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The Bumblebees in Southern Hokkaido and Northernmost Honshu, with Notes on Blakiston Zoogeographical Line[1,4,5]

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Synopsis

Distribution of bumblebees in southern Hokkaido west of Ishikari Lowland and northernmost Honshu (Aomori Pr.) is studied, with a critical examination of subspecific differentiation in species inhabiting the both areas. Based upon numerous capture records, distribution maps are prepared for each species. These maps indicate a poor coincidance of specific distribution boundaries with the Tsugaru Strait, i. e. Blakiston Line. On the other hand, comparison of hair-coat variability among diverse local populations revealed a clinal change of melanism among the north-south direction in four species studied. The trends, however, seem to be disjuncted by the Tsugaru Strait, except for *B. honshuensis*. Consequently, it is concluded that post-glacial segregation of the Strait functioned for subspeciation of some Japanese bumblebees. Nomenclatorially *B. h. tkalcui* in southern Hokkaido is synonymized with *B. honshuensis* of Honshu.

Introduction

The Tsugaru Strait, isolating Hokkaido from Honshu, and known as Blakiston line, segregates distribution areas of many animal species. Although the significance of this zoogeographical line is obvious for some animal groups, e. g. terrestrial mammals (14), its role is often less conspicuous for the animals with high dispersal ability such as winged insects (1, 6).

Among insects, the bumblebees are powerful fliers but are presumed to be sedentary, because of their keeping of the nests, as indicated by the facts that high mountains or only narrowly isolated islands often have endemic color-forms or subspecies (3, 10, 11). This suggests that the bumblebee populations in northern Japan have suffered, and still are suffering, an isolation by this Strait.

The Japanese bumblebee fauna is composed of 14 species, six of which are divided into 13 subspecies. Among these taxa many species have been

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Table 1. Localities and number of individuals (three castes combined). Code No. correspond to the locations shown in Fig. 1. Abbreviations for relative altitude, M: mountains; H: hills; P: plain, (cf. text). Abbreviations for species: div: *B. diversus* Sm.; yez: *B. yezoensis* Mats.; hon: *B. honshuensis* (Tk.); sch: *B. schrencki* Mor.; pse: *B. pseudobaicalensis* Vogt; deu: *B. deuteronymus* Schulz; ard: *B. ardens* Sm; bea: *B. beaticola* (Tk.); hpn: *B. hypnorum* (L.); hpc: *B. hypocrita* Pérez; ign: *B. ignitus* Sm. (subspecies not considered.)

Area locality	(Code No.)	relative altitude	div	yez	hon	sch	pse	deu	ard	bea	hpn	hpc	ign	T	No. records
Hokkaido															
Ishikari															
Ishikari beach	(1)	P				1								1	1
Hoshioki, Teine	(2)	H	1						7	3				11	1
Mt. Teine	(3)	M									1			1	1
Sapporo	(4)	P	40	9		3	27	5	29	1	7	44		165	103
Mt. Moiwa	(5)	H	6			3	6		6			6		27	16
Nopporo	(6)	P	1						8			4		13	7
Mt. Hakken	(7)	H		1					6		1			8	4
Misumai	(8)	H	1				2							2	3
Jozankei	(9)	H	32	20	30		18	2	5	1	30	83		221	72
Usubetsu	(10)	H	15	1								3		19	3
Mt. Muine	(11)	M	5		1					4	5	8		23	6
Otarunai	(12)	H	7	6	1					6	2	8		30	4
Mt. Soranuma	(13)	M	3							26		3		32	6
Mt. Eniwa	(14)	M	13									3		16	1
Lake Shikotsu (Kohan)	(15)	H	2											2	1
Isarigawa	(16)	H	3						2	1		2		8	2
Shiribeshi															
Otaru	(17)	P										1		1	1
Okusawa	(18)	H										3		3	1
Asarigawa Spa	(19)	H								1		2		3	1
Zenibako	(20)	P										1		1	1

