside Kashmir. X – present in the regional lists from world summary grid-squares (see Map 1): AP, western Alps; AR, Armenia and the Caucasus; MG, northern Mongolia; TS, central Tien Shan; HK, Hindu Kush; NP, Nepal; GS, southern Gansu; BM, central Burma; TW, Taiwan.

	Region									
Habitat in Kashmir:	AP	AR	MG	TS	HK	Kashmir	NP	GS	BM	TW
High alpine				X		*oberti*		X		
						personatus	X	X		
						ladakhensis	X	X		
Alpine						*kashmirensis*	X	X		
						himalayanus				
		X	X	X	X	*keriensis*	X	X		
Mesic subalpine						*rufofasciatus*	X	X	X	
			X	X	X	*biroi*				
						lemniscatus	X	X		
						avinoviellus				
Arid subalpine					X	*marussinus*				
				X	X	*subtypicus*				
					X	*semenovianus*				
Steppe			X	X	X	*asiaticus*	X	X		
		X	X	X	X	*melanurus*	X	X		
Upper forest						*lepidus*	X	X		
	X	X	X	X	X	*lucorum*	X	X		
	X	X	X			*hypnorum*	X	X		
						pyrosoma	X	X		X
Lower forest					X	*tunicatus*	X			
						simillimus				
						trifasciatus	X	X	X	X
						haemorrhoidalis	X		X	

tends to follow contours, but throughout this region it consists essentially of bands parallel to the Great Himalaya (e.g. Map 3). So for bumble bees, as for the vegetation and for many other groups of organisms (e.g. Mani, 1986), the fauna apparently changes to a greater extent in a small distance across the Himalaya than it does along them. This supports the familiar idea that distributions are restricted less by the capacity of organisms to spread through a habitat than by their capacity to colonise a different kind of habitat (e.g. Fretwell & Lucas, 1970).

Distribution outside Kashmir

Only the broadest patterns in the distribution of bumble bees outside Kashmir can be discussed without an analysis of the distribution of all bumble bee species (in prep.). Table 6 summarises the distributions of the social bumble bees of Kashmir (i.e. excluding species of the subgenus *Psithyrus*) across some of the mountainous areas of Europe and Asia. The species are listed in a sequence to show their altitudinal distribution and habitat association within Kashmir (see Figs 6 & 12).

The alpine and high alpine species of Kashmir are primarily associated with the Tibetan massif (Table 6: reaching Nepal, Gansu). The distributions of *B. keriensis* and *B. oberti* also extend westwards and northwards through the Pamir to the Tien Shan ranges and, for *B. keriensis*, further to Armenia in the west and to the mountains of northern Mongolia in the north-east.

The subalpine and steppe species of Kashmir are principally associated with the arid mountains to the north in central Asia (Table 6: Hindu Kush, Alai-Tien Shan s.l.). There are also a couple of very widespread, cool temperate and upper montane forest species (*B. lucorum* and *B. hypnorum*). Species of the arid subalpine element are at the south-eastern limits of their distributions in Kashmir. Species of the steppe element are also more widespread in central Asia, but reach beyond Kashmir eastwards into the Tibetan massif. Together with the alpine species these correspond to the 'western hypsobiont element' described from the Himalayan butterfly fauna by Mani (1986).

The remaining species are found in and around the forests at lower altitudes and are more southern and eastern in their distribution outside Kashmir. They are either restricted to the western Himalaya (*B. tunicatus* and *B. simillimus*) or are at the western limit of their distributions (Table 6: reaching eastwards to Nepal and Taiwan). *B. haemorrhoidalis* and *B. trifasciatus* reach eastwards and southwards into the Oriental tropics in the mountains of northern Thailand. Together this group of eastern species corresponds to the 'eastern forest element' described from butterflies by Mani (1986).

Four species are narrowly endemic to the western Himalaya, *B. avinoviellus, B. himalayanus, B. tunicatus* and *B. simillimus*. It is possible that *B. himalayanus* may prove to be conspecific with the central Asian taxa *B. turkestanicus* and *B. marussinus* (see the comments on *B. marussinus* and *B. himalayanus*). The three remaining species are among the more plesiomorphic species within their respective species-groups. If they are relics of a relatively ancient bumble bee fauna that was once more widespread, then it now persists in a region that has been subject to some of the most active mountain building during the last few million years (see Bally, 1983; Mani, 1986). But although the western Himalaya may not appear to have been a particularly stable refuge in this period, the high relief could have provided some buffering against any climatic fluctuations by allowing altitudinal displacement of bumble bee populations.

Overall, the bumble bee fauna of Kashmir includes particularly few of the relatives of the European *B. hortorum* (only *B. trifasciatus*) or *B. pascuorum* (only *B. haemorrhoidalis*), but particularly many of the relatives of the European *B. lapidarius* (8 species of the subgenera *Sibiricobombus* and *Melanobombus*). This pattern (9% *Megabombus* + *Diversobombus* + *Thoracobombus* + *Orientalibombus* : 35% *Sibiricobombus* + *Melanobombus*, Kashmir fauna excluding *Psithyrus*) contrasts markedly with the representation of these groups in the fauna of the European Kalsbach Alps (31% : 6%, Pittioni, 1937), in the fauna of the whole of Europe (34% : 8%, Reinig, 1981) or in the fauna of the western Palaearctic (32% : 10%, Rasmont, 1983*b*).

Relationships between patterns at different spatial scales

Among the social bumble bees, those species that are more widespread world-wide are not generally found at more localities within Kashmir (Fig. 13, which excludes the species of the subgenus *Psithyrus*, Kendall coefficient of rank correlation 0.08, $P > 0.5$ n.s.). It is possible that these data might not be representative because the sampling effort was far from uniform at both spatial scales and the sites in Kashmir were not randomly located but selected by kind of habitat and for ease of access. Nonetheless, there is pattern in the data insofar as species with similar habitat associations (Figs 6 & 12) do tend to occur closer together in Fig. 13. One interpretation is that this pattern in Fig. 13 may show a common limiting effect within the groups of species with similar habitat requirements, which could be just a consequence of the limited availability of the most suitable kinds of habitat for these species at both spatial scales.

From a study of British bumble bees, patterns in local distributions appear to be related to how close the species are to the centres of their world-wide distributions (Williams, 1988). Among the Kashmir fauna, those species that are nearer to the centres of their world-wide distributions (from Maps 5–62: *B. avinoviellus, B. himalayanus, B. melanurus, B. tunicatus, B. asiaticus, B. semenovianus, B. keriensis* and *B. simillimus*) do also tend to occur at more localities within the country (Maps 5–62; Fisher-Pitman randomisation test, $W = 181$, single-tailed $P < 0.01$, see Krauth, 1988). More precisely, those species that are nearer to the centres of their distributions in Britain have been found in a broader range of kinds of habitat. For the fauna of Kashmir, this greater breadth of habitat use for those species that are nearer to the centres of their world-wide distributions is apparent in the greater altitudinal ranges of these species within the country (excluding single altitude records of *B. oberti* and *B. lemniscatus*, Fisher-Pitman randomisation test, $W = 18400$, single-tailed $P < 0.05$).

Fig. 13 also appears to contain information as to how close the species are to the centres of their world-wide distributions. For these data in which the variance is similar in the log(world) and log(kashmir) distribution values, the central/marginal position of a species appears to be related to log(kashmir)-log(world). Since all species tend to occupy more localities nearer to the centres of their distributions, then if the more widespread species world-wide were generally found at more localities within comparable parts of their distributions, perhaps the deviation of the Kashmir species from any underlying positive relationship in Fig. 13 might show some influence of how far Kashmir is from their centres of world-wide distribution.

The relationship between distribution patterns and patterns of local abundance found among British bumble bees (Williams, 1988) is not consistently evident in the samples from Kashmir. Those species that were chosen from the maps to

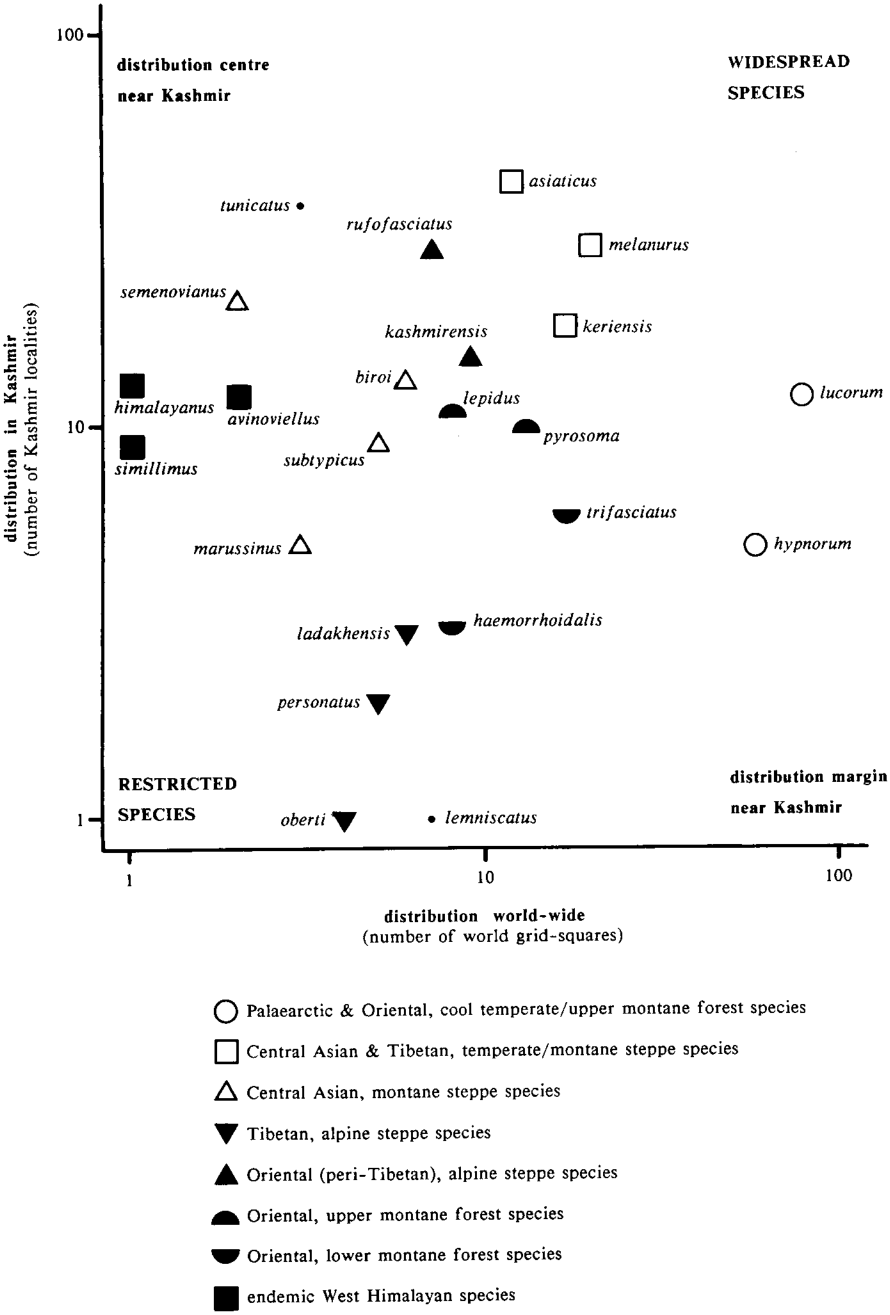

Fig. 13 Plot of how widespread the species of social bumble bees (i.e. excluding species of the subgenus *Psithyrus*) are within Kashmir against how widespread they are world-wide (logarithmic axes). Data are taken from occupancy of the number of localities within Kashmir (see Map 4) and from the number of world summary grid-squares (see Map 1) respectively. The distributions of *B. tunicatus* and *B. lemniscatus* are anomalous.

be nearer to the centres of their world-wide distributions in Kashmir do not appear to be generally more abundant locally in these samples (local abundance for a species estimated as the total numbers of individuals examined from Kashmir / numbers of localities in Kashmir, Fisher-Pitman randomisation test, $W = 145$, single-tailed $P = 0.19$ n.s.). However, there is still a tendency for the more widespread species within Kashmir to be more abundant locally (Kendall coefficient of rank correlation 0.29, single-tailed $P < 0.025$). It is possible that even if there were a relationship with the world-wide pattern, it may have been obscured in these data because the later collections at least were strongly biassed against including many specimens of the common species from each site, whereas the rare species were deliberately sought.

