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The Bumblebee Fauna of the Kurile Islands (Hymenoptera : Apidae)[1,3]

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伊藤誠夫・坂上昭一

Abstract A total of 14 bumblebee taxa (11 species) are recognized from the Kurile Islands, including *Bombus beaticola shikotanensis* ssp. nov. Concerning the distributional patterns, the cool-temperate elements hardly attain northward beyond the Kunashiri Strait, while the boreal elements common to Kamtchatka do not reach south of the Urup Strait. Some factors which are presumably responsible for this chorological gradient are discussed.

Introduction

Although the bumblebees are one of the most outstanding northerly predominant insect groups, their taxonomic and faunistic studies in northern Asia are still far from satisfaction except for Japan (32, 34, 35, 45, 47). As for the Kurile Islands lying between Hokkaido and Kamtchatka, most previous contributions (14, 16, 22, 28, 31, 42) are taxonomically imperfect, involving many misidentifications and use of invalid names. The distribution of each species has also been known from a limited number of records. The present paper aims to give an up-to-date revision on the taxonomy and chorology of the non-parasitic bumblebees, the genus *Bombus*.

Materials Examined

The specimens placed at our disposal belong to the two collections: EIHU (Entomological Institute, Faculty of Agriculture, Hokkaido University), 288 specimens by the courtesy of Dr. Sadao Takagi and Dr. Toshio Kumata. Collected by K. Doi, S. Iwata, H. Kono, S. Kuwayama, I. Masaki, S. Matsumura, Y. Sugihara, S. Sumiyama, K. Takahashi, M. Tatewaki and T. Uchida. HAES (Hokkaido National Agricultural Experiment Station), 163 specimens, by the kind intermediary of Dr. Satoru Kuwayama. Collected by S. Kuwayama, Y. Sugihara and S. Sumiyama. Further, some other specimens from Europe, East Siberia, Kamtchatka and Hokkaido were used for comparison. Among them those loaned from ZASL (Zoological Institute, Academy of Sciences, Leningrad) by the curtesy of Dr. Yu. A. Pesenko were of particular importance. If necessary the specimens of HAES and ZASL are henceforth

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[3] Studies on systematics and zoogeography of Asian Bumblebees II

specified respectively with single and double asterisks.

Before going further, we would like to express our cordial thanks to all the persons cited above who gave us, either directly or indirectly, opportunities to examine the valuable materials.

Explanations

1. The distributional records were available from most of the major Islands (Table 1, Fig. 55 D). Henceforth, the term "record" means a group of specimens collected from the same locality on the same date. 2. The insular names (in Japanese usage) are abbreviated by three capitals (full names given parenthetically). SKT (Shikotan), KNS (Kunashiri), ETR (Etorofu), URP (Urup), CHR (Chiripoi), SSR (Simshir), KET (Ketoi), RSH (Rasshua), SSK (Shashikotan), ONK (Onnekotan), PRM (Paramushir), SMS (Shumshu), ALD (Alaido). 3. Synonymic list involves only the original description and some important contributions. 4. For some poorly known species, the structural diagnoses are given synoptically with allied species, leaving precise redescriptions elsewhere. 5. Coloration always means that of hair coat.

Species Obtained

Bombus* (*Bombus*) *florilegus Panfilov

Bombus terrestris var. *japonicus* Friese 1909 (nec Dalla Torre 1890), Deutsch. Ent. Zeitschr. 1909: 674; Friese & Wagner 1910: 48. —*Bombus japonicus*, Skorikov 1933: 57; Kuwayama 1967: 210; Krivolutskaja 1973: 149. —*Bombus terrestris*, Sakagami 1954 (nec Linné 1758, partim): 84. —*Bombus florilegus* Panfilov 1956: 1334; Tkalců 1962: 92; —1965: 12; Sakagami & Ishikawa 1969: 167.

Specimens examined SKT 1♀ 5♀♀: Shakotan, 7. VII, 1♀; 23. VII '25, 4♀♀; Shikotan 23–27. VII '35, 1♀. KNS 1♀ 1♂; Kotankei, 18. VIII '40, 1♂*; Kunashiri, VIII '36, 1♀. ETR 21♀♀ 59♀♀ 73♂♂: Bettobu 11–13. VII '36, 1♀; Iriribushi, 17. VII '27, 1♀; Naipo, 7. VII '35, 4♀♀; Porosu, 14–15. VII '35, 6♀♀ 1♂; Rubetsu, 28. VIII '40, 16♀♀ 2♂♂*; Rubetsu-Toshimoe, 2–10. VII '35, 1♀; 29. VIII, 5♀♀ 30♂♂*; 29–30. VIII '40, 16♀♀ 16♂♂*, 4♀♀ 5♂♂; Rubetsu-Shana, 31. VIII '40, 1♀ 1♂; Shana, 12. VII, 1♀; 10. VIII '27, 2♀♀; 11–20. VII '35, 5♀♀ 2♀♀; 22–25. VII '36, 1♀; 1–3. IX. 1♀*. IX '40, 1♀; Shibetoru, 5–7. IX, 3♀♀ 1♂*; 6–7. IX '40, 2♀♀ 1♂; 10. VII '27, 2♀♀ 1; Toshimoe, 3–9. VII '35, 1♀; 29. VIII, 1♀ 3♂♂*; 29–30. VIII '40, 2♀♀ 5♀♀ 11♂♂*; Yanketou-Mt. Chirip, 3. IX '40, 1♂*. URP 1♀ 31♀♀ 3♂♂: Onsenzaki, 10. IX '27 1♂; Tokotan, 4. IX '27, 1♂; 27. VIII '29, 1♀ 1♂; 9–23. VIII '36, 1♀ 29♀♀; Urup, 2. IX '27, 1♀. CHR 10♀♀: Sha(?)-Bay, 20. VIII, 8♀♀; VII '37, 2♀♀. SSR 3♀♀ 14♀♀ 1♂: Broutona-Bay, 26. VII, 1♀; 28. VII '28, 1♀; 26. VII, 2♀♀; 29. VII, 1♀; VII, 1♀; 5. VIII '37, 8♀♀ 1♂; Higashi'ura, 2. VIII '37, 1♀ 2♀♀. KET 6♀♀ 1♂: Ketoi, 1. VIII, 1♀; 1. IX, 4♀♀; 2. IX '29, 1♀ 1♂. RSH 5♀♀: Rasshua, 10. VIII, 1♀; 18. VIII '29, 4♀♀. ONK 2♀♀ 2♀♀: Onnekotan, 12. VII, 2♀♀ 1♀; 16. VII '37, 1♀.

Apparently the most predominant species in the southern islands except for KNS (Table 1, Fig. 1 A).

Structure Morphologically distinguished from *B. l. albocinctus* in several

Table 1. Number of records and, in parentheses, of specimens (both sex combined) of each species from each island. Subspecific names are omitted. Islands are ordered approximately from south to north, and species (given by abbreviated subgeneric names) also from southerly to northerly predominants

Species Islands	KNS	SKT	ETR	URP	CHR	SSR	KET	RSH	SSK	ONK	PRM	SMS	ALD	Total no. of records (of specimens)
Th. pseuaobaicalensis	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	1 (1)
Dv. diversus	5 (9)	—	—	—	—	—	—	—	—	—	—	—	—	5 (1)
Mg. yezoensis	5 (6)	—	—	—	—	—	—	—	—	—	—	—	—	5 (6)
Bo. hypocrita	6 (12)	1 (1)	—	—	—	—	—	—	—	—	—	—	—	7 (13)
Pr. beaticola	3 (8)	2 (2)	—	—	—	—	—	—	—	—	—	—	—	5 (10)
Th. schrencki	11 (25)	8 (10)	9 (15)	5 (13)	—	—	—	—	—	—	—	—	—	33 (63)
Pr. hypnorum	1 (1)	—	—	—	—	—	—	—	—	4 (14)	—	—	—	5 (15)
Bo. florilegus	2 (2)	3 (6)	21 (153)	5 (35)	2 (10)	7 (18)	3 (7)	2 (5)	—	2 (4)	—	—	—	47 (240)
Pr. oceanicus	—	—	5 (7)	1 (45)	1 (1)	—	—	—	—	—	2 (2)	—	1 (1)	10 (56)
Bo. lucorum	—	—	—	—	—	1 (3)	1 (1)	1 (1)	1 (2)	3 (9)	8 (10)	3 (3)	1 (4)	19 (33)
Mg. tichenkoi	—	—	—	—	—	—	—	—	—	—	2 (4)	1 (1)	—	3 (5)
Total no. of records	24	13	26	7	2	7	4	2	1	6	10	4	1	107
Total no. of specimens	(64)	(19)	(175)	(93)	(11)	(21)	(8)	(6)	(2)	(27)	(16)	(4)	(5)	(451)
Area (km²)	1500	255	3139	1429	33	343	71	63	122	441	2042	386	156	

characters (Table 2, Figs. 3~31).

Coloration Mostly black, collaris and T$_2$ white to pale yellow. Color variation given by Sakagami (31) actually included two taxa, *B. florilegus* and *B. l. albocinctus*. These composite materials were re-examined together with some others. A remarkable variation is seen in the degree of admixture of pale hairs on apical metasomal terga, particularly T$_5$ (Fig. 2 left). Queens constantly melanic, while workers and males quite variable. In workers and to some degree in males, albinism is most advanced in SKT, followed by ETR and the middle Kuriles (SSR, KET and RSH), but absent in URP and CHR. This indicates the occurrence of a subtle geographical bimodality

Table 2. Synoptic diagnoses of *B. florilegus*, *B. l. albocinctus* and

Female

Character	*florilegus*
Pubescence	slightly sparser
Apical part of clypeal disc	mildly convex
Mandible Area between basal area and the basal end of median furrow Ventral rim Incisula lateralis	weakly elevated, separating the furrow from basal area mildly bent inward weaker (Fig. 3)
Antennal flagella seen laterally	F$_2$ apparently shorter than F$_3$ (Fig. 6)
Hind tibia seen ventrally Apicodorsal angle Bristles along apical margin Apical part of outer surface	indistinctly produced (Fig. 9) slightly longer and denser (Fig. 9) widely flattened, but distinctly sloping ventrally near ventral margin

Male

Size	larger
Maximal length of hairs on dorsal margin of mid tibia	longer than width of tibia
Punctation on disc of T$_4$~T$_6$	denser, with interspaces more or less shagreened
Apical projection of S$_7$	strongly produced with relatively dense hairs (Figs. 13-15)
Basal projection of spatha	relatively broad and short, surface not much polished (Figs. 20, 21)
Apicodorsal end of penis valve	posteriorly extending strongly, laterally bent weakly (Figs. 26, 27)
Subinner-apicodorsal area of stipes	distinctly elevated

in coloration, suggesting the differentiation of white tailed peripheral populations from the black tailed ones in URP and CHR.