Asari Pass	(21)	H	9	4				16	7		8	44	6
Ranshima	(22)	P	1									1	1
Yoichi	(23)	P	1				4				3	8	1
Bikuni	(24)	P			1	2						3	2
Mt. Shakotan	(25)	M	14			4		1	3			22	5
Iwanai	(26)	P									1	1	1
Shimano	(27)	P	1									1	1
Tomari	(28)	P	4			8					1	13	3
Mt. Niseko	(29)	M	2						36			38	3
Suttsu	(30)	P	6									6	1
Wakikata	(31)	H						1				1	1
Kyogoku	(32)	H	11			27	8	4	1	1	36	88	17
Mt. Yotei	(33)	M						1	49	1	8	59	11
Iburi													
Tomakomai (Exp. Forest)	(34)	P	1		10	10	1				35	58	2
Shadai	(35)	P					4					4	1
Mt. Washibetsu	(36)	H						3				3	1
Mt. Tarumae	(37)	M		1							1	2	2
Mt. Showashinzan	(38)	H	1									2	1
Toyako Spa	(39)	H							2			2	1
Hiyama													
Mt. Kariba	(40)	M	14		7			4	39	7	19	20	7
Kenichi Spa	(41)	H			1				3			4	2
Esashi	(42)	P				1						1	1
Motoyama, Esashi	(43)	P	14		2	3						19	1
Kaminokuni	(44)	P	4			10					4	18	1
Nakasuda	(45)	H	80		30	177	1	2			69	359	20
Okushiri Is.	(46)	P	552			21		349			132	1054	47
Oshima													
Mt. Oshamanbe	(47)	H	7		3			1	3		2	16	2
Torizakigawa	(48)	H						1				1	

Area locality	(Code No.)	relative altitude	div	yez	hon	sch	pse	deu	ard	bea	hpn	hpc	ign	T	No. records
Mt. Torizaki	(49)	H	8				2							10	3
Nakayama Pass	(50)	H	11		38				1	5		8		63	1
Niyama	(51)	H	1											1	1
Narukawa	(52)	H	54		4		15	52	22	10		6		163	24
Nanae	(53)	P	1											1	1
Mt. Nanae	(54)	H							1					1	1
Mt. Yokotsu	(55)	M						1	9	64				74	11
Onuma	(56)	P						1	1			1		3	2
Kakkumi	(57)	H	263		51				56			188		558	18
Akagawa	(58)	H	24				81		15			4		124	25
Akanuma	(59)	P					1	1		1				3	3
Shirikishinai	(60)	P	17		3		8	1	7			25		61	10
Hakodate	(61)	P	14				108	72				4		198	31
Mt. Hakodate	(62)	H	349				9	6	334					698	95
Tobetsu	(63)	P	31		33		93		2			47		206	11
Ono	(64)	P	2											2	1
Garo	(65)	H								1				1	1
Yunosato	(66)	H							1					1	1
Gobanzaka	(67)	H	1												1
Fukushima	(68)	P	421		214		233		20	1		57		946	25
Mt. Daisengen	(69)	M	100		21				25	134		21		301	16
Era	(70)	P					1							1	1
Aomori Pref.															
Shimokita															
Oma	(71)	P										1		1	1
Zaimoku	(72)	P	7						1					8	1
Sai	(73)	P	31									3		34	1
Ikokuma	(74)	P			44				7					51	3
Kazamaura	(75)	P	1											1	1