Relationships between the patterns of distribution at different spatial scales form the basis of a simple model for the interaction of those ecological factors that are most likely to govern bumble bee distributions (discussed in Williams, 1988, 1989). It follows from this that where some disturbance of sites causes a major reduction in food availability, it is the species that are nearest to the centres of their world-wide distributions that are most likely to persist. This may provide one explanation for the observation that *B. tunicatus* and *B. asiaticus* are the species that are often found alone in severely over-grazed areas around the edge of the Vale of Kashmir and in the Sind valley.

COLOUR PATTERNS OF THE KASHMIR FAUNA

The colour patterns of bumble bees often vary greatly among individuals of one species (e.g. Fig. 11), but may be closely similar between individuals of unrelated species where these species occur together (Fig. 12; see e.g. Vogt, 1909, 1911; Sakagami & Yoshikawa, 1961; Tkalců, 1968*b*, 1989; Pekkarinen, 1979; Plowright & Owen, 1980). Genetic determination of characteristics of the colour pattern with simple Mendelian inheritance has been demonstrated for the North American *B. melanopygus* and *B. rufocinctus* (Owen & Plowright, 1980; Plowright & Owen, 1980; Owen, 1986). But in the face of such marked regional convergence, several authors have questioned whether variation among colour patterns of individuals within a population is always determined genetically, or whether it is perhaps more often determined directly by environmental factors, such as diet, temperature or humidity during development (e.g. Vogt, 1909, 1911; Reinig, 1935; Pittioni, 1942, 1943).

The pubescence of bumble bees develops during the pupal stage and the colours appear soon after the adults emerge from their cocoons. Adult queen and worker bees invest much time and energy ensuring that the conditions in the nest remain nearly constant, for instance by incubating brood or by fanning air over the nest to regulate temperature as necessary (e.g. Heinrich, 1979). Hence the brood is shielded from many of the possible environmental effects on colour pattern during its development, so colonies usually produce individuals with relatively homogeneous colour patterns. However, if a nest is exposed and moved to a nest box, unusual colour patterns are more often found among the adults that subsequently emerge from pupation (pers. obs.).

The few examples of pronounced caste dimorphisms show that colour patterns are not solely determined by genes, but must also be influenced by the environment. Two examples have been described previously from subtropical environments (*B. ephippiatus* from the mountains of Costa Rica, see Owen & Plowright, 1980; *B. festivus* from the eastern Himalaya, see Ito *et al.*, 1984), in which workers and males from the same colonies share similar colour patterns that differ strongly from those of the queens. Similar differences exist within species of the *rufofasciatus*-group from Kashmir (see Plate 1). For *B. pyrosoma*, males usually also differ in that they have the pubescence predominantly yellow (Figs 424, 427, 430), a characteristic that can be regarded as sex-linked (see Stiles, 1979). But colour variation among the females from Kashmir appears to be related to body size (which increases through Figs 426, 428, 429, 425, see the comments on *B. pyrosoma*) and so to larval food intake. From the material available it seems most likely that the white-tailed queens from Kashmir belong to the same population as the nominal taxon *B. friseanus* from Yunnan (synonymised with *B. pyrosoma* s.l.). These queens from Yunnan have the pubescence of terga IV-V red, so they closely resemble their own workers from Yunnan and also many of the workers from Kashmir. Thus caste dimorphism in colour pattern may exist in only part of the population of *B. pyrosoma* s.l.

Variation of *B. asiaticus* in Kashmir

The *asiaticus*-group is particularly well represented in collections for an investigation of the variation in the colour pattern of the pubescence.

In Kashmir, two principal nominal taxa occur on opposite sides of the Great Himalaya range (Map 48), one with an unbanded yellow thorax (Figs 371–376), the other usually with a black band between the wing bases and an otherwise grey-white thorax (Figs 383–391). These nominal taxa are believed to be parts of a single species (see the comments on *B. asiaticus*).

The basis of this colour variation can be examined where the regional colour patterns occur together. At a few sites at the upper end of the higher valleys in the Great Himalaya, the *B. asiaticus* are not uniformly of one or other of the two principal colour patterns, but instead many individuals show a variety of combinations of their differing character states (Figs 377–382). The largest sample with this kind of variation was collected by F. Schmid from Lal Pani in the upper Kishanganga valley between 2–3.ix.1953 (BMNH: Table 7). This is likely to be a relatively unbiassed sample insofar as he specialised in collecting Trichoptera and not particular bumble bee taxa. I have also collected a small sample that shows similar variation, from Nigagar in the upper Sind valley (9.viii & 17.ix.1986, PW). The occurrence of the black tail-colour state (Figs 379–381) at both of these localities is curious. It is not known for individuals from the adjacent regions of Ladakh or the Vale of Kashmir, although it is common in parts of the Hindu Kush ranges (BMNH).

The ability of simple population genetic models to account for the observed patterns of variation among the specimens from these boundary sites can be tested if certain assumptions are made. Three aspects of the variation are chosen because they appear to be among the most important elements of the bees' colour pattern as they are viewed flying among flowers. It is assumed initially that each character shows either of two states and that these are each determined by one of a pair of alleles at a single locus. In fact the three characters selected do not show entirely discrete states. However, the minority of intermediate specimens from the possible hybrid zone can be assigned to these states for a preliminary analysis (Table 7), at least until further information on modifier effects is available.

Table 7 Numbers of individuals of *B. asiaticus* collected by Schmid from Lal Pani 2–3.ix.1953 with each combination of states of three characters of the colour pattern of the pubescence. The scoring was simplified prior to analysis in order to present discrete states despite some limited intergradation. The black thoracic band is deemed to be present if it appears well defined from the dorsal aspect. The pale colour 'white' includes very pale cream. The 'tail' colour is deemed to be red if the pubescence of at least two of the apical terga is predominantly red.

Thoracic band	Pale bands	Tail colour	Females	Males
present	white	red	7	1*
absent	white	red	–	1
present	white	black	2	1
absent	white	black	1	–
present	yellow	black	3	34
absent	yellow	black	–	13
present	yellow	red	9	37
absent	yellow	red	–	5**

* *B. callophenax* of Richards, not of Cockerell
** *B. longiceps* Smith

Table 8 Association between pairs of character states of the colour pattern among the males of *B. asiaticus* from Lal Pani (see Table 7). None of these comparisons shows significant association (chi-square two-sample test, all comparisons $P>0.05$).

		Pale bands		Tail colour	
		white	yellow	red	black
Thoracic band	present	2	71	38	35
	absent	1	18	6	13
Tail colour	red	2	42		
	black	1	47		

There is no association between the states of the three colour characters among individuals from the top of the Kishanganga valley (Table 8). This apparent independent assortment of the characters shows an absence of the disequilibrium (e.g. Mallet, 1986) that would be expected if gene flow across the coincident character clines in the hybrid zone were large. Hybrid zones are expected to be captured by linear habitat features where population density is particularly low (e.g. Mallet, 1986; Hewitt, 1988). For *B. asiaticus* in Kashmir, this role may be fulfilled by the high ridges and passes of the Great Himalaya range. For instance, where the upper Sind valley reaches the main ridge of the Great Himalaya just above Nigagar, the valley floor rises abruptly by about 700 m at the Zoji-La pass. My small samples from either side of Nigagar, at Sonamarg (2700 m) and above Gumri (3700 m), each consist of material with a single colour pattern (i.e. the alleles may be nearly fixed), so the hybrid zone at the top of the Sind valley may be less than 16 km wide. Such a narrow cline is consistent with the interpretation that there is little gene flow across the hybrid zone at the top of the Kishanganga valley (Table 8). The hybrid zone at the top of the Kishanganga may, nonetheless, be much broader (Map 48, see the comments on variation within Kashmir for *B. asiaticus*).

Table 9 Observed numbers of individuals of *B. asiaticus* from Lal Pani with each state of three colour pattern characters (see Table 7), together with the expected numbers from simple genetic models. Frequencies from a small sample (n = 20) from Nigagar are included for comparison. Deviation from model significant at $P<0.05$ *, $P<0.001$ ***, or not significant ns.

		Observed: females (diploid)	males (haploid)	**Expected:** females – no dominance	females – simple dominance
Thoracic band	present	21	73	17	[est(p) = 73/92] 21
	absent	1	19	5	[est(q) = 19/92] 1
Frequency (absent) Lal Pani		0.05	0.21		
[Frequency(absent) Nigagar		0.00	0.66]		
(Chi-square one-sample test, df = 1)				(4.14)	(0.00)
Probability that deviation of observation from expectation is due to chance				$P<0.05$ *	$P>>0.05$ ns
Pale bands	white	10	3	1	[est(p) = 3/92] 1
	yellow	12	89	21	[est(q) = 89/92] 21
Frequency (yellow) Lal Pani		0.55	0.97		
[Frequency (yellow) Nigagar		0.50	0.66]		
(Chi-square one-sample test, df = 1)				(84.86)	(84.86)
Probability that deviation of observation from expectation is due to chance				$P<<0.05$ ***	$P<<0.05$ ***
Tail colour	red	16	44	11	[est(p) = 44/92] 16
	black	6	48	11	[est(q) = 48/92] 6
Frequency (black) Lal Pani		0.27	0.52		
[Frequency (black) Nigagar		0.14	0.33]		
(Chi-square one-sample test, df = 1)				(4.55)	(0.00)
Probability that deviation of observation from expectation is due to chance				$P<0.05$ *	$P>>0.05$ ns

The frequency of alleles can be estimated and the dominant allele can be determined from the frequencies of the character states, because although female bumble bees are diploid, the males are usually haploid (see Plowright & Pallett, 1979). The frequency of the character states among males in the large sample from Lal Pani is assumed to be representative of the allele frequencies in that local part of the population (which assumes that even if the material was collected in the proximity of only a very few colonies, it still represents a random sample of the local gene pool). These frequencies may differ at other localities in the Kishanganga valley or at Nigagar, so these samples cannot be combined for analysis. If there is simple, complete dominance by one of the two alternative alleles at each locus, then the frequencies of character states should differ between males and females, with higher frequencies of expression for the recessive allele among males. The higher frequencies among males of the lack of a black thoracic band, of yellow pale bands and of black 'tails' at both Lal Pani and Nigagar (Table 9) are consistent with their determination by recessive alleles. Furthermore, the frequencies of characters among males can be used to calculate the frequencies among females that would be expected if there were no dominance (which might result from Hardy-Weinberg equilibrium with co-dominance of both alleles, or from some mechanism other than straightforward Mendelian genetics). These calculated frequencies are found to differ significantly from those observed for all three characters (Table 9).

The observed frequencies of the states of the black thoracic band and of the tail colour among females are consistent with those expected from the Hardy-Weinberg equilibrium model with simple, complete dominance between two alleles (Table 9). However, this is rejected for the pale band colour character, the distribution of which was not consistent with the dominance-free model either. It has to be noted that the chi-square one-sample test is not reliable when an expected frequency is less than 5 (e.g. Siegel, 1956), but the values of chi-square that result here are so large (84.8, df = 1) that the conclusion that the model should be rejected is unlikely to be altered. The reason for the failure of the models must be that their assumptions are violated. In addition to those mentioned above, assumptions of the equilibrium model include insignificant dispersal, random mating and unselective predation.