Specific Distribution Subendemic to Kurile Islands : Middle- and Southern Kuriles, easternmost Hokkaido.

Bombus* (*Bombus*) *lucorum albocinctus Smith

Bombus albocinctus Smith, 1854, Catalog. Hymen. Brit. Mus. II : 397, n. 41 ; Friese 1905 : 517. —*Terrestribombus lucorum albocinctus*, Bischoff 1930 : 4. —*Bombus lucorum* Rasse *albocinctus*, Krüger 1950 : 196. —*Bombus* (s. str.) *albocinctus*, Krivolutskaja 1973 : 149.

Specimens examined SSR 3♀♀ : Higashi'ura, 2. VIII '37. KET 1♀ : Ketoi, 1. X '29. RSH

B. l. lucorum (T = tergum, S = sternum, F = flagellum)

l. albocinctus	*l. lucorum*
slightly denser	=*l. albocinctus*
more or less flattened	intermediate or as in *l. albocinctus*
flattened, not separating the furrow from basal area more strongly bent inward stronger (Fig. 4)	=*florilegus* =*albocinctus* intermediate or as in *albocinctus* (Fig. 5)
F_2 only slightly shorter than F_3 (Fig. 7)	intermediate or as in *albocinctus* (Fig. 8)
more or less distinctly produced (Fig. 10, 11) slightly shorter and sparser more widely flattened, not or little sloping ventrally near ventral margin	=*albocinctus* (Fig. 12) =*albocinctus* (Fig. 12) =*albocinctus*
smaller	=*albocinctus*
shorter than or as long as width of tibia	=*albocinctus*
sparser, with interspaces strongly shagreened	=*albocinctus*
less strongly produced with sparser hairs (Figs. 16, 17)	weakly produced, intermediately haired (Figs. 18, 19)
narrower and longer, surface very polished (Figs. 22, 23)	intermediate or as in *albocinctus* in shape, not much polished (Figs. 24, 25)
posteriorly extending weakly, laterally bent more strongly (Figs. 28, 29)	intermediate or as in *albocinctus* (Figs. 30, 31)
obscurely elevated	=*albocinctus*

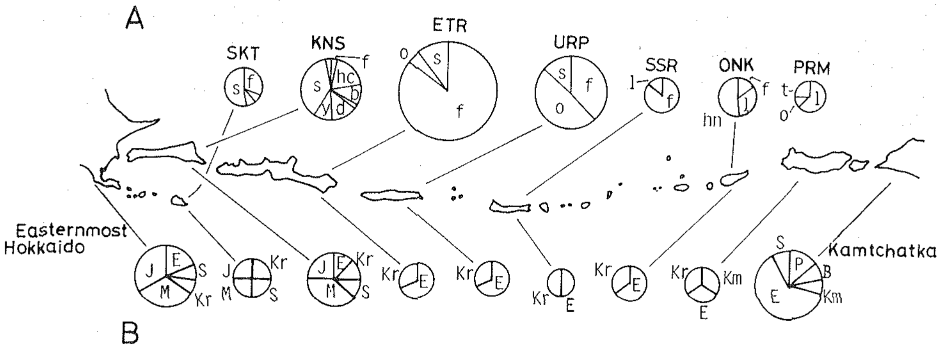


Fig. 1. A. Relative abundance of each species, by the number of individuals. s : *B. schrencki*, f : *B. florilegus*, hc : *B. hypocrita*, y : *B. yezoensis*, b : *B. beaticola*, d : *B. diversus*, o : *B. oceanicus*, hn : *B. hypnorum klutschians*, l : *B. lucorum*, t : *B. tichenkoi*. B. Relative abundance of species group. P : Circumpolar, B : Boreal Eurosiberian, E : Eurosiberian, S : Siberian, M : Manchurian, Km : Endemic or subendemic to Kamtchatka, Kr : Endemic or subendemic to the Kuriles, J : Endemic or subendemic to Japan

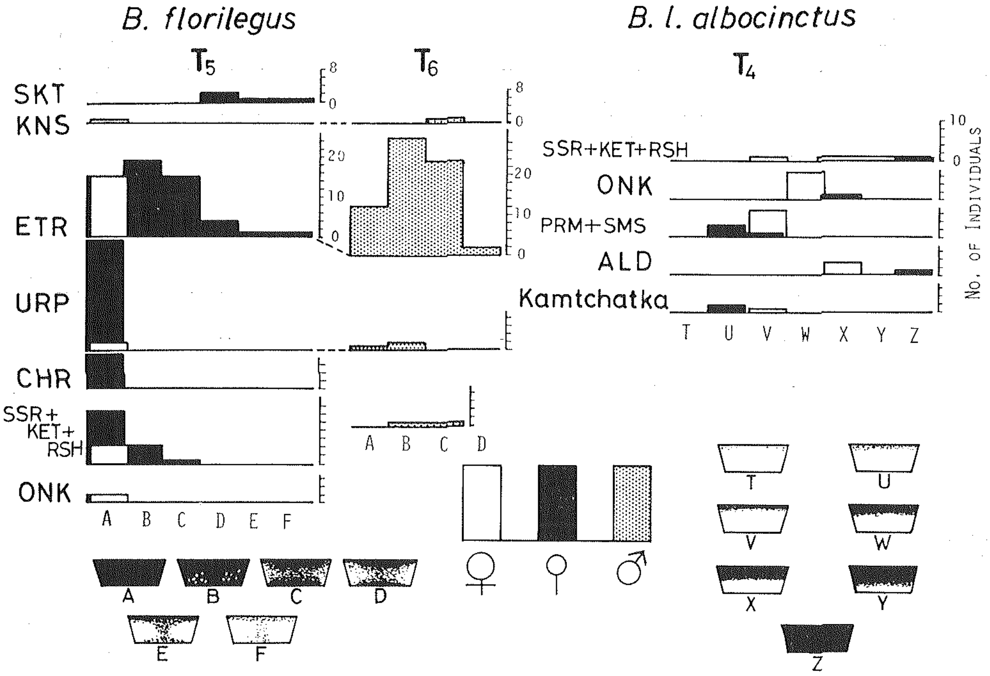


Fig. 2. Color variation in *B. florilegus* (left) and *B. lucorum albocinctus* (right)

1♀ : Rashua, 10. VIII '29. SSK 2♀♀ : Shashikotan, VI '37. ONK 9♀♀ : Onnekotan, 1♀ ; 12. VIII '37, 4♀♀ ; Shakko (?)-gawa, 16. VII '37, 4♀♀. PRM 6♀♀ 4♀♀ : Kujira-Bay, 18. VII '26, 1♀ ; Murakami-Bay, 1♀, 22. VII, 1♀ 1♀ ; 25. VII, 1♀ ; 13. VIII '26, 1♀ ; Noda-Bay, 3. VII, 2♀♀ ; 7. VII '26, 1♀ ; Suribachi, 23. VII '35, 1♀. SMS 1♀ 2♀♀ : Jôgasaki, 8. VIII, 1♀ ; 10. VIII '26, 1♀ ; Shimshubetsu, 14. VII '41, 1♀. ALD 3♀♀ 1♀ : Alaido, '26.

Abundant in northern Islands (Table 1. Fig. 1 A).

Structure Bischoff (2) considered this taxon as a subspecies of *B. lucorum* Linné. Krüger (15) cited it as *B. lucorum* Rasse *albocinctus*, and Tkalců (48) followed Bischoff, while Krivolutskaja (14) regarded it a good species. In the present study we tentatively follow Bischoff because the specimens are similar in many structural characters to those of *lucorum* in Europe (Table 2, Figs. 3～31). The validity of our judgement should be tested by further comparison with the specimens from Siberia connecting the ranges of *albocinctus* and *lucorum.*

Coloration Mostly black ; collaris and T_2 whitish to plae yellowish ; metasomal apex white ($T_4 \sim T_6$ in female, $T_4 \sim T_7$ in male). Variation is seen in the degree of admixture of dark hairs in the pale part. Geographical variation of females was examined for the most variable part, T_4 (Fig. 2, right). Within the available material the population of ALD and some islands of the middle Kuriles (SSR, KET, RSH and ONK) seem to show a weak melanic tendency, again suggesting differentiation in peripherally isolated populations.

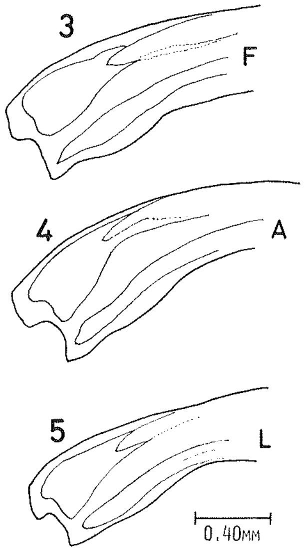
Specific distribution Holarctic. *Subspecific distribution* Kamtchatka, middle and northern Kuriles, Okhotsk, Sakhaline.

Bombus* (*Bombus*) *hypocrita sapporoensis Cockerell

Bombus ignitus var. *hypocrita* Pérez 1905 (partim ?), Bull. Mus. Hist. Nat. Paris, 1905 : 30. —*Bombus sapporoensis* Cockerell, 1911, Proc. U. S. Nation. Mus. 39 : 641 ; Krivolutskaja 1973 : 149. —*Terrestribombus sapporoensis*, Skorikov 1922 : 155. —*Bombus sapporensis*, Matsumura 1932 (nec Cockerell 1911): 4 & 6, pl. 1, fig. 21. —*Bombus hypocrita*, Tkalců 1962 (nec Pérez 1905, partim): 85; —1965: 11; Kuwayama 1967: 210; Krivolutskaja 1973: 149. —*Bombus* (*Bombus*) *hypocrita hypocrita*, Sakagami & Ishikawa 1969 (nec Pérez 1905): 185. —*Bombus* (*Bombus*) *hypocrita sapporoensis*, Sakagami & Ishikawa 1972: 609.