Shimofuro	(76)	P	1							1		5		7		3
Akagawa	(77)	P	88		6							7		101		11
Yagen	(78)	H	137		48				19			59		263		13
Okuyagen	(79)	H	213		154				13			51		449		10
Mt. Osorezan	(80)	H										1		1		1
"Shimokita Pen."									1					1		1
Tsugaru																
Mt. Kinashi	(81)	H					1							1		1
Mt. Bonjuyama	(82)	H										1		1		1
Mt. Iwaki	(83)	M	5		1					70		3		79		13
Hirosaki	(84)	P										1	2	3		3
Mt. Azyariyama	(85)	H	6									16		22		2
Owani	(86)	H	4									2		6		4
Souma	(87)	P										1		1		1
Mt. Kudoji	(88)	H										1		1		1
Ikarigaseki	(89)	H	2		1				2					5		3
Ishinoto near Owani	(90)	H								1		1		2		1
Towada-san near Owani	(91)	H										1		1		1
Oguni	(92)	H	1									1		2		1
Komanodai	(93)	H										1		1		1
Mt. Ohanabe	(94)	M	1							9		1		11		2
Nurukawa Spa	(95)	H	1						1			1		3		1
Okawara	(96)	H	2									3		5		2
Mt. Hakkoda	(97)	M								7				7		2
Sukayu Spa	(98)	H								12		1		13		2
Tsuta Spa	(99)	H							2					2		1
Sanbongi	(100)	P										2	2	3		1
Lake Towada	(101)	H	2		1				2			2		8		5
Utarube	(102)	H										1		1		1
Total			2669	41	696	17	868	159	988	502	55	1018	3	7015		767

presumed to have the Tsugaru Strait as northern or southern distribution boundary of their subspecies. But no detailed studies have been published on the distribution of the bumblebees in this zoogeographically interesting areas.

In the present study, we prepare distribution maps of each species, examine the validity of subspecies, and discuss the significance of Blakiston Line as a geographical barrier for bumblebees.

Materials Examined

The materials used for this study were mainly from the collections deposited in the Institute of Low Temperature Science, (accumulated by Prof. S. F. Sakagami and by Dr. H. Fukuda) and Entomological Institute, Faculty of Agriculture, (accumulated by the late Prof. S. Matsumura and his many successors), Hokkaido University, Sapporo. Further the following collections were also available at our disposal. Tohoku National Agricultural Experiment Station (by Dr. Y. Maeta), Biological Institute, Tohoku-gakuin University (by Mr. K. Goukon), the Laboratory of Entomology, Obihiro University (by Prof. H. Nishijima, Mr. M. Usui and Mr. K. Tagawa), Biological Institute, Kushiro branch, Hokkaido University of Education (by Prof. Y. Akahira), Biological Institute, Hakodate branch, Hokkaido University of Education (by one of us, Mr. M. Munakata). The provenance of the examined specimens is given in Table 1, with the number of individuals. The code numbers for localities are given approximately from north to south, and the locations are mapped in Fig. 1. Most specimens were not accompanied with altitudianl data. In such cases, the relative altitude was given for each locality by the following criteria: M: Mountaineous localities judged to be at more than 1,000 m alt. H: Low mountaineous or hilly localities judged to be at 100～1,000 m. P: Plain and coastal localities judged to be at less than 100 m. Since this procedure inevitably weakens altitudinal information, the aspect of vertical distribution will not be touched.

Results

Distribution boundaries of species The distribution maps for each species (Fig. 2～10) give the following results: (subspecies are not considered unless specified): 1) *B. yezoensis* (Fig. 2) and *hypnorum* (Fig. 3) have not been obtained from Ohima Pen. *B. hypnorum* was collected from Mt. Kariba (1,520 m) while *yezoensis* only from the areas near Sapporo. The collecting effort paid for the northern part of Oshima Pen., the critical zone for these species, is still insufficient (Fig. 1). But, southern boundaries of these two species are certainly at inland, not at the Tsugaru St., because no specimen has been collected from the southernmost part of Oshima Pen. despite intensive collectings there. Their boundaries seem to coincide with Suttsu-Kuromatsunai Phytogeographical Line (Fig. 1) known as the northern boundary of beech and simultaneously the southern boundary of fir (15). 2)