Firm conclusions as to the genetic basis of the patterns of colour variation among these bumble bees cannot be drawn without breeding experiments. This would allow ideas of the pattern of inheritance to be tested, although this is not particularly easy with bumble bees (but see Owen & Plowright, 1980). However, the pattern of variation for two out of three of the characters that have been analysed is consistent with simple genetic models. It is therefore also consistent with the assumption that individuals with these colour patterns are interbreeding as parts of a single population and a single biological species. Thus local climate or diet does not appear to be the proximate factor governing the close convergence in colour pattern between this species and the regionally covarying groups of species on either side of the Great Himalaya.

Convergent colour patterns

It is noticeable that only a few of the possible colour patterns are actually found among bumble bees world-wide, given the range of colours shown by the pale pubescence of bumble bees and the observed patterns of disposition of bands of pale and black pubescence on their bodies (Plowright & Owen, 1980; BMNH, PW). For instance, at least half of all species of bumble bees have some individuals with a 'red-tailed' colour pattern. Other common elements in the colour pattern are a band of black hairs on the thoracic dorsum between the wing bases, and a black band on tergum III. The most widespread colour pattern of the dorsal pubescence among all bumble bees of the world appears to be for the thorax to be yellow with a band of black hairs between the wing bases and for the gaster to be yellow – black – red, from base to apex (cf. Figs 233–235, 242, 243, 298–300, 317, 318, 377, 378, 382, 388, 393, 407, 412–416, 426).

The three principal regions of Kashmir have groups of bumble bee species with characteristic colour patterns of the dorsal pubescence (Fig. 12):

(1A) In the high alpine zone of Ladakh, the most common colour pattern of the pubescence is for the thorax to have yellow transverse bands anteriorly and posteriorly, with a black band between the wing bases. The gaster is yellow (terga I-II) and red (terga III-V), although often with a narrow black band between them (basal quarter or less of tergum III).

(1B) At lower altitudes in the arid steppe of Ladakh, the common colour pattern is for the pubescence of the thoracic dorsum to be uniformly yellow and for the gaster to have a yellow band (terga I-II yellow, or just tergum I yellow, or terga I-II completely black) – black (at least tergum III) – red (usually terga IV-V).

(2A) Around the Vale of Kashmir, above the forests, the most common pattern is for the pubescence of the thoracic dorsum to be grey-white with a black band between the wing bases. The gaster is grey-white (tergum I) – yellow (usually tergum II) – red (terga III-IV, sometimes with white on terga IV-V).

(2B) In the Vale of Kashmir and the surrounding upper montane forest, the common colour pattern is banded and white as for type 2A, but the gaster lacks any yellow and is grey-white (tergum I, sometimes tergum II) – black (at least tergum III) – red (usually terga IV-V).

(3) In the lower montane forests of the Jammu foothills, the common colour pattern is for the pubescence of the thorax to be black and for that of the gaster to be yellow (terga I-II) and red (terga III-V), but without an obvious black band.

The type 1A colour pattern deviates only slightly from the widespread bumble bee pattern of three yellow bands and a red 'tail' by the replacement of much of the black on tergum III by red. This type 1A pattern is otherwise most predominant among individuals from the Pyrenees in Europe.

The type 1B pattern differs from the widespread pattern principally in the absence of a black band on the thorax, although it retains an extensive black area on the gaster. It is predominant in the Hindu Kush and occurs elsewhere in the Caucasus (*B. (Melanobombus) lapidarius*) and quite independently in South America (*B. (Fervidobombus) bellicosus* Smith).

The type 2A pattern differs from the widespread pattern by a change in the pale pubescence from yellow to grey-white on all but tergum II. The type 2A pattern is perhaps most predominant in Kashmir, but is also found around the southern and eastern margins of the Tibetan massif.

The type 2B pattern completes the transition of all of the yellow pubescence of the widespread pattern to grey-white. Individuals with this colour pattern occur widely in the Himalaya, the central Asian mountains and westwards in the Caenozoic mountains of southern Europe to as far west as the Alps (*B. (Pyrobombus) brodmannicus*) and the

Atlas mountains of North Africa (*B. lapidarius*). Males from populations with the type 2B pattern often retain the common banded yellow pattern (e.g. *B. wurflenii* and *B. lapidarius* from the Caucasus, *B. brodmannicus* from the Alps, *B. lapidarius* from the Atlas, BMNH). A variant of the type 2B pattern has tergum II or terga I-II dark chocolate-brown. This is seen in the Himalaya only among the males and workers of *B. tunicatus* (Figs 348, 349, 351, 352, 354) and *B. simillimus* (Figs 418, 420, 421), but it is also known from the Caucasus mountains for *B. (Thoracobombus) mlokosievitzii* Radoszkowski (BMNH, PW).

The type 3 pattern differs from the widespread pattern by the replacement of the pale pubescence on the thoracic dorsum by black and by the reduction of the black band on the gaster. In the western Himalaya individuals with this pattern are restricted to the outer foothills. Further east in Uttar Pradesh the same pattern is shared by *B. (Alpigenobombus) breviceps* and *B. (Pyrobombus) rotundiceps*.

So what is responsible for the apparent constraints on the range of bumble bee colour patterns that are actually observed? Why do these colour patterns appear to have converged especially closely among many species within each geographical region? These species are often not closely related, as shown by differences in their male genitalia. Colour pattern had no effect on acceptance of females by patrolling males of British *B. pratorum* (L.) (Free, 1971). Stiles (1979) suggested that colour affects radiative properties that may be crucial to thermoregulation in extreme climates. Sakagami & Ito (1981) challenged this interpretation of sexual dimorphism in colour pattern, because the two faunas compared by Stiles were dominated by different groups of species. Within each of these subgenera, *Fervidobombus* and *Pyrobombus*, no regional trends were found. However, there may be differences in the kind of habitat and in mate-searching behaviour between the species of these two groups that could also affect the relative advantages of the two kinds of colour patterns. The peculiar behaviour of males of some species of the subgenus *Fervidobombus* has been described by Lloyd (1981) and by Villalobos & Shelly (1987). It could be that many of these differences between the two groups, including differences in colour pattern, are each related to an underlying difference in physiology that is linked to their regional patterns of distribution more directly.

Many species of bumble bees commonly produce individuals that are entirely black, but these are most often predominant in tropical environments (Franklin, 1913). These species include *B. (Rufipedibombus) rufipes*, *B. (Megabombus) melanopoda* Cockerell and workers and males of *B. (Senexibombus) senex* Vollenhoven in the East Indies (BMNH), and *B. (Fervidobombus) brevivillus* Franklin, *B. (Fervidobombus) niger* Franklin [= *B. atratus* Franklin, preoccupied name], *B. (Fervidobombus) pullatus* Franklin and *B. (Fervidobombus) morio* (Swederus) in South America (BMNH, PW). An extensively black body is likely to have a lower reflectance even in the infra-red part of the spectrum and so should have a higher rate of approach to thermal equilibrium with the environment by an exchange of long-wave radiation. This may be an advantage to actively foraging bumble bees in a warm environment, because they produce a lot of excess heat from the flight muscles and so might otherwise suffer from heat stress. The subtropical black bees listed above may often be forest-dwelling. In the shade they can escape the additional problem of rapid overheating that could arise from an equally efficient absorption by black pigments of the short-wave radiation in direct sunlight. So this likely advantage of the black pubescence for bees foraging in a shaded warm environment may account for why the type 3 pattern, with a black thorax, the source of the endogenous heat, predominates among bumble bees at the lowest altitudes at which they occur in Kashmir (Fig. 12). It is very noticeable that near their lower altitudinal and latitudinal limits in Kashmir these bees (*B. trifasciatus* and *B. haemorrhoidalis*) forage particularly both in the shade and during the cooler periods of the day (see the discussion of the distribution of the fauna with altitude). However, further south in their distributions in South East Asia, these same species have extensively orange-brown colour patterns of the thoracic pubescence (Fig. 11). More information is needed on the foraging behaviour of these bees in South East Asia, where there is a tendency among the few large nocturnal bees and wasps to have an orange-brown colour pattern (M. C. Day, pers. comm.; Roubik, 1989). There is also clearly a need for measurements of the radiative properties of bumble bee colour patterns in general.

Male bumble bees that patrol in the higher forest on Mt Apharwat tend to be almost uniformly bright yellow (Fig. 6 and see the comments on *B. pyrosoma*, *B. lucorum* and *B. hypnorum*). This may also be true of those males that patrol in forests, but not in open habitats, at higher latitudes (see Pekkarinen, 1979: fig. 7, cf. Løken, 1973: fig.2). In contrast to black, a pale, highly reflective body colour should reduce the rate of approach to thermal equilibrium with the environment by an exchange of long-wave radiation, so that following an active warm-up, a sufficiently high excess thoracic temperature for flight can be reached quickly and maintained in a shaded cool environment. In contrast, males of those species that patrol in the forests at low altitudes, in open areas outside the forest or in a broad range of habitats in Kashmir tend to be darker and share the colour pattern of the females (Fig. 6). Uniform bright yellow may be disadvantageous in open areas beyond the forest, for instance in alpine and arctic zones, because it is very conspicuous to predators. This could be a particular problem for the more sedentary 'perch and sprint' males (e.g. *B. asiaticus* and *B. rufofasciatus*, see the introduction on mate-searching behaviour of male bumble bees in Kashmir) and those males that aggregate at nest entrances (which includes several species of *Fervidobombus*, e.g. review by Schremmer, 1972; Lloyd, 1981; Villalobos & Shelly, 1987). Yet the most uniformly light-coloured female bumble bees in Kashmir, which belong to the type 1A pattern-group, are found at the highest altitudes sampled for bumble bees, in Ladakh. This trend towards lighter colours in cooler environments is the reverse of that described by Pekkarinen (1979) from European species.

Regional convergences in the finer details of the colour pattern between bumble bee species are likely to be the result of selective predation. Predators with perception of colour and great visual acuity, perhaps certain birds, may avoid the familiar common colour patterns of these insects because the females can inflict a painful sting, and preferentially attack any individuals with unusual colour patterns. This kind of selection could bring about Müllerian mimicry among the colour patterns on the dorsa of the females (Plowright & Owen, 1980) and Batesian automimicry by the colour patterns on the dorsa of the stingless males (Stiles, 1979). The putative models for this process would be the colour patterns of the females of the most abundant species. In Kashmir, these species tend to be regionally restricted and relatively invariant in their colour patterns (type 1A, *B. oberti*, Figs 392, 393; type 1B, *B. semenovianus*, Figs 397, 398, 400, 401; type 2A, *B. rufofasciatus*, Figs 431, 432, 434, 435, 438; type 2B, *B. tunicatus*, Figs 350, 353; type 3, *B. haemorrhoidalis*, Figs 279, 280; see Fig. 12). Many of the mimics occupy the middle classes of abundance, but are often more widespread among the regions of Kashmir. These species covary in their colour patterns among the regions so that they show the protective livery of the local model (e.g. *B. avinoviellus*, Figs 232–241; *B. himalayanus*, Figs 242–253; *B. kashmirensis*, Figs 295–310; *B. lepidus*, Figs 327, 328, 330, 331, 333, 334; *B. biroi*, Figs 335–346; *B. asiaticus*, Figs 371–391).