Specimens examined KNS 3♀♀ 9♀♀ : Furukamappu, 13~14. VIII '40, 6♀♀ ; Furukamappu-Seseki, 15. VIII '40, 1♀* ; Kunashiri, VIII '36, 2♀♀ ; Nikshiro, 11. VIII '25, 1♀ ; 17–22. VII '35, 1♀ ; Seseki-Nakanokotan, 16. VIII '40, 1♀. SKT 1♀ : Shikotan, 27–31. VIII '36.

Recorded only from two southernmost islands, KNS and SKT. Kuwayama (16) recorded *B. hypocrita* Pérez from SKT, while Krivolutskaja (14) *B. sapporoensis* Cockerell from the same island. Although she also cited *B. hypocrita* from Kuwayama (16) the two are apparently one and the same taxon, *Bombus hypocrita sapporoensis* Cockerell (Sakagami and Ishikawa, 35). In coloration the southern Kurile population shows no remarkable differentiation from that in Hokkaido. As for variability of this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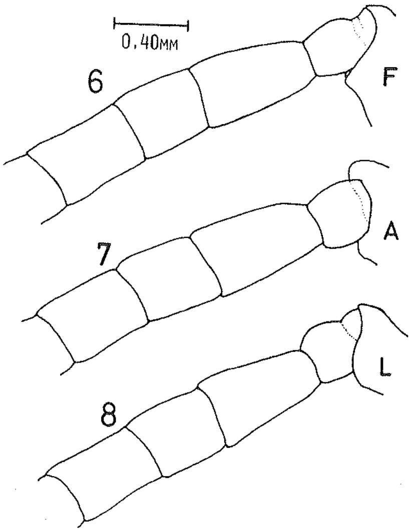
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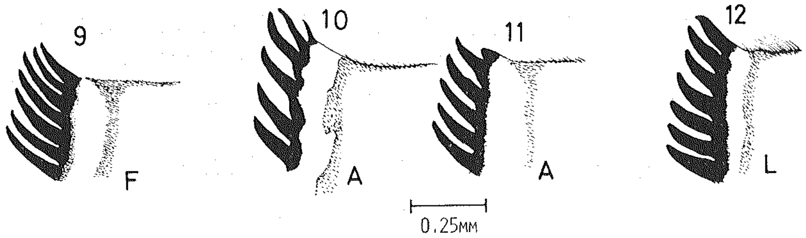
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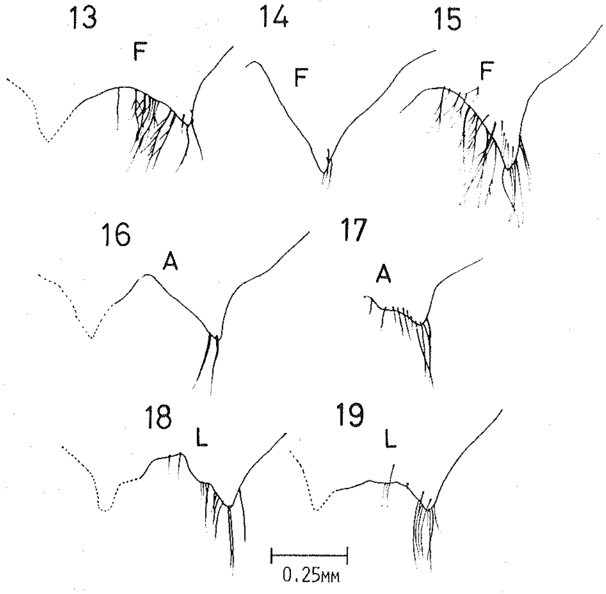
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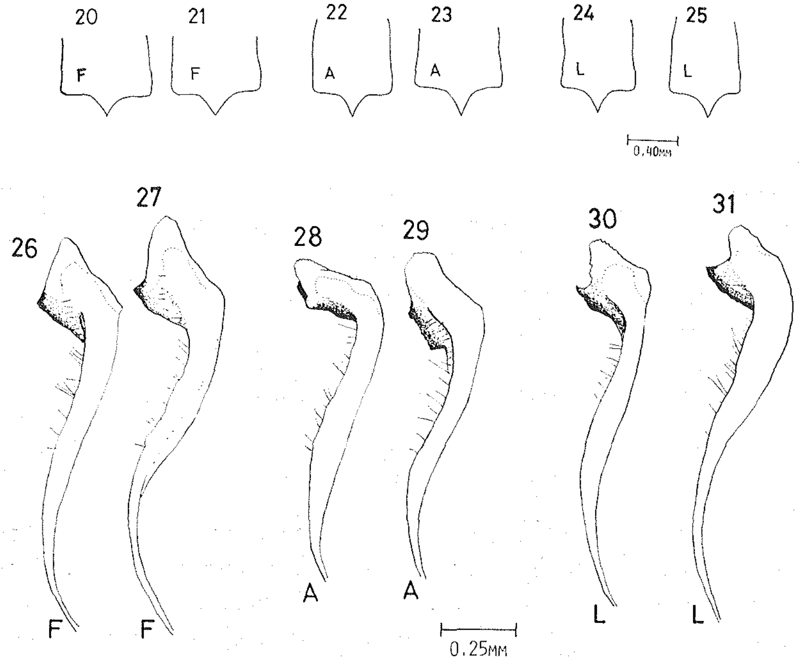


Figs. 3–31. Some structural characters of *Bombus* (*B.*) *florilegus* (=F), *B.* (*B.*) *lucorum albocinctus* (=A) and *B.* (*B.*) *lucorum lucorum* (=L). Figs. 3–5: Incisura lateralis of left mandible in queens: Figs. 6–8: Antennal flagella $F_1 \sim F_3$ (right) of queens: Figs. 9–12: Apicodorsal angle and bristles nearby of left hind tibia of queens; Figs. 13–19: Apical projection of the 8th sternum (St_8) in male. Figs. 20–25: Basal projection of spatha in male genitalia. Figs. 26–31: Right penis valve in male genitalia (dorsal view)

species in Hokkaido, see Ito and Munakata (10).
Specific distribution Manchurian. *Subspecific distribution* Ussuri, Manchuria, Korea, Sakhaline, Hokkaido, Kunashiri and Shikotan.

Bombus* (*Pyrobombus*) *beaticola moshkarareppus
Sakagami et Ishikawa

Bombus (*Pyrobombus*) *beaticola moshkarareppus* Sakagami and Ishikawa 1969: 176. —*Bombus* (*Pratobombus*) sp. 1 ?, Krivolutskaja 1973: 149.

Specimens examined KNS 1♀ 4♀♀ 2♂♂: Furukamappu, 13–14, VII 5♀♀ 2♂♂*; 18. VIII '40, 1♀; Nikishiro, 17–22. VII '35, 1♀.

B. beaticola was recorded from the two southernmost islands KNS and SKT like as *B. h. sapporoensis*. The specimens from KNS do not show any remarkable difference from those of eastern Hokkaido and are identified to *B. b. moshkarareppus*. On the other hand, the population of SKT exhibits a noteworthy melanism in coat coloration as already touched by Sakagami and Ishikawa (34), deserving to be recognized as a new subspecies described

below. Beside *B. hypnorum*, Krivolutskaja (14) mentioned three *Pratobombus* (=*Pyrobombus*) species without giving names, each from one island of the southern Kuriles, sp. 1 (KNS), sp. 2 (SKT) and sp. 3 (ETR). Although she did not refer to their characters, from the coincidence of the localities we regard that they correspond to our species as follows: *B.* sp. 1=*B. b. moshkarareppus*, *B.* sp. 2=*B. b. shikotanensis* ssp. nov. and *B.* sp. 3= *B. oceanicus* (see also the remarks on the last species).
Coloration See Sakagami and Ishikawa (34).
Specific distribution Subendemic to Japan. *Subspecific distribution* Hokkaido, Is. Kaibato, Kunashiri.

Bombus* (*Pyrobombus*) *beaticola shikotanensis ssp. nov.

Bombus (*Pyrobombus*) *beaticola moshkarareppus* Sakagami and Ishikawa 1969 (partim): 176. —*B.* (*Pratobombus*) sp. 2 ?, Krivolutskaja 1973: 149.

Head, pleura, ventral sides of meso- and metasoma, legs, wide interalaris, T_3, T_4 and basal half of T_5 dark; narrow collaris and scutellaris, T_2 whitish yellow; apical half of T_5 very faded orange; T_1 dark and light hairs mixed; apical periphery of T_2 dark. The most remarkable difference from *B. b. moshkarareppus* is the entirely dark T_4 and basally dark T_5.
Holotype: Queen, Kiritôshi, Notoro, Is. Shikotan, 30. VII. 1940.
Paratypes: Aimisaki, Is. Shikatan, 29. VII. 1940, 1♀*; Tiboi Aimisaki, 20. VII '40, 1 ♀. (Holotype and the second paratype are paratypes of *B. b. moshkarareppus* Sakagami and Ishikawa 1969).

Bombus* (*Pyrobombus*) *oceanicus Friese

Bombus pratorum var. *oceanicus* Friese, 1909, Deutsch. ent. Zeitschr., 1909: 675. —*Pyrrhobombus oceanicus*, Tkalců 1965: 2. —*Bombus* (*Pyrobombus*) sp., Kuwayama 1967: 210. —*Bombus* (*Pratobombus*) sp. 3 ?, Krivolutskaja 1973: 149.

Specimens examined ETR 1♀ 4♀♀ 2♂♂: Rubetsu Toshimoe, 29. VIII, 1♀; 29–30. VIII '40, 1♂; Shana, 11–20. VII '35, 1♀; Shana-Bettobu, 21. VII '36, 3♀♀; Yanketou-Mt. Chirip, 3. IX '40, 1♂. URP 45♀♀: Tokotan, 9–23. VIII '36. CHR (North Is.) 1♀: Sha (?)-Bay, 20. VIII '37. PRM 2♀♀: Shiomi, 7. VII '41, 1♀; Suribachi, 23. VII '35, 1♀. ALD 1♀: Alaido, '26.