Only three individuals of *B. ignitus* have been obtained from Aomori Pr. (Table 1), all not from Shimokita Pen. in spite of intense surveys there (Fig. 1, 3). Anyhow, it is certain that this species reaches the Tsugaru St., but is quite rare there. 3) Three Japanese species have not obtained from the areas concerned. *B. florilegus* is confined to the easternmost Hokkaido (10). *B. consobrinus* and *ussurensis* are also not found in Iwate

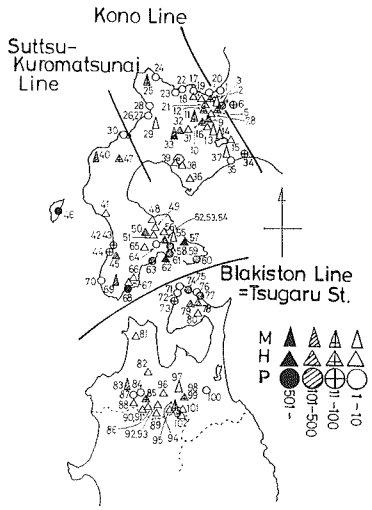

Fig. 1. Areas studied. Localities given by code number. Thick solid lines are biogeographical demarcations so far proposed. Cf. Table 1

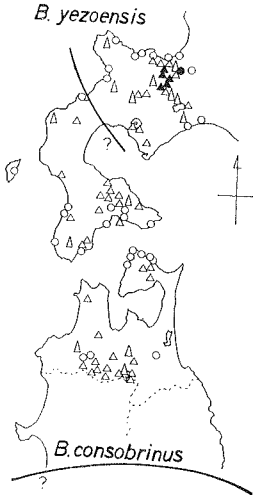

Fig. 2. Distribution map for *B. yezoensis* Matsumura and *B. consobrinus* Dahlbom in localities given in Fig. 1. In this and subsequent figures, blank: not collected; dark: collected. Thick solid lines show approximate distributional boundaries.

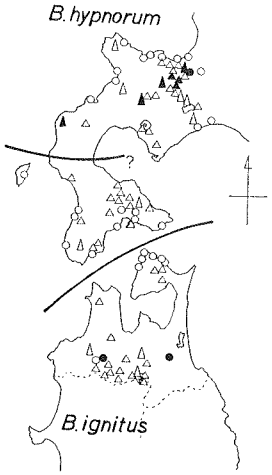

Fig. 3. Distribution map for *B. hypnorum* (L.) and *B. ignitus* Smith. Cf. legend for Fig. 2

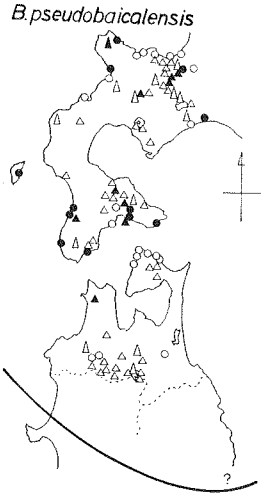

Fig. 4. Distribution map for *B. pseudobaicalensis* Vogt. Cf. legend for Fig. 2

Pr. (7). The northernmost record of *B. consobrinus* is in Sendai, Miyagi Pr. (Mt. Aoba, Sendai, coll. by. K. Goukon), and that of *B. ussurensis* is Tochigi Pr. (E. Katayama, pers. comm.). Their northern boundaries are estimated at inland of Honshu. 4) Recently *B. pseudobaicalensis* and *B. d. maruhanabachi* were discovered from some localities in Iwate Pr. (7). *B. pseudobaicalensis* is one of the commonest species (Table 1) in lowlands of Hokkaido, but had not been obtained from Honshu. In the present study, it was also found from Aomori Pr. (Table 1, Fig. 4). Thus, its southern boundary is obviously at inland of Honshu. It is still difficult to determine precisely the range of *B. d. maruhanabachi*. But, by the absence of any