A subtle difference between the colour patterns of *B. kashmirensis* and *B. rufofasciatus* could be interpreted as further circumstantial evidence in support of the mimicry hypothesis for colour convergence. Workers of these two species appear to be identical (type 2A colour pattern) when they are seen manoeuvring slowly from flower to flower in the alpine and subalpine zones of the mountains around the Vale of Kashmir. Most workers of *B. rufofasciatus* have the hairs of gastral terga III-IV almost uniformly red and those of tergum V uniformly white (Fig. 435). The *B. kashmirensis* from the same region often have all three terga (III-V) covered with hairs that are red at the base, but which become more extensively white-tipped towards the apex of the gaster (Fig. 303). This achieves the same white-tailed effect as for *B. rufofasciatus*, because the apex of the gaster curves slightly towards the ventral for bumble bees.

Colour variation within many of the bumble bee species of Kashmir does appear to be much greater than within the bumble bee species of Britain, or even within the more variable species of the Alps. This may be blamed on taxonomic 'lumping' in this review. But if bumble bee colour patterns have converged into separate and distinctive mimetic groups within each of the neighbouring regions of Asia, then the position of Kashmir at the frontier between the large and divergent Oriental and Palaearctic faunas (which are still to some extent separated even inside Kashmir by the divide of the Great Himalaya) may account in part for the great diversity of colour pattern within some of the Kashmir species.

Acknowledgements. I am very grateful to all of those who gave advice, with special thanks to B. Bolton and M. C. Day. D. Agosti, N. H. Barton, R. L. Blackman, S. A. Corbet, A. O. Divers, W. G. Eberhard, P. J. Eggleton, K. Gaston, C. J. Humphries, L. S. Kimsey, R. P. Macfarlane, A. Pekkarinen, R. C. Plowright, P. Rasmont, M. J. Scoble and R. I. Vane-Wright commented on parts of the manuscript. C. R. Betts, G. R. Else, N. D. M. Fergusson, L. Ficken, M. G. Fitton, P. Gilbert, P. M. Hammond, J. M. Harvey, B. R. Pitkin, A. Polaszek, J. Spratt, N. D. Springate, D. A. Sutton, B. C. Townsend, C. R. Vardy, S. L. Ward and D. B. Williams helped with equipment, library searches and translations. M. A. Mir (No. 1 Guide, Gulmarg) provided support in the field and C. A. Chadwell helped with certain plant determinations. I am very grateful to the Keeper of Entomology for providing facilities for this work.

I am also much indebted to the following who helped by lending material: A. V. Antropov (ZMMU), K. Arakaki (BPBM), E. Diller (ZS), M. Fischer (NM), W. Hogenes (ITZ), F. Koch and I. Wegener (MNHU), J.-P. Kopelke (NMS), J. Macek (NMP), K. C. McGiffen (INHS), R. J. McGinley and B. B. Norden (USNM), C. D. Michener (SEMK), J. Papp (TM), B. Petersen (ZM), V. Raineri (MCSN), P. Rasmont (FA), B. Tkalců, S.-f. Wang (IZ), J. C. Weulersse (MNHN) and especially Y. A. Pesenko and M. V. Podbolotskaya (ZI). N. R. Bogatyrov, W. Budenburg, C. A. Chadwell, C. S. Cockell, R. Desmier de Chenon, A. O. Divers, R. W. Husband, A. Hutchings, M. Ito, L. W. Macior, S. Martin, H. Osmaston, B. Petersen, N. Saville, G. S. Vick and S.-f. Wang kindly donated or exchanged other Asian specimens used here.

The work was carried out during a Postdoctoral Research Fellowship funded by the Natural Environment Research Council, which also awarded a grant towards publication costs. Additional assistance for the purchase of a microscope was provided from the Entomological Fund, and assistance for the purchase of computer hardware for the automated mapping system was provided by the Systematics Association.

REFERENCES

Abrol, D. P. 1987. Influence of thermal and energetic constraints on the pollination activity of carpenter bee *Xylocopa pubescens*. *Environment and Ecology* **5**: 90–93.

Ackery, P. R. & Vane-Wright, R. I. 1984. *Milkweed butterflies, their cladistics and biology, being an account of the natural history of the Danainae, a subfamily of the Lepidoptera, Nymphalidae*. ix+425 pp. London.

Alcock, J. & Alcock, J. P. 1983. Male behaviour in two bumblebees, *Bombus nevadensis auricomus* and *B. griseicollis* [sic] (Hymenoptera: Apidae). *Journal of Zoology* **200**: 561–570.

Alford, D. V. 1975. *Bumblebees*. xii+352 pp. London.

Awram, W. J. 1970. *Flight route behaviour of bumble bees*. 173 pp. Ph.D. thesis, University of London.

Ball, F. J. 1914. Les bourdons de la Belgique. *Annales de la Société entomologique de Belgique* **58**: 77–108.

Bally, A. W. 1983. Geological and ecological studies of Qinghai-Xizang (Tibet) Plateau. [Review.] *American Scientist* **71**: 189–190.

Barton, N. H. 1988. Speciation. *In* Myers, A. A. & Giller, P. S.: *Analytical biogeography, an integrated approach to the study of animal and plant distributions*, pp. 185–218. London.

Bergström, G., Kullenberg, B. & Ställberg-Stenhagen, S. 1973. Studies on natural odoriferous compounds. VII. Recognition of two forms of *Bombus lucorum* L. (Hymenoptera, Apidae) by analysis of the volatile marking secretion from individual males. *Chemica Scripta* **4**: 174–182.

Bergström, G., Svensson, B. G., Appelgren, M. & Groth, I. 1981. Complexity of bumble bee marking pheromones: biochemical, ecological and systematical interpretations. *In* Howse, P. E. & Clement, J.-L.: *Biosystematics of social insects*, pp. 175–183. The Systematics Association, Special Volume No. 19. London.

Bingham, C. T. 1897. *The fauna of British India, including Ceylon and Burma. Hymenoptera. – Vol. I. Wasps and bees*. xxix+579 pp. London.

Bischoff, H. 1930. Entomologische Ergebnisse der schwedischen Kamtchatka-Expedition 1920–1922. 29. Bombinae. (Hymen.) *Arkiv för zoologi* **21**: 1–6.

—— 1931. Entomologische Ergebnisse der deutsch-russischen Alai-Pamir-Expedition 1928 (II). 4. Hymenoptera VII. Zur Kenntnis einiger Hummelnester aus dem Pamir. *Mitteilungen aus dem Zoologischen Museum in Berlin* **16**: 860–864.

—— 1935. Genus *Bombus* (Apidae, Hymen.). *In: Wissenschlaftliche Ergebnisse der niederlandischer Expedition in den Karakorum und die angrenzenden Gebiete in den Jahren 1922, 1925 und 1929/30* **1**: 255–256. Leipzig.

—— 1936. Schwedisch-chinesische wissenschaftliche Expedition nach den nordwestlichen Provinzen Chinas, unter Leitung von Dr. Sven Hedin und Prof. Sü Ping-chang. Insekten gesammelt vom schwedischen Arzt der Expedition Dr. David Hummel 1927–1930. 56. Hymenoptera. 10. Bombinae. *Arkiv för zoologi* **27**: 1–27.

Bischoff, H. & Hedicke, H. 1931. Über einige von Illiger beschriebene Apiden (Hym.). *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* **1930**: 385–392.

Blüthgen, P. 1918. *Psithyrus vestalis* Geoffr. und *bohemicus* Seidl (*distinctus* Pérez) (Hym.). *Entomologische Mitteilungen* **7**: 188–197.

Boulangé, H. 1924. Recherches sur l'appareil copulateur des hyménoptères et spécialement des chalastogastres. *Mémoires et Travaux des facultés Catholiques de Lille* **28**: 444 pp.

Bowers, M. A. 1985. Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah. *Ecology* **66**: 914–927.

Chang, D. H. S. 1981. The vegetation zonation of the Tibetan Plateau. *Mountain Research and Development* **1**: 29–48.

Chiu, S. C. 1948. Revisional notes on the Formosan bombidfauna (Hymenoptera). *Notes d'entomologie chinoise* **12**: 57–81.

Cockerell, T. D. A. 1905. Descriptions and records of bees. – I. *Annals and Magazine of Natural History* (7) **16**: 216–225.

—— 1906. Descriptions and records of bees. – XII. *Annals and Magazine of Natural History* (7) **18**: 69–75.

—— 1909. Descriptions and records of bees. – XXIII. *Annals and Magazine of Natural History* (8) **4**: 393–404.

—— 1910. Some bees from high altitudes in the Himalaya mountains. *Entomologist* **43**: 238–239.

—— 1911. The humble-bees of Formosa. *Entomologist* **44**: 100–102.

—— 1917. New social bees. *Psyche* **24**: 120–128.

—— 1922. Bees in the collection of the U.S. National Museum. *Proceedings of the United States National Museum* **60**: 20 pp.

Cresson, E. T. 1863. List of the North American species of *Bombus* and *Apathus*. *Proceedings of the Entomological Society of Philadelphia* **2**: 83–116.

—— 1864. Descriptions of several new species of North American Apidae. *Proceedings of the Entomological Society of Philadelphia* **3**: 38–43.

Dalla Torre, K. W. von 1880. Unsere hummel-(*Bombus*) Arten. *Der Naturhistoriker* **2**: 40–41.

—— 1882. Bermerkungen zur Gattung *Bombus* Latr., II. 3. Zur Synonymie und geographischen Verbreitung der Gattung *Bombus* Latr. *Bericht des Naturwissenschaftlich-medizinischen Vereins in Innsbruck* **12**: 14–31.

—— 1890. Hymenopterologische Notizen. *Wiener entomologische Zeitung* **9**: 139.

—— 1896. *Catalogus hymenopterorum hucusque descriptorum systematicus et synonymicus. Volumen X: Apidae (anthophila)*. viii+643 pp. Lipsiae.

Darwin, C. 1859. *On the origin of species by means of natural* *selection, or the preservation of favoured races in the struggle for life*. ix+490 pp. London.

Day, M. C. 1979. The species of Hymenoptera described by Linnaeus in the genera *Sphex, Chrysis, Vespa, Apis* and *Mutilla*. *Biological Journal of the Linnean Society* **12**: 45–84.

Delmas, R. 1981. Systematics and geographical variation in the Bombinae. *In* Howse, P. E. & Clement, J.-L.: *Biosystematics of social insects*, pp. 223–229. The Systematics Association, Special Volume No. 19. London.

Dobzhansky, T. 1937. *Genetics and the origin of species*. xvi+364 pp. New York.

Dover, C. 1922. A note on bees of the genera *Xylocopa* and *Bombus* in the Indian Museum. *Record of the Indian Museum* **24**: 85–89.

Eberhard, W. G. 1985. *Sexual selection and animal genitalia*. xvii+244 pp. London.

Erlandsson, A. 1979. *Bombus canariensis* Pérez, 1895 n. stat and *Bombus maderensis* n. sp. from the Macaronesian Islands. *Entomologica scandinavica* **10**: 187–192.

Eversmann, E. 1852. Fauna hymenopterologica Volgo-Uralensis. (Continuatio). Familia anthophilarium seu apidarum. *Izvêstiya Moskovskago éntomologicheskago obshchestva* **3**: 3–137.

Fabricius, J. C. 1775. *Systema entomologiae, sistens insectorvm classes, ordines, genera, species, adiectis synonymis, locis, descriptionibvs, observationibvs*. 32+832 pp. Flensbvrgi & Lipsiae.

—— 1781. *Species insectorvm exhibentes eorvm differentias specificas, synonyma avctorvm, loca natalia, metamorphosin adietis observationibvs, descriptionibvs*. **1**: viii+552 pp. Hambvrgi & Kilonii.

—— 1787. *Mantissa insectorvm sistens eorvm species nvper detectas adiectis characteribvs genericis, differentiis specificis, emendationibvs, observationibvs*. **1**: xx+348 pp. Hafniae.