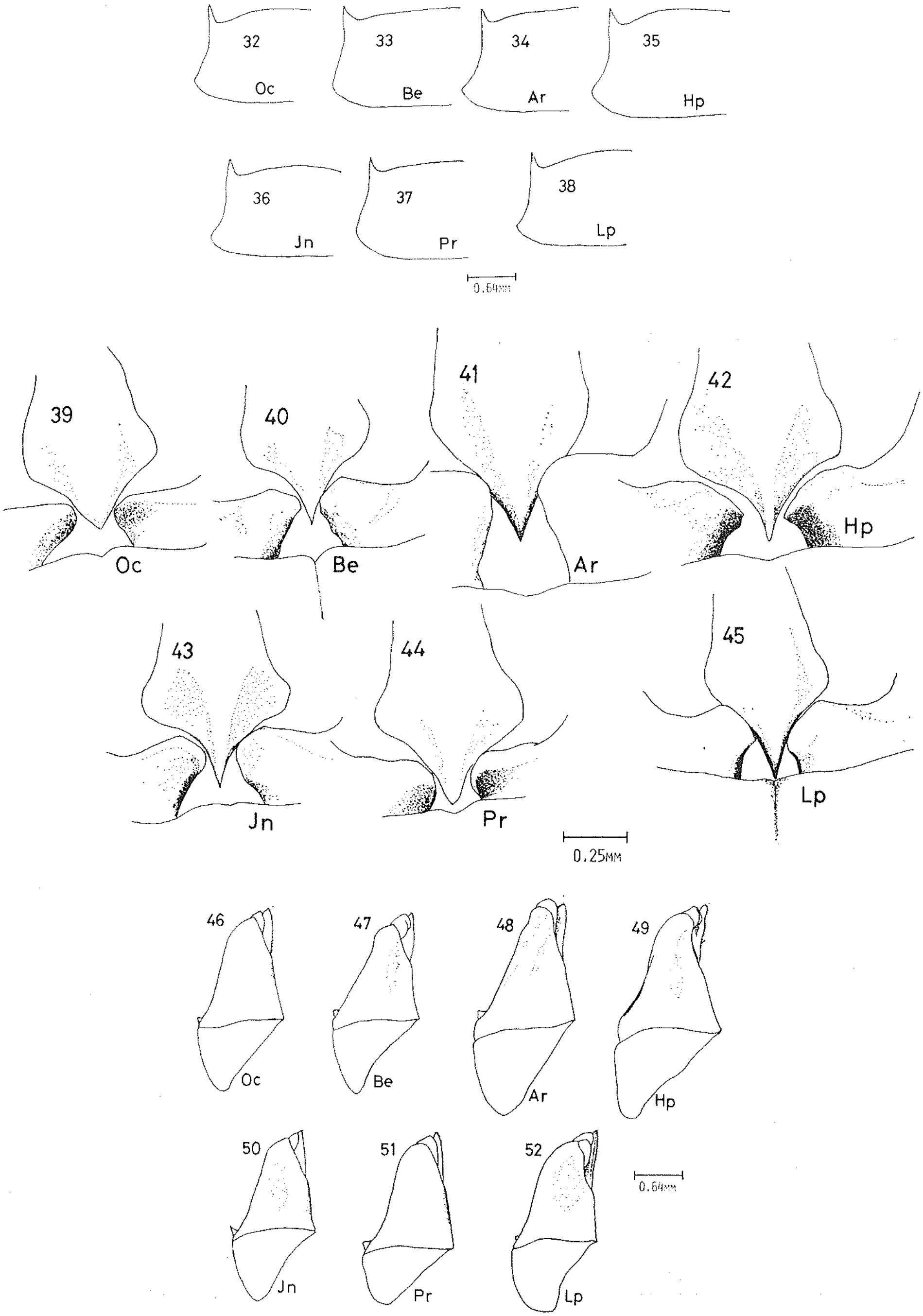
After the poor original description by Friese this species had long been ignored until Tkalců (45) recorded it from "Yeso" (= Hokkaido), with a photo but without detailed description. According to recent collecting efforts in Japan (6, 10, 33, 49, 50) its occurrence in Hokkaido is dubious. In our materials this species was recorded in three southern (ETR, URP and CHR) and two northernmost islands (PRM and ALD). The distribution might be discontinuous in the middle Kuriles. Many specimens were obtained from URP and ETR (Table 1 and Fig. 1 A), suggesting its predominance in these two islands. *Bombus* (*Pratobombus*=*Pyrobombus*) sp. 3 which Krivolutskaja (14) recorded only from URP is probably this species. *Bombus*

Table 3. Synoptic diagnoses of seven *Pyrobombus* species (Queen)

	oceanicus	*beaticola*	*ardens*	*hypnorum*	*jonellus*	*pratorum*	*lapponicus*
Provenance Character	Kuriles	Japan	Japan	Europe and Japan	Europe	Europe	Europe
Impunctate area of scutal disc	wide, rather ill-defined	moderately wide, ill-defined	moderate to wide, relatively well-defined	variable, ill-defined	moderate, relatively well-defined	moderate, ill-defined	very narrow, very ill-defined
Integumental color of clypeal disc	reddish with dark purple tint	black with weak reddish purple tint	black	=*oceanicus*	=*ardens*	=*oceanicus*	=*beaticola*
Shape of labral furrow	V shaped or intermediate to U and V	V shaped	U shaped	=*ardens*	=*beaticola*	intermediate	=*oceanicus*
Punctation on basal area of mandible	dense; mostly fine with a few large	dense; fine to medium	rather sparse; fine to large, with irregular sculptural striation	dense; mostly fine, some ones medium or large	rather dense; fine and large with irregular sculptural striation	moderately dense	sparse; fine and large, weak, irregularly distributed
Parorbital punctate band and its punctures	narrow, one or two rowed; sparse; small or fine	moderately wide, obscurely two rowed; sparse	narrow, one rowed; relatively sparse	wide, two or three rowed; dense	wide, two rowed; relatively dense	narrow, one rowed; moderately dense	very wide, two or three rowed; dense
Apical tip of T_6	entirely covered with fine plumose hairs	slightly exposed	exposed	=*ardens*	=*oceanicus*	=*oceanicus*	=*oceanicus*
Integument of T_6	dull	=*oceanicus*	=*oceanicus*	shining	somewhat dull	=*oceanicus*	=*ardens*
Basodorsal margin of hind basitarsus	weakly constricted (Fig. 32)	linear (Fig. 33)	very weakly constricted or as in *beaticola* (Fig. 34)	distinctly constricted (Fig. 35)	=*oceanicus* (Fig. 36)	linear or very subtly constricted (Fig. 37)	gradually constricted (Fig. 38)

Table 4. Synoptic diagnoses of seven Pyrobombus species (Male) (F=flagellum)

Character	*oceanicus*	*beaticola*	*ardens*	*hypnorum*	*jonellus*	*pratorum*	*lapponicus*
Parorbital punctate band and its puncure	narrow ; very sparse	norrow ; sparse	relatively narrow ; dense	moderately wide; relatively sparse	wide ; relatively sparse	narrow ; relatively dense	wide , dense
Inter-ocellar punctate band	moderate or relatively narrow, posteriorly 3-, anteriorly 1-rowed	=*oceanicus*	narrow, posteriorly 2-, anteriorly 1- rowed	very narrow with one row throughout	very wide, posteriorly 5-, anteriorly 3-rowed	moderately wide, posteriorly 3-, anteriorly 2- rowed	relatively wide, posteriorly 3-, anteriorly 2-rowed
Length/width of F_7	1.5	1.5	2.0	1.9～2.0	1.6～1.7	1.3～1.6	1.5～1.6
Pilosity on outer surface of hind tibia	relatively sparse, uniform, apical one-third sparser or bare	apical two-thirds bare	mostly bare	=*oceanicus*	=*oceanicus*	=*oceanicus*	=*oceanicus*
Sculpture on T_5	shagreened	more or less shagreened	shagreened	weakly shagreened	strongly shagreened	shagreened	shagreened
Longest hair on dorsal margin of hind basitarsus relative to tarsal width	longer than tarsal width	slightly shorter than or two thirds as long as tarsal width	short, half of tarsal width	two thirds as long as tarsal width	=*oceanicus*	as long as tarsal width or slightly longer	much longer than tarsal width
Basal projection of spatha	wide, short, not much pointed (Fig. 39)	wide, long, sharply pointed (Fig. 40)	wide, very long, more or less pointed (Fig. 41)	moderately wide, long, more or less pointed (Fig. 42)	relatively narrow, relatively long, sharply pointed (Fig. 43)	wide, moderately long, not much pointed (Fig. 44)	moderately wide, very long, sharply pointed (Fig. 45)
Profile of stipes	not much tapered apically (Fig. 46)	rather strongly tapered apically (Fig. 47)	strongly tapered, with specific apical distortion (Fig. 48)	strongly tapered apically, with specific apical distortion (Fig. 49)	intermediate to *oceanicus* and *beaticola* (Fig. 50)	not much tapered apically (Fig. 51)	not much tapered apically with specific apicoventral distortion (Fig. 52)



Figs. 32–52. Some structural characters of seven *Pyrobombus* species. *B. oceanicus* (=Oc), *B. beaticola moshkarareppus* (=Be), *B. ardens sakagamii* (=Ar), *B. hypnorum koropokkrus* (=Hp), *B. jonellus* (Jn), *B. pratorum* (Pr), *B. lapponicus* (Lp). Figs. 32–38. Basodorsal margin of hind basitarsus (in queen). Figs. 39–45. Basal part of spatha of male genitalia (in dorsal view). Figs. 46–52. Profile of male genitalia

(*Pyrobombus*) sp. in Kuwayama (16) was identified to this species, based upon re-examination of his specimens.

Structure This species is morphologically distinct from all the species inhabiting the northern Palaearctic region which were available for comparison. Among these species it was closest to *B. pratorum* (Table 3 and 4, Figs. 32~52). Reinig (25) placed a boreo-eurosiberian species *B. cingulatus* in *pratorum* group. If his opinion is valid, *B. oceanicus* might have been derived from this taxon.