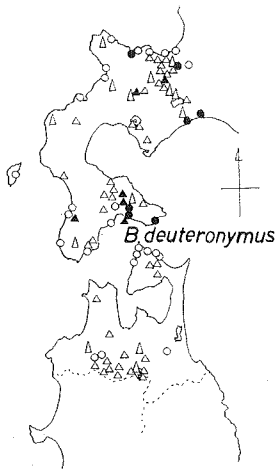

Fig. 5. Distribution map for *B. deuteronymus* Schulz. Cf. legend for Fig. 2

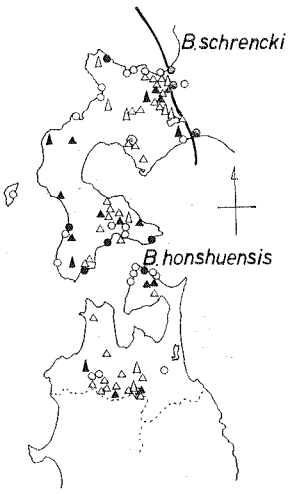

Fig. 6. Distribution map for *B. honshuensis* (Tkalců) and *B. schrencki* Morawitz. Cf. legend for Fig. 2

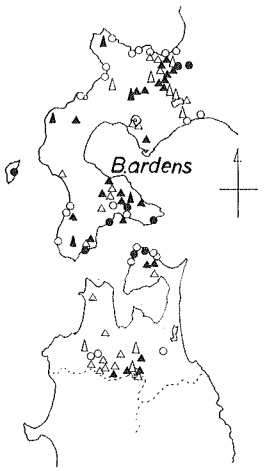

Fig. 7. Distribution map for *B. ardens* Smith. Cf. legend for Fig. 2

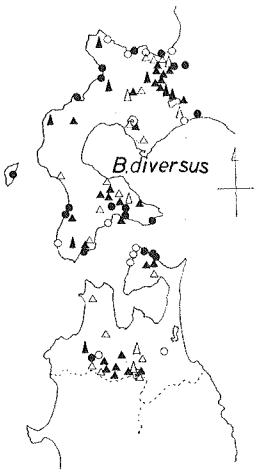

Fig. 8. Distributin map for *B. diversus* Smith. Cf. legend for Fig. 2

effective geographical barriers between Iwate Pr. and the Tsugaru St. we tentatively assume its occurrence near the areas facing the Strait. 5) Sakagami and Ishikawa (10) reported that *B. schrencki* is vicarious with *B. honshuensis*, separated by Ishikari Lowland i. e. Kono Line (14). The present study revealed its occurrence on the hills west of the lowland (Table 1, Fig. 6) giving a slight change to previous information. 6) Five species, (*B. honshuensis, ardens, diversus, hypocrita* and *beaticola*) have been collected amply from the studied area Fig. 6～10). It is noteworthy that all these species are separated into a pair of subspecies, each inhabiting Honshu and Hokkaido, and is separable only by the difference of coloration (10, 11, 12, 13). This requires re-examination of the subspecific difference, before the analysis of their distribution.

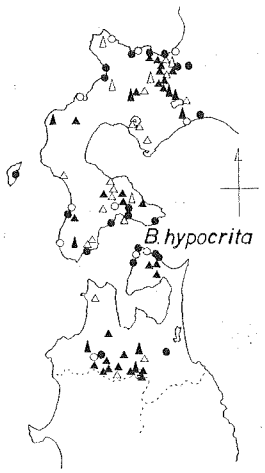

Fig. 9. Distribution map for *B. hypocrita* Pérez. Cf. legend for Fig. 2

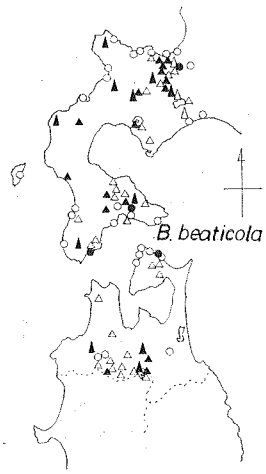

Fig. 10. Distribution map for *B. beaticola* (Tkalcû). Cf. legend for Fig. 2

Hair-coat variability of subspecies The validity of subspecies in the areas concerned was examined by comparing hair-coat coloration among diverse local populations. The selected populations are henceforth cited by abbreviations given below. The boundaries of these populations cannot be distinctly defined unless geographically isolated by effective barriers.