—— 1793. *Entomologia systematica emendata et aucta. Secundum classes, ordines, genera, species adjectis synonimus, locis observationibus, descriptionibus*. **2**: viii+519 pp. Hafniae.

—— 1804. *Systema piezatorum secundum ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus*. xiv+439 pp. Brunsvigae.

Fisher, R. M. 1987. Queen-worker conflict and social parasitism in bumble bees (Hymenoptera: Apidae). *Animal Behaviour* **35**: 1026–1036.

Franklin, H. J. 1911. New North American Bombidae. *Transactions of the American Entomological Society* **37**: 157–168.

—— 1913. The Bombidae of the New World. *Transactions of the American Entomological Society* **38**(1912): 177–486.

Free, J. B. 1971. Stimuli eliciting mating behaviour of bumblebee (*Bombus pratorum* L.) males. *Behaviour* **40**: 55–61.

Freeman, R. B. 1968. Charles Darwin on the routes of male humble bees. *Bulletin of the British Museum (Natural History)* (Historical) **3**: 179–189.

Fretwell, S. D. & Lucas, H. L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta biotheoretica* **19**: 16–36.

Friese, H. 1905. Neue oder wenig bekannte Hummeln des russischen Reiches (Hymenoptera). *Ezhegodnik Zoologicheskago muzeya* **9**(1904): 507–523.

—— 1909. Neue Varietäten von *Bombus* (Hym.). *Deutsche entomologische Zeitschrift* **1909**: 673–676.

—— 1913. Über einige neue Apiden (Hym.). *Archiv für Naturgeschichte* **78**(1912)(A,12): 85–89.

—— 1916. Über einige neue Hummelformen (*Bombus*), besonders aus Asien (Hym.). *Deutsche entomologische Zeitschrift* **1916**: 107–110.

—— 1918. Über Hummelformen aus dem Himalaja. *Deutsche entomologische Zeitschrift* **1918**: 81–86.

—— 1924. Über auffallende Hummelformen. (Hym. Apid.). *Deutsche entomologische Zeitschrift* **1924**: 437–439.

—— 1931. Über *Bombus* und *Psithyrus*. *Konowia* **10**: 300–304.

Friese, H. & Wagner, H. von 1910. Zoologische Studien an Hummeln. I. Die Hummeln der deutschen Fauna. *Zoologische Jahrbucher, Systematik, Ökologie und Geographie der Tiere* **29**(1909): 1–104.

Frison, T. H. 1927. A contribution to our knowledge of the relationships of the Bremidae of America north of Mexico (Hymenoptera). *Transactions of the American Entomological Society* **53**: 51–78.

—— 1933. Records and descriptions of *Bremus* and *Psithyrus* from India (Bremidae: Hymenoptera). *Record of the Indian Museum* **35**: 331–342.

—— 1934. Records and descriptions of *Bremus* and *Psithyrus* from Formosa and the asiatic mainland. *Transactions of the Natural History Society of Formosa* **24**: 150–185.

—— 1935. Records, notes and descriptions of *Bremus* from Asia (Bremidae: Hymenoptera). *Record of the Indian Museum* **37**: 339–363.

Gerstaecker, A. 1869. Beiträge zur näheren Kenntniss einiger Bienen-Gattungen. *Stettiner entomologische Zeitung* **30**: 315–367.

Ghiselin, M. 1975. A radical solution to the species problem. *Systematic Zoology* **23**(1974): 536–544.

Grütte, E. 1937. Zur Kenntnis zentralasiatischer Arten von *Psithyrus* Lep. (Hym. Apid.). *Mitteilungen der Deutschen entomologischen Gesellschaft* **7**: 103–109.

Gurcharan Singh & Kachroo, P. 1976. *Forest flora of Srinagar and plants of neighbourhood*. x+278 pp. Dehra Dun.

Haas, A. 1976. Paarungsverhalten und Nestbau der alpinen Hummelart *Bombus mendax* (Hymenoptera: Apidae). *Entomologica germanica* **3**: 248–259.

Handlirsch, A. 1888. Die Hummelsammlung des k. k. naturhistorischen Hofmuseums. *Annalen des Naturhistorischen Museums in Wien* **3**: 209–250.

Harris, M. 1776. *An exposition of English insects, with curious observations and remarks, wherein each insect is particularly described; its parts and properties considered; the different sexes distinguished, and the natural history faithfully related*. viii+166 pp. London.

Heinrich, B. 1979. *Bumblebee economics*. viii+245 pp. Massachusetts.

Hengeveld, R. 1988. Mayr's ecological species criterion. *Systematic Zoology* **37**: 47–55.

Hennig, W. 1981. *Insect phylogeny*. [Translated by Pont, A. C.; revisionary notes by Schlee, D.] xxii+514 pp. Chichester.

Hewitt, G. M. 1988. Hybrid zones – natural laboratories for evolutionary studies. *Trends in Ecology and Evolution* **3**: 158–167.

Honk, C. G. J. van, Velthuis, H. H. W. & Röseler, P.-F. 1978. A sex pheromone from the mandibular glands in bumblebee queens. *Experientia* **34**: 838–839.

Hull, D. L. 1980. Individuality and selection. *Annual Review of Ecology and Systematics* **11**: 311–332.

Illiger, J. C. W. 1806. William Kirby's Familien der bienenartigen Insekten, mit Zusätzen, Nachweisungen und Bemerkungen. *Magazin für Insektenkunde* **5**: 28–175.

Inouye, D. W. 1977. Species structure of bumblebee communities in North America and Europe. *In* Mattson, W. J.: *The role of arthropods in forest ecosystems*, pp. 35–40. New York.

International Commission on Zoological Nomenclature 1939. Opinion 135. The suppression of the so-called 'Erlangen List' of 1801. *Opinions and Declarations rendered by the International Commission on Zoological Nomenclature* **2**: 7–12.

—— 1954. Opinion 220. Validation, under the plenary powers, of the generic name *Bombus* Latreille, 1802 (class Insecta, order Hymenoptera), in so far as the use of those powers is required to provide that name with the status of availability. *Opinions and Declarations rendered by the International Commission on Zoological Nomenclature* **4**: 103–114.

—— 1985. *International code of zoological nomenclature*. 3rd edn. xx+338 pp. Berkeley.

Ito, M. 1983. *Supraspecific classification of bumblebees based on* *the characters of male genitalia*. 247 pp. Ph.D. thesis, Hokkaido University.

—— 1985. Supraspecific classification of bumblebees based on the characters of male genitalia. *Contributions from the Institute of Low Temperature Science, Hokkaido University* (B) **20**: 143 pp.

—— 1987. Geographic variation of an east Asian bumblebee *Bombus diversus* in some morphometric characters (Hymenoptera, Apidae). *Kontyû* **55**: 188–201.

Ito, M., Matsumura, T. & Sakagami, S. F. 1984. A nest of the himalayan bumblebee *Bombus (Festivobombus) festivus*. *Kontyû* **52**: 537–539.

Ito, M. & Sakagami, S. F. 1985. Possible synapomorphies of the parasitic bumblebees (*Psithyrus*) with some nonparasitic bumblebees (*Bombus*) (Hymenoptera: Apidae). *Sociobiology* **10**: 105–119.

Jonghe, R. de 1982. Copulations interspécifiques en captivité d'espèces du genre *Bombus* Latreille (sensu stricto) (Hymenoptera, Apidae, Bombinae). *Bulletin et Annales de la Société royale entomologique de Belgique* **118**: 171–175.

Jonghe, R. de & Rasmont, P. 1983. Kreuzungsexperiment mit Hummeln des Genus *Bombus* Latreille sensu stricto (Hymenoptera, Apidae). *Phegea* **11**: 7–10.

[Jurine] 1801. Nachricht von einen neuen entomologischen Werke des Hrn. Prof. Jurine in Geneve. *Intelligenzblatt der Literatur-Zeitung* No. 21: 160–165.

Kim, C.-W. & Ito, M. 1987. On the bumblebees from the Korean Peninsula (Hymenoptera, Bombidae). *Entomological Research Bulletin* **13**: 1–42.

Kimsey, L. S. 1984. A re-evaluation of the phylogenetic relationships in the Apidae (Hymenoptera). *Systematic Entomology* **9**: 435–441.

Kirby, W. 1802. *Monographia apum angliae; or, an attempt to divide into their natural genera and families, such species of the Linnean genus* Apis *as have been discovered in England: with descriptions and observations*. **2**: 388 pp. Ipswich.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution* **36**: 1–12.

Kopelke, J.-P. 1982. Funktion der Genitalstrukturen bei *Bombus*-Arten am Beispiel von *B. lapidarius* (Linnaeus 1758) und deren Bedeutung für die Systematik (Insecta: Hymenoptera: Apidae). *Senckenbergiana biologica* **62**(1981): 267–286.

Krauth, J. 1988. *Distribution-free statistics: an application-oriented approach*. Techniques in the behavioral and neural sciences 2: xiv+381 pp. Oxford.

Krüger, E. 1917. Zur Systematik der mitteleuropäischen Hummeln (Hym.). *Entomologische Mitteilungen* **6**: 55–66.

—— 1943. Über die Genitalanhänge einiger Männchen der Untergattung *Pratobombus* O. Vogt. *Zeitschrift für Morphologie und Ökologie der Tiere* **39**: 527–545.

—— 1951. Phänoanalytische Studien an einigen Arten der Untergattung *Terrestribombus* O. Vogt (Hymen. Bomb.). I. Teil. *Tijdschrift voor Entomologie* **93**(1950): 141–197.

—— 1954. Phaenoanalytische Studien an einigen Arten der Untergattung *Terrestribombus* O. Vogt (Hymenoptera, Bombidae). II. Teil. *Tijdschrift voor Entomologie* **97**: 263–298.

—— 1956. Phaenoanalytische Studien an einigen Arten der Untergattung *Terrestribombus* O. Vogt (Hymenoptera, Bombidae). II. Teil. *Tijdschrift voor Entomologie* **99**: 75–105.

—— 1958. Phaenoanalytische Studien an einigen Arten der Untergattung *Terrestribombus* O. Vogt (Hymenoptera, Bombiidae). III. Teil. *Tijdschrift voor Entomologie* **101**: 283–344.

Kruseman, G. 1952. Subgeneric division of the genus *Bombus* Latr. *Transactions of the 9th International Congress of Entomology, Amsterdam* **1**:101–103.

Labougle, J. M. & Ayala, R. 1985. A new subgenus and species of *Bombus* (Hymenoptera: Apidae) from Guerrero, Mexico. *Folia Entomológica Mexicana* **66**: 47–55.

Latreille, P. A. 1802*a*. *Histoire naturelle des fourmis, et recueil de mémoires et d'observations sur les abeilles, les araignées, les faucheurs, et autres insectes*. xvi+445 pp. Paris.

—— 1802*b*. *Histoire naturelle, générale et particulière des crustaces et des insectes*. **3**: xii+467 pp. Paris.

Lepeletier de Saint-Fargeau, A. L. M. 1832. Observations sur l'ouvrage intitulé: 'bombi scandinaviae monographice tractato, etc., à Gustav. Dahlbom.'. *Annales de la Société Entomologique de France* **1**: 366–382.

—— 1836. *Histoire naturelle des insectes. Hyménoptères*. **1**: 547pp.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 823 pp. Holmiae.

—— 1761. *Fauna svecica sistens animalia svecica regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per classes & ordines, genera & species, cum differentiis specierum, synonymis auctorum, nominibus incolarum, locis natalium, descriptionibus insectorum*. [45]+578 pp. Stockholmiae.

Lloyd, J. E. 1981. Sexual selection: individuality, identification, and recognition in a bumblebee and other insects. *Florida Entomologist* **64**: 89–118.