Coloration Face, ventral part of meso- and metasoma, basal segments of legs, pleura mostly, interalaris, T_3 and T_4, T_2 apically, and often T_1, T_5 and T_6 dark; collaris, scutellaris, pleura above, T_2 basally, sometimes T_1 faded pale yellow and T_5 and T_6 white. Individual variation in melanism is remarkable (Fig. 53). In the lightest form, entire mesosomal dorsum, T_1 and basal two thirds of T_2 pale yellow and T_4~T_6 white. In the darkest form, wide interalaris and entire metasoma dark. As the materials from the northern Kuriles were insufficient, geographical variation could not fully be tested.

Specific distribution Endemic to Kurile Islands.

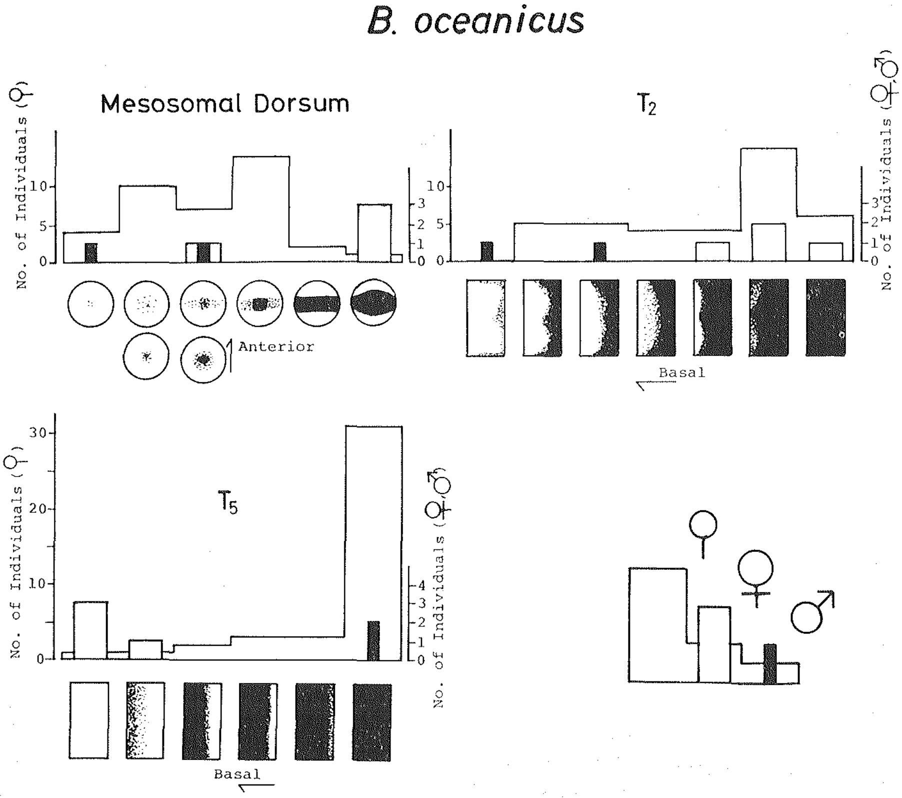


Fig. 53. Variation of *B.* (*Pyrof.*) *oceanicus* on mesosomal dorsum, T_2 and T_5

Bombus* (*Pyrobombus*) *hypnorum klutschianus Bischoff

Pratobombus hypnorum klutschianus Bischoff 1930: 2. —*Bombus hypnorum calidus,* Sakagami 1954 (nec Erichson 1951, partim): 86; Kuwayama 1967 (partim): 210.

Specimens examined ONK 14♀♀: Onnekotan, 12. VII, 8♀♀; 16. VII, 3♀♀; 20. VII, 1♀; Shakko(?)-gawa. 20. VII '37, 1♀.

B. hypnorum was recorded from two islands KNS and ONK very remote from each other. Krivolutskaja (14) obtained only one specimen from KNS, mentioning its extreme rarity. Within the records available, it is difficult to determine whether its range is continuous or interrupted in the Kuriles. But, the latter alternative seems more probable because the specimens from these two islands differ in coloration. As reviewed by Reinig (26), this species exhibits a remarkable geographical variation in Boreo-palaearctic region. Bischoff (2) described *B. h. klutschianus* from Kamtchatka as being lighter than *B. h. calidus* inhabiting Ussuri and East Siberia. As all the specimens (workers) from ONK bear one of its important characters, white $T_4 \sim T_6$, they are identified to *klutschianus*. Sakagami (31) regarded the same specimens as *calidus* mentioning that they lack two other important characters of *klutschianus*, lightly colored head and corbicular fringe. But, in the original description, Bischoff described that the workers of *klutschianus* were dark and unseparable from *calidus* in these two characters. As to the specimens from KNS, see below.
Specific distribution Boreo-palaearctic. *Subspecific distribution* Kamchatka, northern Kuriles (Onnekotan).

Bombus* (*Pyrobombus*) *hypnorum koropokkrus
Sakagami et Ishikawa

Bombus (*Pratobombus*) *hypnorum calidus,* Sakagami 1954 (nec Erichson 1851, partim): 86; Krivtoluskaja 1967: 148. —*Bombus* (*Pyrobombus*) *hypnorum calidus,* Kuwayama 1967 (nec Erichson 18-51, partim): 210. —*Pyrobombus hypnorum calidus,* Tkalců 1965 (nec Erichson 1851, partim): 1. —*Bombus* (*Pyrobombus*) *hypnorum insularis* Sakagami & Ishikawa 1969 (nec Friese 1924): 170. —*Bombus* (*Pyrobombus*) *hypnorum koropokkrus* Sakagami & Ishikawa 1972: 610.

Specimens examined KNS 1♂: Chinomiji, 5. VIII '40.

Only one male from KNS. It was not typically white tailed as in the males of *B. h. klutschianus* or *B. h. hypnorum.*
Coloration Head, mesosoma together with basal segments of legs and metasoma below entirely orange or orange yellow. Tibiae and basitarsi brownish or chocolate. T_1 orange, T_2 orange with a few black hairs discally, T_3 orange with some black hairs medially. T_4 and T_5 black with admixture of yellowish hairs, discally sparse, laterally dense. T_6 as in T_4 and T_5 but laterally predominated by pale yellowish hairs, T_7 whitish yellow. In the

population of Hokkaido (*B. h. koropokkrus*) a typical male with $T_1 \sim T_3$ orange, T_4 predominantly orange, T_5 light and dark mixed in the same amount, and T_6 entirely dark. The melanic T_4 and pale T_6 in the KNS specimen suggest the subspecific differentiation of the population from those of both Hokkaido and ONK. But, as no female specimens from KNS are available, the concerned specimen is tentatively identified to *B. h. koropokkrus*. *Subspecific distribution* Hokkaido, Kunashiri.

Bombus* (*Diversobombus*) *diversus tersatus Smith

Bombus tersatus Smith 1869, Entomologist 62: 207. —*Bombus* (*Diversobombus*) *diversus*, Sakagami (nec Smith 1869, partim): 186; Krivolutskaja 1973: 148. —*Diversobombus diversus tersatus*, Tkalců 1965: 4. —*Bombus* (*Diversobombus*) *diversus* subsp., Kuwayama 1967: 210. —*Bombus* (*Diversobombus*) *diversus tersatus*, Sakagami and Ishikawa 1969: 183; 1972: 607. —*Bombus* (*Diversobombus*) *atrocaudatus*, Krivolutskaja 1973 (nec Vogt 1909): 148.

Specimens examined KNS 9♀♀: Chinomiji-Pondomari, 9. VIII, 1♀*; Furukamappu, 13. VIII '40, 1♀*; Nikishiro, 17–22. VII '35, 5♀♀; Pondomari, 10. VIII, 1♀*; Tomari, 21. VIII '40, 1♀*.

Kuwayama (16) reported the occurrence of *B. diversus* in KNS as the unique *Diversobombus* species from the Kuriles. Re-examination of his specimens revealed that they were all *B. diversus tersatus* Smith (45). In coloration and several metric characters the population shows no difference from that in the easternmost Hokkaido (Ito, unpubl.). *B. atrocaudatus* recorded by Krivolutskaja (14) seems to be *B. d. tersatus*, as *atrocaudatus* was originally described from Sakhaline, the population of which is, based upon some specimens at our disposal, slightly darker than *B. d. tersatus*, but not so as *B. d. diversus*.
Coloration See Sakagami and Ishikawa (35) and Ito and Munakata (10).
Specific distribution Subendemic to Japan (Record from North Korea is dubious, as discussed by Sakagami, 32). *Subspecific distribution* Hokkaido, southern part of Sakhaline, Kunashiri.

Bombus* (*Megabombus*) *yezoensis Matsumura

Bombus yezoensis Matsumura 1932: 45, pl. 1, fig. 1. —*Hortobombus przewalskiellus* Skorikov 1933: 59. —*Diversobombus yasumatsui* Skorikov 1933: 60. —*Bombus* (*Hortobombus*) *tersatus*, Sakagami 1954 (nec Smith 1869): 89; Kuwayama 1967: 210; Krivolutskaja 1973: 148. —*Hortobombus yezoensis*, Tkalců 1962: 99. —*Megabombus yezoensis*, Tkalců 1965: 13. —*Bombus* (*Hortobombus*) *yezoensis*, Sakagami & Ishikawa 1969: 182; Kuwayama 1967: 210; Krivolutskaja 1973: 148.

Specimens examined KNS 4♀♀ 2♀♀: Chinomiji, 5. VIII '40, 2♀♀*; 16. IX '41, 1♀*; Nikishiro, 17–22. VII '35, 1♀; Pondomari, 10. VIII '40, 1♀*; Yambetsu, 24–25, VII '35, 1♀.

One of us (Sakagami, 31) recorded once *B.* (*Hortobombus*) *tersatus* from the southern Kuriles and Hokkaido, and described its subspecies *B. t. kurilensis* from the northern Kuriles. Kuwayama (16) and Krivolutskaja

(14) cited these taxa without giving further remarks. Later, Tkalců (45) mentioned that *B. yezoensis* Matsumura should be applied to the *Megabombus* species in Hokkaido. (As for *kurilensis*, see the remarks on *B. tichenkoi*).
Coloration See Sakagami (31). No remarkable difference between populations of KNS and Hokkaido.
Specific distribution Manchurian (?) : Ordos, Hokkaido and Kunashiri.