EH : Eastern Hokkaido, mainly from Obihiro, Kushiro, and its vicinity; Sa : Sapporo and its vicinity, from the areas covering Ishikari-, Shiribeshi and Iburi Provinces; Ok : Okushiri Is.; Os : Oshima Peninsula, Oshima and Hiyama Provinces; Sh : Shimokita Peninsula, mainly from Yagen, Okuyagen and a few localities of northernmost coast; Ao : Aomori Pr., excluding Shimokita Pen.; Iw : Iwate Pr. and Miyagi Pr., mainly from Morioka and its environs; Ka : Kanto Province, mainly from Tochigi Pr.; Na : Nagano Pr., mainly from Ina district; SJ : Southern Japan, various localities south of Tokyo and/or west of Nagano Pr.

Not all local populations were compared for each species. Often some populations were combined for getting a sufficient number of individuals for comparison. In such cases the combined populations are expressed by Sh+Ao, or Iw+Ka+SJ, etc.

Abbreviations HOK and HON are used to designate the populations of Hokkaido and Honshu, respectively. The variation analysis of *B. beaticola* is not given in the present paper, by the insufficiency of materials.

Comparison of hair-coat variability among local populations were carried out by the following step: 1) Variability on chosen body parts was classified into several stages, by the degree of adminxture of black or dark hairs (Fig. 11, T_n=metasomal tergum n. 2) Number of individuals belonging to each stage was couted, and the resulting frequency distributions were compared one another. 3) Difference of frequency distribution (henceforth DFD) was compared statistically by χ^2-test. Frequency distributions are halved, or rarely diveded into three parts to get a number of individuals necessary for the test. 4) To avoid arbitrariness in dividing, χ^2 was calculated for all possible ways of dividing. The devision point of stages was expressed parenthetically, e. g. (0~3/4~7). 6) The results are expressed according to the level of significance as follows: highly significant ++ $p<0.1\%$, significant + $p<2\%$, more or less significant + $p<5\%$ and insignificant − $p\geq 5\%$ (p: probability of chance occurrence). 7) Pairs of populations for

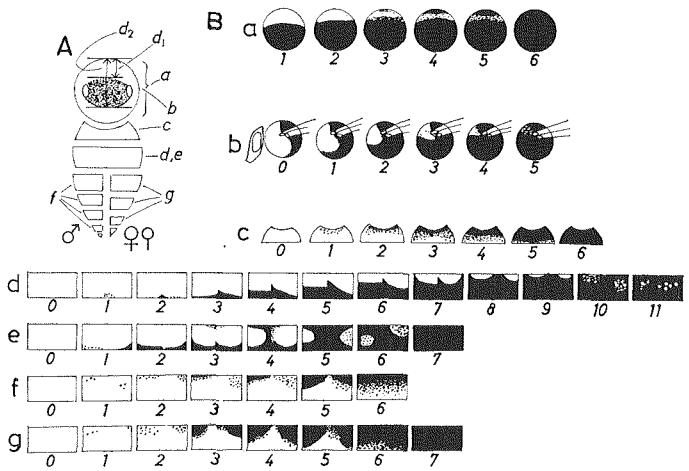

Fig. 11. (A) Body parts studied. Each alphabetical character corresponds to that in (B); d_1 and d_2: distance measured for estimation of width of collaris (explanations in text). (B). Degree of mixture of dark hairs on; a: mesosomal dorsum (*B. ardens*); b: pleura (*B. hypocrita* queen); c: T_1, (*B. ardens* and *B. hypocrita*); d: T_2, (*B. hyporita*); e: T_2, (*B. ardens*); f: T_3 and T_4, (*B. ardens*, male); g: $T_{2\sim6}$ (*B. honshuensis*, *B. diversus*). Unsymmetrical patterns in each stage of d~g show variety within it.

which χ^2-test was not applicable will not be proposed as principle.