Løken, A. 1961. Observations on Norwegian bumble bee nests (Hymenoptera, Apidae, *Bombus*). *Norsk entomologisk Tidsskrift* **11**: 255–268.

—— 1966. Notes on Fabrician species of *Bombus* Latr. and *Psithyrus* Lep., with designations of lectotypes (Hym., Apidae). *Entomologiske Meddelelser* **34**: 199–206.

—— 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). *Norsk entomologisk Tidsskrift* **20**: 1–218.

—— 1984. Scandinavian species of the genus *Psithyrus* Lepeletier (Hymenoptera: Apidae). *Entomologica scandinavica* suppl. 23: 45 pp.

Maa, T. 1948. On some eastern asiatic species of the genus *Psithyrus* Lepel. (Hymenoptera: Bombidae). *Notes d'entomologie chinoise* **12**: 17–37.

Mallet, J. 1986. Hybrid zones of *Heliconius* butterflies in Panama and the stability and movement of warning colour clines. *Heredity* **56**: 191–202.

Mani, M. S. 1986. *Butterflies of the Himalaya*. x+181 pp. Lancaster.

Mayr, E. 1963. *Animal species and evolution*. xiv+797 pp. Massachusetts.

Medler, J. T. 1962. Morphometric analyses of bumblebee mouthparts. *Transactions of the 11th International Congress of Entomology, Vienna* **2**: 517–521.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bulletin of the American Museum of Natural History* **82**: 157–326.

Michener, C. D. & Amir, M. 1977. The seasonal cycle and habitat of a tropical bumble bee. *Pacific Insects* **17**: 237–240.

Milliron, H. E. 1960. Recognition of bumblebee type specimens, with notes on some dubious names (Hymenoptera: Apidae). *Bulletin of the Brooklyn Entomological Society* **55**: 87–99.

—— 1961. Revised classification of the bumblebees – a synopsis (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* **34**: 49–61.

—— 1971. A monograph of the western hemisphere bumblebees (Hymenoptera: Apidae; Bombinae). I. The genera *Bombus* and *Megabombus* subgenus *Bombias*. *Memoirs of the Entomological Society of Canada* **82**: 80 pp.

Morawitz, F. 1875. [Bees.] (Mellifera). *In* Fedtschenko, A.: *Reise in Turkestan. II Zoologischer Teil*. 303 pp. Berlin.

—— 1880. Ein Beitrag zur Bienen-Fauna Mittel-Asiens. *Izvêstiya Imperatorskoi akademii nauk* **26**: 337–379.

—— 1883. Neue russisch-asiatische *Bombus*-Arten. *Trudy Russkago éntomologicheskago obshchestva* **17**: 235–245.

—— 1886. Insecta in itinere cl. N. Przewalskii in Asia centrali novissime lecta. I: Apidae. *Trudy Russkago éntomologicheskago obshchestva* **20**: 195–229.

—— 1890. Insecta a cl. G. N. Potanin in China et in Mongolia novissime lecta. XIV. Hymenoptera Aculeata. III. Apidae. *Trudy Russkago éntomologicheskago obshchestva* **24**: 349–385.

—— 1894. Supplement zur Bienenfauna Turkestans. *Trudy Russkago éntomologicheskago obshchestva* **28**: 1–87.

Morice, F. D. & Durrant, J. H. 1915. The authorship and first publication of the 'Jurinean' genera of Hymenoptera: being a reprint of a long-lost work by Panzer, with a translation into English, an introduction, and bibliographical and critical notes. *Transactions of the Entomological Society of London* **47**(1914): 339–436.

Morse, D. H. 1982. Behavior and ecology of bumble bees. *In* Hermann, H. R.: *Social insects*, **3**: 245–322. London.

Nelson, G. 1972. Phylogenetic relationship and classification. *Systematic Zoology* **21**: 227–231.

Newman, E. 1835. Attempted division of British insects into natural orders. *Entomological Magazine* **2**(1834): 379–431.

Nylander, W. 1848. Adnotationes in expositionem monographicam apum borealium. *Meddelanden af Societatis pro fauna et flora fennica* **1**: 165–282.

Obrecht, E. & Scholl, A. 1984. *Bombus lucorum* auct. ein Artenkomplex – Enzymelektrophoretische Befunde (Hymenoptera, Bombidae). *Verhandlungen der Deutschen zoologischen Gesellschaft* **77**: 266.

Owen, R. E. 1986. Gene frequency clines at X-linked or haplodiploid loci. *Heredity* **57**: 209–219.

Owen, R. E. & Plowright, R. C. 1980. Abdominal pile color dimorphism in the bumble bee, *Bombus melanopygus*. *Journal of Heredity* **71**: 241–247.

Pamilo, P., Pekkarinen, A. & Varvio, S.-L. 1987. Clustering of bumblebee subgenera based on interspecific genetic relationships (Hymenoptera, Apidae: *Bombus* and *Psithyrus*). *Annales zoologici fennici* **24**: 19–27.

Pamilo, P., Varvio-Aho, S.-L. & Pekkarinen, A. 1984. Genetic variation in bumblebees (*Bombus*, *Psithyrus*) and putative sibling species of *Bombus lucorum*. *Hereditas* **101**: 245–251.

Panfilov, D. V. 1951. [Bumble bees of the subgenus *Cullumanobombus* Vogt (Hymenoptera, Apoidea).] *Trudy Vsesoyuznogo entomologicheskogo obshchestva, Akademiya nauk SSSR* **43**: 115–128.

—— 1957. [On the geographical distribution of bumble bees (*Bombus*) in China.] *Acta geographica sinica* **23**: 221–239.

—— 1981. [Maps 91–97.] *In* Gorodkov, K. B.: [*Provisional atlas of the insects of the European part of the U.S.S.R.* Maps 73–125.] Leningrad.

—— 1982. [Maps 147–150.] *In* Gorodkov, K. B.: [*Provisional atlas of the insects of the European part of the U.S.S.R.* Maps 126–178.] Leningrad.

—— 1984. [Maps 186–192.] *In* Gorodkov, K. B.: [*Provisional atlas of the insects of the European part of the U.S.S.R.* Maps 179–221.] Leningrad.

Panzer, G. W. F. [1801]. *Favnae insectorvm germanicae initia oder Deutschlands Insecten gesammelt und herausgegeben.* **85**: 24 pls. Nurnberg.

Paterson, H. E. H. 1980. A comment on 'mate recognition systems'. *Evolution* **34**: 330–331.

—— 1985. The recognition concept of species. *In* Vrba, E. S.: *Species and speciation*, pp. 21–29. Transvaal Museum Monograph No. 4. Pretoria.

Pekkarinen, A. 1979. Morphometric, colour and enzyme variation in bumblebees (Hymenoptera, Apidae, *Bombus*) in Fennoscandia and Denmark. *Acta zoologica fennica* No. 158: 60 pp.

Pekkarinen, A., Teräs, I., Viramo, J. & Paatela, J. 1981. Distribution of bumblebees (Hymenoptera, Apidae: *Bombus* and *Psithyrus*) in eastern Fennoscandia. *Notulae Entomologicae* **61**: 71–89.

Pendlebury, H. M. 1923. Four new species of *Bombus* from the Malay Peninsular. *Journal of the Federated Malay States Museums* **11**: 64–67.

Pittioni, B. 1937. Die Hummelfauna des Kalsbachtales in Ost-Tirol. Ein Beitrag zur Ökologie und Systematik der Hummeln Mitteleuropas. *Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand* **3**: 64–115.

—— 1938. Die Hummeln und Schmarotzerhummeln der Balkan-Halbinsel mit besonderer Berücksichtigung der Fauna Bulgariens. I. Allgemeiner Teil. *Izvestiya na Tsarskite prirodonauchni instituti v Sofiya* **11**: 12–69.

—— 1939*a*. Die Hummeln und Schmarotzerhummeln der Balkan-Halbinsel. II. Spezieller Teil. *Izvestiya na Tsarskite prirodonauchni instituti v Sofiya* **12**: 49–115.

—— 1939*b*. Neue und wenig bekannte Hummeln der Paläarktis (Hymenopt., Apidae). *Konowia* **17**(1938): 244–263.

—— 1939*c*. *Tanguticobombus* subg. nov. (Hymenopt., Apidae). *Zoologischer Anzeiger* **126**: 201–205.

—— 1942. Die boreoalpinen Hummeln und Schmarotzerhummeln (Hymen., Apidae, Bombinae). I. Teil. *Izvestiya na Tsarskite prirodonauchni instituti v Sofiya* **15**: 155–218.

—— 1943. Die boreoalpinen Hummeln und Schmarotzerhummeln (Hymen., Apidae, Bombinae). II. Teil. *Izvestiya na Tsarskite prirodonauchni instituti v Sofiya* **16**: 1–77.

—— 1949. Beiträge zur Kenntnis der Bienenfauna SO-Chinas. Die Hummeln und Schmarotzerhummeln der Ausbeute J. Klapperich (1937/38). (Hym., Apoidea, Bombini). *Eos* **25**: 241–284.

Plowright, R. C. & Laverty, T. M. 1984. The ecology and sociobiology of bumble bees. *Annual Review of Entomology* **29**: 175–199.

Plowright, R. C. & Owen, R. E. 1980. The evolutionary significance of bumble bee color patterns: a mimetic interpretation. *Evolution* **34**: 622–637.

Plowright, R. C. & Pallett, M. J. 1979. Worker-male conflict and inbreeding in bumble bees (Hymenoptera: Apidae). *Canadian Entomologist* **111**: 289–294.

Plowright, R. C. & Stephen, W. P. 1973. A numerical taxonomic analysis of the evolutionary relationships of *Bombus* and *Psithyrus* (Apidae: Hymenoptera). *Canadian Entomologist* **105**: 733–743.

Podbolotskaya, M. V. in press. [The types of the species of bumble bees described by A. S. Skorikov and F. Morawitz in the collection of the Zoological Institute, Leningrad.]

Polunin, O. & Stainton, A. 1984. *Flowers of the Himalaya.* xxx+580 pp. Oxford.

Popov, V. B. 1927*a*. Zur geographischen Verbreitung von *Psithyrus vestalis* Fourcr. und *P. distinctus* Pér. (Hymenoptera, Psithyridae). *Russkoe entomologicheskoe Obozrenie* **21**: 128–132.

—— 1927*b*. New forms of the genus *Psithyrus* Lep. *Konowia* **6**: 267–274.

—— 1931. Zur Kenntnis der paläarktischen Schmarotzerhummeln (*Psithyrus* Lep.). *Eos* **7**: 131–209.

Queiroz, K. de & Donoghue, M. J. 1988. Phylogenetic systematics and the species problem. *Cladistics* **4**: 317–338.

Quilis-Pérez, M. 1927. Los apidos de España genero *Bombus* Latr. *Anales del Instituto Nacionale, Valencia* **15**: 1–119.

Radoszkowski, O. 1859. Sur quelques hyménoptères nouveaux ou peu connus de la collection du Musée de l'Académie des Sciences de St. Pétersbourg. *Byulleten' Moskovskogo obshchestva ispytatelei prirody* **32**: 479–486.

—— 1862. Sur quelques hyménoptères nouveaux ou peu connus. *Byulleten' Moskovskogo obshchestva ispytatelei prirody* **32**: 589–598.

—— 1884. Révision des armures copulatrices des mâles du genre *Bombus*. *Byulletin' Moskovskogo obshchestva ispytatelei prirody* **59**: 51–92.

—— 1893. Descriptions d'hyménoptères nouveaux. *Revue d'entomologie* **12**: 241–245.