Bombus* (*Megabombus*) *tichenkoi (Skorikov)

Hortobombus tichenkoi Skorikov 1925 : 115. —*Bombus* (*Hortobombus*) *tersatus kurilensis* Sakagami 1954: 92, syn. nov.; Kuwayama 1967: 210. —*Bombus* (*Hortobombus*) *tichenkoi*, Krivolutskaja 1973 : 146.

Specimens examined PRM 4♀♀ : Noda-Bay, 7. VII, 3♀♀ ; 31. VII '26, 1♀. SMS 1♀ : Bettobi, 23. VIII '35. (All holo- and paratypes of *B. t. kurilensis*.)

Recorded only from two northernmost islands, PRM and SMS. Krivolutskaja (14) mentioned its occurrence in KNS. But her specimens are possibly *B. yezoensis* by the following three reasons : 1) absense of *yezoensis* in her collection from KNS ; 2) absense of *tichenkoi* in our collection from the middle and southern Kuriles, especially from KNS and ETR, in spite of many collecting records there (Table 1) ; 3) resemblance of *tichenkoi* and dark individuals of *yezoensis*, especially in workers.
Structure Comparison between the holotype of *B. tersatus kurilensis* Sakagami and the syntype of *B. tichenkoi* Skorikov** revealed their identity. The localities of the allotype and the morphotype of *B. t. kurilensis*, erroneously printed in the original description as "Is. Shumshir", are corrected here to "Is. Shumshu". In the original description Skorikov (41) placed this species closest to *B. argillaceus* Scopoli. The comparison of several queen characters clearly demonstrate its difference from the latter (Table 5). The closest relative is possibly *B. sushkini*, an East Siberian species (48). They might be vicarious for each other in northeastern Siberia.
Coloration Females : Blackish, collaris and scutellaris fulvous. In coloration the specimens we examined are identical with the syntype of *B. t. karaginensis*** from Is. Karagin, not with *B. t. tichenkoi* from Kamtchatka. This suggests an advanced melanism in the two peripheral populations remote from each other. But as little information on geographical and individual variations of this species is available, the subpecific system is not adopted here. No remarkable variation exists among four Kurile specimens.
Specific distribution Subendemic to Kamtchatka : Kamtchatka, Is. Karagin, northern Kuriles (Paramushir, Shumshu).

Table 5. Synoptic diagnoses of four *Megabombus* species (Queen).

	tichenkoi
Provenance	Kuriles and Kamtchatka
No. of specimens examined	6
Character	
Head width	m = 4.90 mm
Pubescence	long
Parocular sculpture	very subtly shagreened
Parocular impunctate area	moderately wide, with wider parorbital punctate band
OP/OE	1.47～1.67
Clypeal disc	relatively flattened
Punctation on clypeal disc	very sparse and weak
Mediobasal punctate band of clypeus	narrow, distinctly depressed, with small weak punctures
Malar length/Malar width	very long, 1.84～1.91
Punctation on basal area of mandibles	dense, weak, mostly fine and a few distinctly large
Impunctate area on scutal disc	very narrow, ill-defined

Bombus (*Thoracobombus*) *schrencki kuwayamai*
Sakagami et Ishikawa

Bombus (*Agrobombus*) *schrencki* subsp. 2, Kuwayama 1967: 210. —*Bombus* (*Agrobombus*) *schrencki*, Krivolutskaja 1973 (nec Morawitz 1881, partim). —*Bombus* (*Agrobombus*) *schrencki kuwayamai* Sakagami & Ishikawa 1969: 164.

Specimens examined KNS 3♀♀ 21♀♀ 2♂♂: Furukamappu, 13–14, VIII, 1♀ 1♂; 15. VIII '40, 1♀; Kotankei, 18. VIII, 1♀; 18–19. VIII '40, 1♀: Tofutsu, 17. VIII, 1♀; 17–18. VIII '40, 1♀; Tomari, 1. VII '25, 1♀; 21. VIII, 2♀♀*; 21–23. VIII '40, 12♀♀ 1♂; 1. IX '41, 1♀; Kunashiri, 17–22. VII '35, 1♀ (Holotype); VIII '36, 1♀. (Except the specimens belonging to HAES all others are holotype and paratypes.)

Recorded only from KNS as the most abundant taxon there (Table 1, Fig. 1 A).

OP: Ocelloccipital distance. OE: Ocellocular distance

yezoensis	*argillaceus*	*sushkini*
Hokkaido	Italy	E. Siberia
5	1	1
m = 4.86 mm	m = 5.36 mm	m = 4.78 mm
long	short	long
irregularly shagreened	distinctly shagreened	subtly and irregularly shagreened
a little wider, with narrower parorbital punctate band	narrow, with wide parorbital punctate band	=*yezoensis*
1.68～1.79	1.83	1.63
moderately convex	distinctly convex	=*tichenkoi* or slightly more convex
sparse, weak	relatively dense, strong	virtually absent except very weak ill-defined ones.
broad, little depressed, with relatively large and strong punctures	narrow, depressed, with relatively large and strong punctures	moderately wide, depressed, with small and weak punctures
long, 1.75～1.87	relatively short, 1.59	very long, 1.88
relatively sparse, moderately strong, fine to medium	dense, strong, small to medium	=*tichenkoi*, but slightly denser and stronger
wider, well-defined	narrow, relatively ill-defined	very narrow, ill-defined

Coloration Geographic variation of *B. schrencki* was described by Sakagami and Ishikawa (34). Variation was here studied with respect to the degree of admixture of dark hairs on $T_3 \sim T_5$ and pleura (Fig. 54). The color of $T_3 \sim T_5$ are subtly lighter than *B. s. albidopleuralis* in Hokkaido, while pleura is not melanic as in *B. s. konakovi* in SKT, ETR and URP. *Specific distribution* East Siberian. *Subspecific distribution* Kunashiri.

Bombus (***Thoracobombus***) ***schrencki konakovi*** Panfilov

Bombus (*Adventoribombus*) *konakovi* Panfilov 1956: 1330; Krivolutskaja 1973: 148. —*Bombus* (*Agrobombus*) *schrencki* subsp. 1. Kuwayama 1967: 210.

Specimens examined SKT 6♀♀ 3♂♂: Kirimishi (?), 31. VII, 1♀*; Notoro, Shakotan, 31. VII '40, 1♀*; Shakotan, 12. VII, 1♀; 23. VII '25, 1♂; 23. VIII '27, 2♂♂; 23–27. VII '35, 2♀♀; Shikotan, 27. VII 1♀*; 25. VII '40, 1♀*. ETR 5♀♀ 9♀♀ 1♂: Porosu, 14–15. VII '36, 1♀;

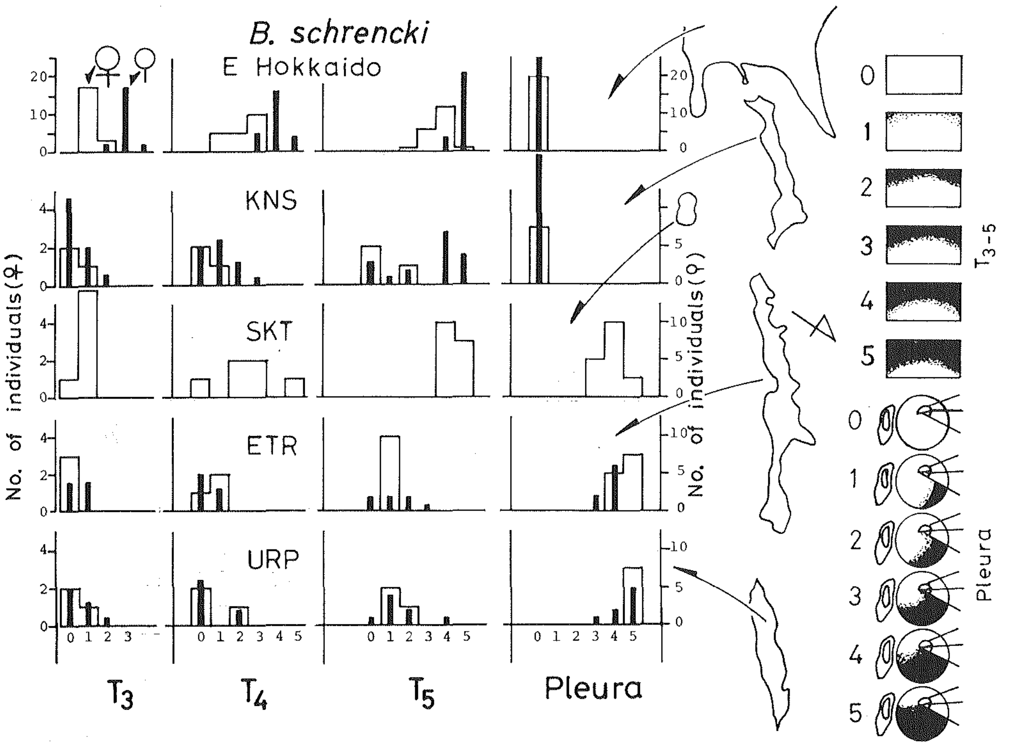


Fig. 54. Variation of *B.* (*Thoracob.*) *schrencki* on $T_3 \sim T_5$ and pleura

Rubetsu, 2–10. VII '35, 1♀; 28. VIII '40, 3♀♀*; Rubetsu-Toshimoe, 29. VII, 4♀♀*; Seseki (Bettobu), 16–18. VII '36, 1♀; Shana, 11–20. VII '35, 1♀; 3. IX '40, 1♀*; Shana, Bettobu, VII '36, 1♀; Yanketou- Mt. Chirip, 3. IX '40, 1♀ 1♂. URP 3♀♀ 9♀♀ 1♂: Onsenzaki, 17. IX '27, 1♀; Tokatan, 29. VIII, 1♀; 2. IX, 1♀ 1♀; 4. IX '27, 1♀ 1♂; 9–23. VIII '36, 2♀♀ 5♀♀.