B. honshuensis: *B. honshuensis tkalcui* was described mainly based upon the intense admixture of black hairs on $T_{4,5}$:

	h. honshuensis	*h. tkalcui*
T_4	absent or very sparse	sparse
T_5	sparse	more abundant.

Results obtained for three terga of all castes are shown in Fig. 12.

Queen The position and/or mode of frequency distribution gradually changed with a trend of northward melanism for all examined terga (usually no black hairs on other terga). But an insufficient number of individuals makes statistical test difficult except for Os/(Ka+Na+SJ) where, T_3 ±(0-1/2-3) and T_5 ++(0-4/5-7; 0-5/6-7), giving a highly significant DFD.

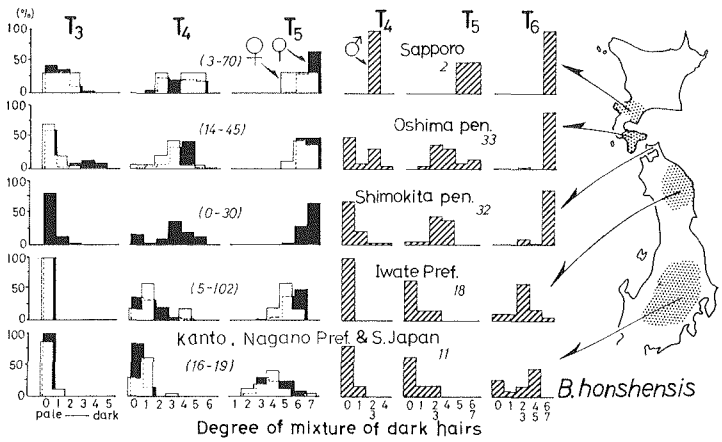

Fig. 12. Frequency distribution (in %) of color variation in diverse local populations of *B. honshuensis*. In this and subsequent figures, Queen: left, blank column; worker: left, black column; male: right, slanted column. Numerals in parentheses: number of individuals examined, queen (left) and worker (right). Numerals without parentheses: ditto, male

Worker The same trend was more obvious for all three terga (Fig. 12, left, black column):

T_3

	Os	Sh	Iw	Ka+Na+SJ
Sa	—	++(0/1-5)	++(0/1-5)	++(0/1-5)
Os		++(0-1/2-5) ±(0/1-5)	++(0/1-5)	++(0/1-5)

T_4

	Os	Sh	Iw	Ka+Na+SJ
Sa	—	±(0-4/5-6) −(0-1/2-6; 0-2/3-6)	++(0/1-6; 0-1/2-6; 0-2/3-6 0-3/4-6)	++(0-1/2-6; 0-2/3-6; 0-3/4-6)

Os	—	++(0/1-6; 0-1/2-6; 0-2/3-6; 0-3/4-6)	++(0/1-6; 0-1/2-6; 0-2/3-6; 0-3/4-6)
Sh		++(0-1/2-6) ±(0/1-6)	++(0/1-6; 0-1/2-6; 0-2/3-6)
Iw			+(0/1-6)

T_5

	Os	Sh	Iw	Ka+Na+SJ
Sa	—	—	++(0-5/6-7; 0-6/7)	++(0-6/7)
Os		—	++(0-5/6-7; 0-6/7)	++(0-6/7)
Sh			++(0-5/6-7; 0-6/7)	++(0-5/6-7; 0-6/7)
Iw				++(0-5/6-7)

DFD for T_3 was insignificant in Sa/Os, significant or more or less significant in Os/Sh, and highly significant in other all pairs. T_4 and T_5 showed a similar trend. DFD between three neighboring northern populations was insignificant, but mostly highly significant between three neighboring southern populations. DFD between pairs of any remote populations always was highly significant except for in T_4 Sa/Sh.