Rasmont, P. 1981. Redescription d'une espèce méconnue de bourdon d'Europe: *Bombus lucocryptarum* Ball, 1914 n. status (Hymenoptera, Apidae, Bombinae). *Bulletin et Annales de la Société royale entomologique de Belgique* **117**: 149–154.

—— 1983*a*. Notes taxonomiques sur les bourdons (Hymenoptera, Apidae). *Bulletin et Annales de la Société royale entomologique de Belgique* **119**: 167–170.

—— 1983*b*. Catalogue commenté des bourdons de la région ouest-paléarctique (Hymenoptera, Apoidea, Apidae). *Notes Fauniques de Gembloux* **7**: 71 pp.

—— 1984. Les bourdons du genre *Bombus* Latreille sensu stricto en Europe occidentale et centrale (Hymenoptera, Apidae). *Spixiana* **7**: 135–160.

—— 1988. *Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae)*. 309+lxi pp. Ph.D. thesis, Faculté des Sciences agronomiques de l'Etat, Gembloux.

Rasmont, P., Scholl, A., Jonghe, R. de, Obrecht, E. & Adamski, A. 1986. Identité et variabilité des mâles de bourdons du genre *Bombus* Latreille sensu stricto en Europe occidentale et centrale (Hymenoptera, Apidae, Bombinae). *Revue suisse Zoologie* **93**: 661–682.

Reinig, W. F. 1930. Untersuchungen zur Kenntnis der Hummelfauna des Pamir-Hochlandes. Zoologische Ergebnisse der deutsch-russischen Alai-Pamir-Expedition der Notgemeinschaft der Deutschen Wissenschaft und der Akademie der Wissenschaften der U.d.S.S.R. *Zeitschrift für Morphologie und Ökologie der Tiere* **17**: 68–123.

—— 1934. Entomologische Ergebnisse der deutsch-russischen Alai-Pamir-Expedition, 1928 (III). 7. Hymenoptera VIII (Gen. *Bombus* Fabr.). Nachtrag. *Deutsche entomologische Zeitschrift* **1933**: 163–174.

—— 1935. On the variation of *Bombus lapidarius* L. and its cuckoo, *Psithyrus rupestris* Fabr., with notes on mimetic similarity. *Journal of Genetics* **30**: 321–356.

—— 1936. Beiträge zur Kenntnis der Hummelfauna von Mandschukuo (Hym. Apid.). *Mitteilungen der Deutschen entomologischen Gesellschaft* **7**: 2–10.

—— 1937. Entomologische Sammelergebnisse der deutschen Hindukusch-Expedition 1935 der deutschen Forschungsgemeinschaft. Hymenoptera. Apidae. *Arbeiten über morphologische und taxonomische Entomologie aus Berlin-Dahlem* **4**: 190.

—— 1939. Die Evolutionsmechanismen, erläutert an den Hummeln. *Verhandlungen der Deutschen zoologischen Gesellschaft* Suppl. **12**: 170–206.

—— 1940. Beiträge zur Kenntnis der Hummelfauna von Afghanistan. (Hym., Apid.). (Ergebnisse der Reise von H. und E. Kotzsch in den Hindukusch im Jahre 1936.) *Deutsche entomologische Zeitschrift* **1940**: 224–235.

—— 1967. Zur Kenntnis der Hummelfaunen einiger Gebirge West-Kleinasiens (Hym., Apidae). *Nachrichtenblatt der Bayerischen Entomologen* **16**: 81–90.

—— 1970. Bastardierungszönen und Mischpopulationen bei Hummeln (*Bombus*) und Schmarotzerhummeln (*Psithyrus*). (Hymenopt., Apidae). *Mitteilungen der Münchener entomologischen Gesellschaft* **59**: 1–89.

—— 1971. Zur Faunistik und Zoogeographie des Vorderen Orients. 3. Beitrag zur Kenntnis der Hummeln und Schmarotzerhummeln Anatoliens (Hym., Apidae). *Veroffentlichungen der Zoologischen Staatssammlung* **15**: 139–165.

—— 1974. Faunistische und zoogeographische Studien in Kleinasien. 5. Auf Hummelfang im Taurus (*Bombus* Latr., 1802 et *Psithyrus* Lep., 1832; Hym., Apidae). *Nachrichtenblatt der Bayerischen Entomologen* **23**: 67–80.

—— 1981. Synopsis der in Europa nachgewiesenen Hummel- und Schmarotzerhummelarten (Hymenoptera, Bombidae). *Spixiana* **4**: 159–164.

Reinig, W. F. & Rasmont, P. 1988. Beitrag zur Kenntnis der Bergwaldhummel *Alpigenobombus wurfleini* [sic] (Radoszkowski, 1859) (Hymenoptera, Apidae, Bombinae). *Spixiana* **11**: 37–67.

Rice, W. R. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *In* Rosenzweig, M. L.: Habitat selection and evolutionary processes. A symposium. *Evolutionary Ecology* **1**: 301–314.

Richards, K. W. 1973. Biology of Bombus polaris *Curtis and* B. hyperboreus Schönherr at Lake Hazen, Northwest Territories (Hymenoptera: Bombini). *Quaestiones entomologicae* **9**: 115–157.

Richards, O. W. 1927*a*. Sexual selection and allied problems in the insects. *Biological Reviews* **2**: 298–364.

—— 1927*b*. The specific characters of the British humblebees (Hymenoptera). *Transactions of the Entomological Society of London* **75**: 233–268.

—— 1928*a*. *Bombus* and *Volucella* in the Himalayas. *Entomologist's Monthly Magazine* **64**: 107–108.

—— 1928*b*. On a collection of humble-bees (Hymenoptera, Bombidae) made in Ladakh by Col. R. Meinertzhagen. *Annals and Magazine of Natural History* (10) **2**: 333–336.

—— 1928*c*. A revision of the European bees allied to *Psithyrus quadricolor*, Lepeletier (Hymenoptera, Bombidae). *Transactions of the Entomological Society of London* **76**: 345–365.

—— 1929*a*. On two new species of humble-bees in the collection of the British Museum, constituting a new group of the genus *Psithyrus*, Lep. (Hymenoptera, Bombidae). *Annals and Magazine of Natural History* (10) **3**: 139–143.

—— 1929*b*. A revision of the humble-bees allied to *Bombus orientalis*, Smith, with the description of a new subgenus. *Annals and Magazine of Natural History* (10) **3**: 378–386.

—— 1930. The humble-bees captured on the expeditions to Mt. Everest (Hymenoptera, Bombidae). *Annals and Magazine of Natural History* (10) **5**: 633–658.

—— 1931. A new species of Indian humble-bee in the collection of the British Museum (Hymenoptera, Bombidae). *Annals and Magazine of Natural History* (10) **8**: 529–533.

—— 1934. Some new species and varieties of oriental humble-bees (Hym. Bombidae). *Stylops* **3**: 87–90.

—— 1951. The 3rd Danish expedition to Central Asia. Zoological results 5. Bombidae (Insecta) from Afghanistan. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn* **113**: 191–199.

—— 1968. The subgeneric divisions of the genus *Bombus* Latreille (Hymenoptera: Apidae). *Bulletin of the British Museum (Natural History)* (Entomology) **22**: 209–276.

Rosen, D. E. 1979. Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. *Bulletin of the American Museum of Natural History* **162**: 267–375.

Roubik, D. W. 1989. *Ecology and natural history of tropical bees*. x+514 pp. Cambridge.

Ruttner, F. 1988. *Biogeography and taxonomy of honeybees*. xii+284 pp. London.

Sakagami, S. F. 1972. Bumble bees collected by the California Academy-Lingnan dawn-redwood expedition to central west China, 1948. (Hymenoptera: Apidae). *Pan-Pacific Entomologist* **48**: 153–174.

—— 1975. Some bumblebees from Korea with remarks on the Japanese fauna (Hymenoptera, Apidae). *Annales historico-naturales Musei nationalis hungarici* **67**: 293–316.

—— 1976. Specific differences in the bionomic characters of bumblebees. A comparative review. *Journal of the Faculty of Science, Hokkaido University* (6) **20**: 390–447.

Sakagami, S. F. & Ishikawa R. 1969. Note préliminaire sur la répartition géographique des bourdons japonais, avec descriptions et remarques sur quelques formes nouvelles ou peu connues. *Journal of the Faculty of Science, Hokkaido University* (6) **17**: 152–196.

Sakagami, S. F. & Ito, M. 1981. Specific and subgeneric variations in tibial corbiculation of male bumblebees (Hymenoptera:

Apidae), an apparently functionless character. *Entomologica scandinavica* Suppl. **15**: 365–376.

Sakagami, S. F. & Yoshikawa, K. 1961. Bees of Xylocopinae and Apinae collected by the Osaka City University Biological Expedition to Southeast Asia 1957–58, with some biological notes. *Nature and Life in Southeast Asia* **1**: 409–444.

Sandhouse, G. A. 1943. The type species of the genera and subgenera of bees. *Proceedings of the United States National Museum* **92**: 519–619.

Schmid, F. 1958. Trichoptères du Pakistan. *Tijdschrift voor Entomologie* **101**: 181–221.

Schmiedeknecht, H. L. O. 1882. *Apidae europaeae (die Bienen Europa's) per genera, species et varietates, dispositae atque descriptae.* **1**(4): pp. 235–314. Berlin.

Scholl, A. & Obrecht, E. 1983. Enzymelektrophoretische Untersuchungen zur Artabgrenzung im *Bombus lucorum* – Komplex (Apidae, Bombini). *Apidologie* **14**: 65–78.

Schremmer, F. 1972. Beobachtungen zum Paarungsverhalten der Männchen von *Bombus confusus* Schenck. *Zeitschrift für Tierpsychologie* **31**: 503–512.

Schweinfurth, U. 1957. *Die horizontale und vertikale Verbreitung der Vegetation im Himalaya.* xii+372 pp. Bonn.

Searle, M. P., Cooper, D. J. W. & Rex, A. J. 1988. Collision tectonics of the Ladakh-Zanskar Himalaya. *Philosophical Transactions of the Royal Society of London* (A) **326**: 117–150.

Seidl, W. B. 1837. Die in Böhmen vorkommenden Hummelarten. *Beiträge zur gesammten Natur-und Heilwissenschaft* **2**: 65–73.

Shapiro, A. M. & Porter, A. H. 1989. The lock-and-key hypothesis: evolutionary and biosystematic interpretation of insect genitalia. *Annual Review of Entomology* **34**: 231–245.

Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences.* xvii+312 pp. London.

Skorikov, A. S. 1910*a*. [*Bombus mendax* Gerst. and its variations (Hymenoptera, Bombidae).] *Russkoe éntomologicheskoe Obozrênie* **9**(1909): 328–330.

—— 1910*b*. [New forms of bumble bees (Hymenoptera, Bombidae).] *Russkoe éntomologicheskoe Obozrênie* **9**(1909): 409–413.

—— 1912*a*. *Bombus lapponicus* (F.) et ses formes ([queens] et [workers]) (Hymenoptera, Bombidae). *Russkoe éntomologicheskoe Obozrênie* **12**: 95–102.

—— 1912*b*. Neue Hummelformen (Hymenoptera, Bombidae). IV. *Russkoe éntomologicheskoe Obozrênie* **12**: 606–610.

—— 1914*a*. Les formes nouvelles des bourdons (Hymenoptera, Bombidae). VI. *Russkoe éntomologicheskoe Obozrênie* **14**: 119–129.

—— 1914*b*. *Subterraneobombus fedtschenkoi* (F. Mor.), un bourdon de Turkestan peu connu (Hymenoptera, Bombidae). *Russkoe éntomologicheskoe Obozrênie* **14**: 287–292.

—— 1914*c*. *Pratobombus leucopygos* [sic] (F. Mor.) et ses variations (Hymenoptera, Bombidae). *Russkoe éntomologicheskoe Obozrênie* **14**: 293–294.