Melanic form of *B. schrencki* (22, 34), recorded from SKT, ETR and URP, and considerably abundant there (Table 1, Fig. 1 A).

Coloration Characterized by entirely melanic meso- and metasomal venter and very melanic pleura (Fig. 54). Coloration on $T_3 \sim T_5$ rather lighter than *B. s. albidopleuralis* in Hokkaido. The population of SKT slightly more melanic than those of the other two islands, especially on T_5.

Subspecific distribution Shikotan, Etorofu and Urup.

***Bombus* (*Thoracobombus*) *pseudobaicalensis* Vogt**

Bombus (*Agrobombus*) *equestris* Rasse *pseudobaicalensis* Vogt 1911, SB. Ges. Naturf. Fr. Berlin, 1911: 43, 53. —*Agrobombus gilvus* Skorikov 1925: 117; —1933: 55. —*Bombus* (*Agrobombus*) *senilis*, Sakagami 1951 (nec Smith 1879, partim): 603. —*Agrobombus pseudobaicalensis*, Tkalců 1962: 96; —1965: 13. —*Bombus* (*Agrobombus*) *pseudobaicalensis*, Sakagami & Ishikawa 1969: 184.

Specimens examined KNS 1♀: Tomari, 1. VII '25.

Only one queen labelled "Tomari, Japan". Based upon the same specimen Sakagami and Ishikawa (34) cited the occurrence of this species in the Kuriles (Fig. 9) without any remarks. Although there are several localities called Tomari in Japan, the provenance of this specimen is judged to be from KNS, because one specimen with the exactly same label of *B. s. kuwayamai*, which occurrs only in this island, is known.

Coloration See Tkalců (45) and Sakagami and Ishikawa (34, Fig. 9). No remarkable difference from the specimens in Hokkaido.

Specific distribution East Siberian: Mongol, Manchuria, Ussuri, Korea, Sakhaline, northern Honshu, Hokkaido and Kunashiri.

Beside the species mentioned above, the following two species have so far been recorded from the Kurile Islands: *B.* (*Diversobombus*) *ussurensis* Radoszkowski from PRM (Skorikov, 42) and *B.* (*Pratobombus*=*Pyrobombus*) *jonellus* Kirby from ALD (Krivolutskaja, 14). Sakagami (32) doubted the former record, because of its absence in Kamtchatka and Okhotsk. His judgement is followed here. As for *B. jonellus*, its occurrence in the northern Kuriles is likely, because it is widespread in Boreo-palaearctic region including Kamtchatka (17).

Faunistic Remarks

In this section the species are cited by abbreviated subgeneric names as follows (The subgeneric system follows Richards, 27): *Bombus* (= *Bo.*), *Alpinobombus* (= *Al.*), *Pyrobombus* (= *Pr.*), *Melanobombus* (= *Ml.*), *Mendacibombus* (= *Md.*), *Megabombus* (= *Mg.*), *Diversobombus* (= *Dv.*), and *Thoracobombus* (= *Th.*).

From the geographical position of the Kuriles which interconnect Hokkaido and Kamtchatka with a chain of about 30 small islands, it is self-evident that their biota was formed by receiving the colonizers from those of the two land masses. To examine such bilateral invasions, the Kurile Islands offer the best situation in the world as far as the bumblebees are concerned. The bumblebee fauna of Hokkaido is fairly well known and consists of 11 forms, among which only *Th. honshuensis* is confined to S. Western Hokkaido (11, 34, 35). As to the fauna of Kamtchatka, our knowledge is not yet complete, but at least 14 good taxa have been recorded (2, 15, 17, 22, 24, 25, 26, 37, 38, 41, 42, 46). Species recorded in those two areas are given below. Specific distributional patterns are mentioned in parentheses (Those for the species common to the Kuriles were given previously). Parentheses for the authors are valid for the generic names, not for the subgenera. The taxa endemic to either of these two areas are asterisked.

Hokkaido: *Th. honshuensis* (Tkalců)* (Endemic to Japan), *Pr. ardens sakagamii* (Tkalců)* (Endemic to Japan), *Th. d. deuteronymus* Schulz (Eurosiberian: Balkan, Siberia, Manchuria, Korea, Japan), *Th. pseudobaicalensis* Vogt, *Dv. diversus tersatus* Smith, *Mg. yezoensis* Matsumura, *Pr. hypnorum koropokkrus* Sakagami & Ishikawa*, *Pr. beaticola moshkarareppus*

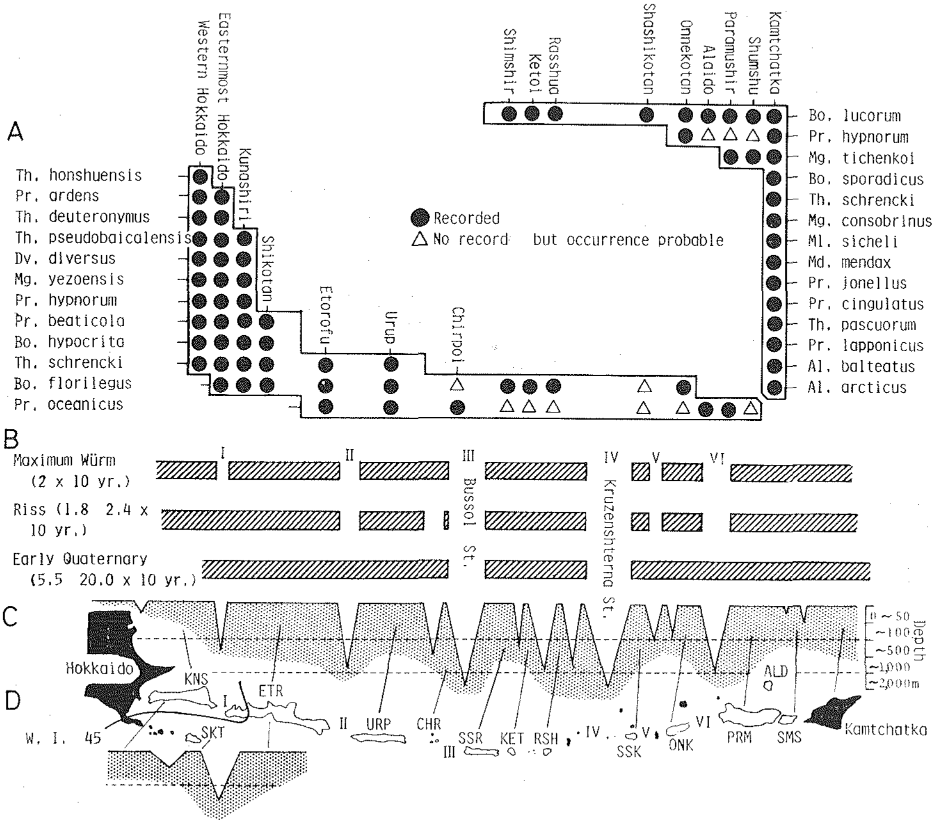


Fig. 55. Distribution of bumblebees in the Kuriles and adjacent areas (A), with geological (B) and geographical conditions (C, D). B: Openings of various straits in the geological ages. C: Extent of each island and strait, together with the depth of strait. D: Map of the Kurile Islands (black = no collecting records); W. I. 45 means isotherm for warmth index 45. I–VI Major straits in the Kuriles

Sakagami & Ishikawa*, *Bo. hypocita sapporoensis* Cockerell, *Bo. florilegus* Panfilov. Kamtchatka: *Bo. lucorum albocinctus* Smith*, *Pr. hypnorum klutchianus* Bischoff*, *Mg. tichenkoi* (Skorikov)*, *Bo. sporadicus malaisei* Bischoff* (Eurosiberian: Eastern Europe, Siberia, Ussuri, Manchuria, Korea, northern China), *Th. pascuorum flavobarbatus* Morawitz (Eurosiberian: Europe, Siberia, Manchuria, Ussuri, Korea), *Th. schrencki albidopleuralis* Skorikov, *Mg. consobrinus wittenburgi* Vogt (Eurosiberian: Europe, Siberia, Sakhaline, Manchuria, Ussuri, Korea, Honshu), *Ml. sicheli sicheli* Radoszkowski (Eurosiberian: Europe, Siberia, Manchuria, Ussuri, Sakhaline, Korea), *Md. mendax mendax* Gerstaecker (Eurosiberian, in mountaneous region: Mountains in Europe, Pamir, Himalaya, northern and western China, Siberia), *Pr. jonellus* Kirby (Eurosiberian: northern Europe, Siberia), *Pr. cingulatus tilingi* Morawitz* (Eurosiberian: Northern Europe, Siberia), *Pr. lapponicus kamtshaticus* Skorikov* (Boreal Eurosiberian: Northern Europe, Siberia), *Al. balteatus* Dahlbom (Circumpolar), *Al. arcticus* Kirby (Circumpolar).

Although the designation of distributional patterns is still provisional for some species, it is certain that the fauna of Hokkaido is characterized by many Manchurian elements while that of Kamtchatka is mostly composed of the northern elements without admixture of the Manchurian (Fig. 1 B).

Omitting *Dv. ussurensis* and *Pr. jonellus* not examined by us the species recorded from the Kuriles are in the present paper classified into three faunal elements.

H: Species common to Hokkaido, i. e. the northward invaders. (*Th. pseudobaicalensis, Dv. diversus, Mg. yezoensis, Pr. hypnorum koropokkrus, Pr. beaticola, Bo. hypocrita, Th. schrencki*). E: Endemic or subendemic species (*Pr. oceanicus, Bo. florilegus*). K: Species common to Kamtchatka, i. e. the southward colonizers. (*Bo. lucorum, Pr. hypnorum klutschianus, Mg. tichenkoi.*)

The distribution of these elements on the major islands is as follows (HE: H species subspecifically differentiated in the Kuriles):

Island	No. species	H	HE	E	K
KNS	8	7	1	1	
SKT	4	3	2	1	
ETR	3	1	1	2	
URP	3	1	1	2	
SSR	2			1	1
ONK	3			1	2
PRM	3			1	2

From this Table and Fig. 1 A and B, the following facts are recognized: 1) KNS is richest in species and shares about 80% species with Hokkaido. 2) H abruptly diminish between KNS and ETR, i. e. at the Kunashiri St. 3) SKT is the second richest, with slightly more species than much larger ETR or URP. 4) The fauna of southern islands south of URP are entirely composed of H and E, lacking K. 5) ETR shares the same elements with URP, including one HE. 6) All the species of ETR and URP are either specifically (2 species) or subspecifically different from the mother population of Hokkaido. 7) H completely disappear in the northern islands north of Bussol. St. between URP (CHR) and SSR. 8) K are relatively few even in the northern islands near Kamtchatka. 10) E are very few in number, only two. 11) All the islands have either or both of the two E. Despite the difficulty of faunistic interpretation due to the northward poverty as in most animal groups, these results are basically similar to those so far reported in various other insect groups in this area (9, 12, 16). All previous studies agree in the predominance of H in the southern islands, abrupt diminution of H between southern and middle Kuriles, few endemics through the Islands and low species diversity especially in the middle and northern Islands where K are predominant. The present results are above all comparable with the butterfly fauna reviewed by Shiokawa (36) as given below:

Island	species No. of	No. of species common to Northeast Hokkaido
NE-Hokkaido	65	—
KNS	53	53
SKT	22	22
ETR	19	19
URP	12	12
PRM	7	5

Between the butterflies and bumblebees, the items 1, 2, 3, 4, 5, 8 and 9 mentioned above, coincide with each other even if not exactly. The conincidence is very weak or absent in 6, 10 and 11, but the most remarkable difference is observed in the item 7, i. e. many H attain even PRM in butterflies. The difference might indicate that bumblebees tend to be more affected by geographical barriers than butterflies. This may be partly true, but the situation is not so simple as suggested by the following chorological inference.

The Kurile Islands began to be formed at the middle of the Miocene (7, 11, 19). According to the paleogeographical maps prepared by Minato (19, Fig. 31), they have been gradually insulated since early Quatenary. Fig. 55 shows approximate ages of strait formation in the area (B), together with approximate depth of sea barriers (C, cited from 1, 20). Among them the two oldest straits (III, IV) had been opened since the early Quaternary, and the three next oldest ones (II, V, VI) since the Riss ice age. The interinsular distance are more or less proportional to the ages of the straits (Fig. 55 B, C). Their relative importance functioning as geographical barriers in the time and space is hence III≑IV>II≑V≑VI>I> all other straits (Fig. 55 B, D). By comparing Fig. 55 A with B it is evident that the ranges of few species are restricted by the older straits with possible exceptions of *Th. schrencki* at III, *Pr. hypnorum klutschianus* at V and *Mg. tichenkoi* at VI. The species inhabiting throughout many islands across one or more old barriers (henceforth abbreviated as *r* species) are *Bo. florilegus, Bo. lucorum, Pr. oceanicus, Pr. hypnorm klutschianus* and *Th. schrencki*. The continuous distribution of these species can be explained alternatively by either invasion before openings of those straits or later oversea colonization. The first alternative seems hardly probable for the most if not all *r* species. The middle Kuriles (SSR, KET, RSH, Matsuwa, etc.) had been isolated for more than 2,000,000 years (Fig. 55 B). If *r* species had been isolated there for such a long time they should have fairly differentiated in the course of adaptation to the violent climatic and other environmental changes repeated in these islands. As mentioned previously, however, no remarkable differentiation is recognized in the populations between these and the adjacent islands.

Although the available basic data are still insufficient, the oversea dispersal by bumblebees seems physiologically not inconceivable. According to

Heinrich (8), the flight speed of the foragers of *B. vosnesenski* is 11～20 km/h, and its fully filled honey crop can contain nectar equivalent to 90 perecent of its body weight and the sugar concentration is about 20～30%. Further, the maximal metabolic rate of the queen under adverse thermal conditions (5°C) is estimated as 75 cal/h. Assuming that all these figures are also applicable for a founding queen weighing 500 mg, of the Kurile species in flight, then, she has about 90～135 mg of sugar in the crop, being equivalent to 360～540 cal, which allows her a continuous flight of 4.8～7.2 hrs and of ca. 53～144 km, if the rapid use of the sugar in the crop is possible as in honey bees (3). The widest straits in the Kurile are III (the Bussol St.) and IV (the Kruzenshterna St.), both about 80 km, having the distance which can physiologically be accessible by bumblebees. A shorter oversea flight was actually observed in the foraging workers of *B.* (*Fervidobombus*) *morio* Swedrius, who travelled the Bay of Guaratuba (Parana, S. Brasil), (about 2.5 km distant; observed by Michener and Moure, cf. Moure and Sakagami, 22). As shown in Fig. 56 the number of species gradually drops with increasing distance from Hokkaido. This suggests that the fauna of each island might be formed mainly by the oversea colonization, which tends to make the species curve well correlating to the distance.

Obviously, the afore-mentioned physiological possibility would rarely be realized. The dispersal might be aided partly by winds. But such passive dispersal may not be much common in big and strong active fliers such as bumblebees. The difference from the distribution of butterflies mentioned above (item 7) might reflect this particularity of bumblebees. Consequently, all the straits have more or less functioned as effective barriers only crossed by a rare chance. The occurrence of some interinsular differentiation in coat coloration favors this interpretation. Panfilov (23) postulated the formation of most recent species groups of the north Eurasian bumblebees by their isloation in the refuges during the Dniepr (= Riss) ice age. Based upon his postulate Sakagami (32) assumed the formation of the bumblebee

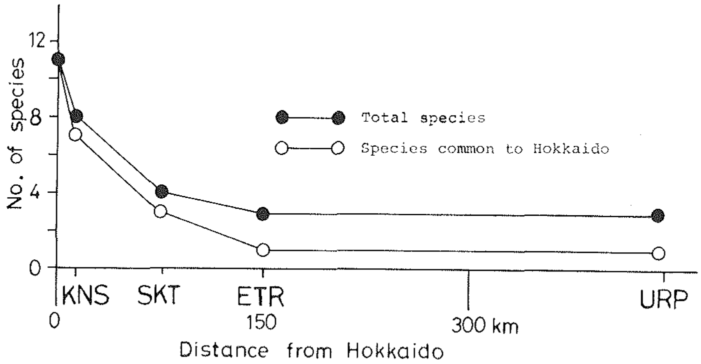


Fig. 56. Gradual decrease of the number of species in the southern Kuriles, with increasing distance from Hokkaido

fauna of Japan as an outcome of invasion of continental stocks in the Riss age or later. It is interesting here that all H species except *Th. schrencki* stop at I (the Kunashiri St.) which opened after the Riss age. This may indicate their arrival after the opening of the strait, i. e. after the Riss age, reinforcing Sakagami's speculation.

On the other hand, the limits of the specific ranges do not clearly coincide with other ecological or climatic clines steepened in the area concerned. In phytogeography Tatewaki (43) proposed Miyabe Line separating boreal East-Siberian and temperate Manchurian regions at II (the Etorofu St.), citing the disappearance of many temperate species there (82% of the species which have the northern limits within the Kurile Islands). This line also represents the northern boundary of the coniferous forest (43, 44). In some insect groups the importance of this line has been indicated (12, 16). But, no bumblebee species have this strait as the boundary of distribution. The steepest change of mean air temperature during active seasons (4) occurrs at II (Fig. 57, after 4), coinciding with Miyabe Line. Shiokawa (34) asserted thermal factor represented by the warmth index (13) as the most important factor to the faunal change of butterflies in Hokkaido and the southern Kuriles. However, the isotherm for warmth index 45°C (Fig. 55 D, from Shiokawa 36) does not coincide clearly with the distribution of bumblebees.

From the discussion given above, it is concluded that the bumblebee fauna in the Kuriles is an outcome of a struggle between the straits as barriers and ability of oversea colonization in the bees, both being effective but only imperfectly. The early comers, species having more powerful flight capacity, wider physiological and/or ecological tolerance, or higher reproductive ability would have more chance for successful oversea colonization. The occurrence of *r* species crossing one or more old straits, as well as the remarkable decrease of species at I, may be explained in this way.

Finally the faunal peculiarity of SKT is briefly mentioned. This small island has four species, all shared with East Hokkaido and KNS. It is noteworthy that three of them show some differentiation in coat coloration, two are melanic (*Pr. beaticola* and *Th. schrencki*) and one white-tailed (*Bo.*

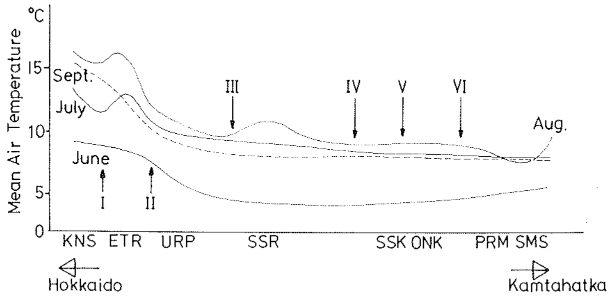


Fig. 57. Mean air temperature of the warm season in the Kuriles (cited from 4). I–VI are the straits (cf. Fig. 55).

florilegus). As for the latter two, the population of ETR shows more or less similar trends, while those in KNS not. Such a similarlity to ETR or difference from KNS has been reported in phytogeography by Tatewaki (43), too. He subdivided the Southern Kurile District into two subareas, Kunashiri subarea and Etorofu-Shikotan subarea, based upon the presence of *Larix Gmelini* Ledeb. and the absence of *Toisusu Urbaniana* (Seem.) Kimura, *Ulmus laciniata* (Trautv.) Mayr, *Quercus dentata* Thumb. etc. in the latter. Hori and Tamanuki (19) indicated a similar trend for butterflies based upon the absence of the species of apparently southern origin in SKT and ETR. Kuwayama (16) also mentioned it in his review on the insect fauna of the southern Kuriles. This similarity both in flora and fauna between these two islands cannot be elucidated by the age of strait formation, because the strait between SKT and ETR is much deeper than those between SKT and KNS or Hokkaido (Fig. 55 C), suggesting its older age. Possibly local climatic or ecological conditions common to SKT and ETR should affect the parallel evolution in coat coloration during a relatively short time span. In this case, the line of warmth index 45 might have some effects, because it separates KNS and East Hokkaido from SKT and the most part of ETR (Fig. 55 D).

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