—— 1914*d*. Contribution à la faune des bourdons de la partie méridionale de la province Maritime. *Russkoe éntomologicheskoe Obozrênie* **14**: 398–407.

—— 1922. [Palaearctic bumble bees. Part I. General biology (including zoogeography).] *Izvestiya Severnoi oblastnoi stantsii zashchity rastenii ot vreditelei* **4**: 1–160.

—— 1931. Die Hummelfauna Turkestans und ihre Beziehungen zur zentralasiatischen Fauna (Hymenoptera, Bombidae). *Abhandlungen der Pamir-Expedition 1928* **8**: 175–247.

—— 1933*a*. Zur Hummelfauna Japans und seiner Nachbarländer. *Mushi* **6**: 53–65

—— 1933*b*. Zur Fauna und Zoogeographie der Hummeln des Himalaya. *Doklady Akademii nauk SSSR* **5**: 243–248.

—— 1938*a*. Zoogeographische Gesetzmässigkeiten der Hummelfauna im Kaukasus, Iran und Anatolien (Hymenoptera, Bombinae). *Entomologicheskoe Obozrenie* **27**: 145–151.

—— 1938*b*. Vorläufige Mitteilung über die Hummelfauna Burmas. *Arkiv för zoologi* **30B**: 1–3.

Smith, E. L. 1970. Evolutionary morphology of the external insect genitalia. 2. Hymenoptera. *Annals of the Entomological Society of America* **63**: 1–27.

Smith, F. 1852*a*. Descriptions of some new and apparently undescribed species of hymenopterous insects from north China, collected by Robert Fortune, Esq. *Transactions of the Entomological Society of London* **2**: 33–45.

—— 1852*b*. Descriptions of some hymenopterous insects from northern India. *Transactions of the Entomological Society of London* **2**: 45–48.

—— 1854. *Catalogue of hymenopterous insects in the collection of the British Museum. Part II. Apidae.* 266(199–465) pp. London.

—— 1878*a*. *Scientific results of the Second Yarkand Mission. Hymenoptera.* 22 pp. Calcutta.

—— 1878*b*. List of the Hymenoptera obtained by Mr Ossian Limborg east of Maulmain, Tenasserim Provinces, during the months of December 1876, January, March and April 1877, with descriptions of new species. *Journal of the Asiatic Society of Bengal* **47**: 167–169.

—— 1879. *Descriptions of new species of Hymenoptera in the collection of the British Museum.* xxi+240 pp. London.

Snodgrass, R. E. 1941. The male genitalia of Hymenoptera. *Smithsonian Miscellaneous Collections* **99**(14): 86 pp.

Splitter, L. J. 1982. *Natural kinds and biological species.* 289 pp. D.Phil. thesis, University of Oxford.

Stiles, E. W. 1979. Evolution of color pattern and pubescence characteristics in male bumblebees: automimicry vs. thermoregulation. *Evolution* **33**: 941–957.

Svensson, B. G. 1979. Patrolling behaviour of bumble bee males (Hymenoptera, Apidae) in a subalpine/alpine area, Swedish Lapland. *Zoon* **7**:67–94.

Templeton, A. R. 1981. Mechanisms of speciation – a population genetic approach. *Annual Review of Ecology and Systematics* **12**: 23–48.

—— 1989. The meaning of species and speciation: a genetic perspective. *In* Otte, D. & Endler, J. A.: *Speciation and its consequences*, pp. 3–27. Sunderland.

The Times Atlas of the World 1987. Comprehensive edn, 7th edn. xlvii+123 pls+228 pp. London.

Thomson, C. G. 1872. *Hymenoptera scandinaviae. (*Apis *Lin.).* **2**: 286 pp. Lund.

Thornhill, R. & Alcock, J. 1983. *The evolution of insect mating systems.* ix+547 pp. London.

Thorp, R. W. 1969. The identity of *Bombus vandykei* (Hymenoptera: Apidae). *Pan-Pacific Entomologist* **45**: 87–96.

Thorp, R. W., Horning, D. S. & Dunning, L. L. 1983. Bumble bees and cuckoo bumble bees of California (Hymenoptera: Apidae). *Bulletin of the California Insect Survey* No. 23: viii+79 pp.

Tkalců, B. 1959. Eine neue Art der Gattung *Psithyrus* Lep. aus Korea (Hymenoptera, Bombinae). *Casopis Ceskoslovenské spolecnosti entomologické* **56**: 251–254.

—— 1960. Remerques sur quelques espèces de bourdons de Chine (Hymenoptera, Bombinae). *Bulletin de la Société entomologique de Mulhouse* **1960**: 66–71.

—— 1961. Zur Hummelfauna der Umgebung Kuku-Nors (Hymenoptera, Bombinae). *Casopis Ceskoslovenské spolecnosti entomologické* **58**: 344–379.

—— 1962. Contribution à l'étude des bourdons du Japon (I) (Hymenoptera, Apoidea). *Bulletin de la Société entomologique de Mulhouse* **1962**: 81–100.

—— 1965. Contribution à l'étude des bourdons du Japon (II) (Hymenoptera, Apoidea). *Bulletin de la Société entomologique de Mulhouse* **1965**: 1–14.

—— 1967. Sur deux espèces de bourdons décrites par William Nylander (Hymenoptera, Apoidea: *Bombus*). *Bulletin de la Société entomologique de Mulhouse* **1967**: 41–58.

—— 1968*a*. Neue Arten der Unterfamilie Bombinae der paläarktischen Region (Hymenoptera, Apoidea). *Sborník Entomologického oddeleni Národního musea v Praze* **65**: 21–51.

—— 1968*b*. Revision der vier sympatrischen, homochrome geographische Rassen bildenden Hummelarten SO-Asiens (Hymenoptera, Apoidea, Bombinae). *Annotationes Zoologicae et Botanicae* **52**: 1–31.

—— 1969*a*. Beiträge zur Kenntnis der Fauna Afghanistans (Sammelergebnisse von O. Jakes 1963–64, D. Povolny 1965, D. Povolny & Fr. Tenora 1966, J. Simek 1965–66, D. Povolny, J. Geisler, Z. Sebek & Fr. Tenora 1967). Bombinae, Apoidea, Hym. *Casopis Moravského musea v Brne* **53**(1968): 189–210.

—— 1969*b*. Ergebnisse der Albanien-Expedition 1961 des Deutschen Entomologischen Institutes. 78. Beitrag. Hymenoptera: Apidae IV (Bombinae). *Beiträge zur Entomologie* **19**: 887–916.

—— 1972. Arguments contre l'interprétation traditionelle de la phylogénie des abeilles (Hymenoptera, Apoidea). Première partie, introduction et exposés fondamentaux. *Bulletin de la Société entomologique de Mulhouse* **1972**: 17–28.

—— 1973. Taxonomie von *Pyrobombus brodmannicus* (Vogt) (Hymenoptera, Apoidea, Bombinae). *Acta entomologica bohemoslovaca* **70**: 259–268.

—— 1974*a*. Ergebnisse der 1. und 2. mongolisch-tschechoslowakischen entomologisch-botanischen Expedition in der Mongolei. Nr. 29: Hymenoptera, Apoidea, Bombinae. *Sborník faunistickych prací Entomologického oddelení Národního musea v Praze* **15**: 25–57.

—— 1974*b*. Eine Hummel-Ausbeute aus dem Nepal-Himalaya (Insecta, Hymenoptera, Apoidea, Bombinae). *Senckenbergiana biologica* **55**: 311–349.

—— 1975. Beitrag zur Kenntnis der Hummelfauna der französischen Basses-Alpes (Hymenoptera, Apoidea, Bombinae). *Sborník Slovenského Narodného Muzea* **20**(1974): 167–186.

—— 1987. Nouveaux synonymes chez les Bombinae (Hymenoptera, Apoidea). *Bulletin de la Société entomologique de Mulhouse* **1987**: 59–64.

—— 1989. Neue Taxa asiatischer Hummeln (Hymenoptera, Apoidea). *Acta entomologica bohemoslovaca* **86**: 39–60.

Troll, C. 1972. The three-dimensional zonation of the himalayan system. *In* Troll, C.: *Geoecology of the high-mountain regions of Eurasia*, pp. 264–275. Proceedings of the Symposium of the International Geographical Union Commission on High-Altitude Geoecology November, 20–22, 1969 at Mainz, Band 4. Wiesbaden.

Verrell, P. A. 1988. Stabilizing selection, sexual selection and speciation: a view of specific-mate recognition systems. *Systematic Zoology* **37**: 209–215.

Villalobos, E. M. & Shelly, T. E. 1987. Observations on the behavior of male *Bombus sonorus* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* **60**: 541–548.

Vogt, O. 1909. Studien über das Artproblem. 1. Mitteilung. Über das Variieren der Hummeln. 1. Teil. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* **1909**: 28–84.

—— 1911. Studien über das Artproblem. 2. Mitteilung. Über das Variieren der Hummeln. 2. Teil. (Schluss). *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* **1911**: 31–74.

Vrba, E. S. 1985. Introductory comments on species and speciation. *In* Vrba, E. S.: *Species and speciation*, pp. ix–xviii. Transvaal Museum Monograph No. 4. Pretoria.

Walckenaer, C. A. 1802. *Faune Parisienne, insectes. Ou histoire abrégée des insectes des environs de Paris, classés d'après le système de Fabricius; précédée d'un discours sur les insectes en général, pour servir d'introduction à l'étude de l'entomologie.* **2**: xxii+438 pp. Paris.

Wang, S.-f. 1979. Three new species of bumble bees from Tibet. *Acta entomologica sinica* **22**: 188–191.

—— 1982. Hymenoptera: Apidae – *Bombus*. *Insects of Xizang* **2**: 427–447.

—— 1987. *Bombus*. *In* Huang, F.-s.: *Forest insects of Yunnan*, pp. 1378–1381. Yunnan.

—— 1988. Hymenoptera: Apidae – genus *Bombus*. *In* Huang, F.-s.: *Insects of Mt. Namjagbarwa region of Xizang*, pp. 553–557. Beijing.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* **58**: 155–183.

Wille, A. & Michener, C. D. 1973. The nest architecture of stingless bees with special reference to those of Costa Rica (Hymenoptera, Apidae). *Revista de biología tropical* **21** suppl. 1: 278 pp.

Williams, P. H. 1981. *On the evolution and ecology of bumblebees (Hymenoptera: Apidae)*. 60 pp. Undergraduate dissertation, University of Cambridge.

—— 1985. A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae). *Systematic Entomology* **10**: 239–255.

—— 1988. Habitat use by bumble bees (*Bombus* spp.). *Ecological Entomology* **13**: 223–237.

—— 1989. Why are there so many species of bumble bees at Dungeness? *Botanical Journal of the Linnean Society* **101**: 31–44.

Willmer, P. G. 1983. Thermal constraints on activity patterns in nectar-feeding insects. *Ecological Entomology* **8**: 455–469.

Wilson, E. O. & Brown, W. L. 1953. The subspecies concept and its taxonomic application. *Systematic Zoology* **2**: 97–111.

Winston, M. L. & Michener, C. D. 1977. Dual origin of highly social behavior among bees (Hymenoptera/Apidae/phylogeny). *Proceedings of the National Academy of Sciences of the United States of America* **74**: 1135–1137.

Yasumatsu, K. 1951. *Bombus* and *Psithyrus* of Shansi, N. China (Hymenoptera, Apidae). *Mushi* **22**: 59–62.

Zander, E. 1900. Beiträge zur Morphologie der männlichen Geschlechtsanhänge der Hymenopteren. *Zeitschrift für wissenschaftliche Zoologie* **67**: 461–489.