Male The same northward melanism was repeated for all examined terga (Fig. 12, right). The results of χ^2-test were:

T_4

	Sh	Iw	Ka+Na+SJ
Os	+(0-1/2-4)	++(0/1-4)	++(0/1-4)
Sh		++(0/1-4)	−(0/1-4)

T_5

	Sh	Iw	Ka+Na+SJ
Os	+(0-2/3-7) −(0-3/4-7)	++(0-1/2-7; 0-2/3-7; 0-3/4-7)	++(0-3/4-7)
Sh		++(0-/3-7; 0-/4-7)	++(0-3/4-7)

T_6

	Sh	Iw	Ka+Na+SJ
Os	—	++(0-5/6-7; 0-6/7)	++(0-5/6-7)
Sh		++(0-3/4-7; 0-5/6-7; 0-6/7)	++(0-6/7)

T_4: For all pairs except Sh/(Ka+Na+SJ), DFD was significant (+ or ++). T_5 and T_6: Highly significant for all pairs (except for Os/Sh) for which χ^2-test was applicable.

Summarizing, the advanced northward melanism was seen in all three castes. DFD in Os/Sh, separated by the Tsugaru Strait, was not particularly greater than that between the pairs in HOK or HON. These results indicate a clinal variation in this species and the invalidity of *B. h. tkalcui*

Sakagami and Ishikawa. Kendall's rank correlation for the rank of the local populations concerning the melanism among three terga also was statistically significant for two-third of six pairs:

	worker			male	
	T_4	T_5		T_5	T_6
T_3	$p>8.4\%$	$p<1.7\%$	T_4	$p<1.7\%$	$p<1.7\%$
T_4		$p<8.4\%$	T_5		$p<1.7\%$

Bombus* (*Thoracobombus*) *honshuensis (Tkalců, 1968) status nov.

Megabombus honshuensis Tkalců 1968: 47.

Bombus honshuensis tkalcui Sakagami and Ishikawa 1969: 160, syn. nov.

Geographical distribution: Hokkaido west of Ishikari Lowland, Honshu, Shikoku.

B. ardens: Sakagami and Ishikawa (10) compared the hair-coat variability of queens for diverse local populations as for mesosomal dorsum, T_1 and T_2, and concluded a gradation of southward melanism, with an intermediate condition in Aomori Pr. and with a notable exception in Okushiri Is. where no queen developed yellow bands.

We examined all the characters mentioned in females, and the admixture of black hairs on T_3 and T_4 as well as the coloration in the latter in males (Fig. 11).

Queen χ^2-test was applicable only for following characters and population pairs:

Mesosomal dorsum

	Ao+Iw	Ka	Ok
Os	++(0-2/3-6; 0-3/4-6)	++(0-2/3-6; 0-3/4-6)	++(0-2/3-6; 0-3/4-6; 0-4/5-6)

T_2

	Ao+Iw	Ka	Ok
Os	++(0-1/2-7; 0-2/3-7; 0-3/4-7)	++(0-1/2-7; 0-2/3-7; 0-3/4-7)	++(for every halving)
Ao+Iw		—	not applicable
Ka			++(0-6/7)

It is noticeable that DFD between Os (pale) or Ok (dark) and the all other populations (excluding Sh where χ^2-test unapplicable) was always highly significant, obviously also in Os/OK. While that in (Ao+Iw)/Ka was not significant (Fig. 13).

worker The above trend was repeated in workers for all parts, especially between Ok and all other populations:

Mesosomal dorsum

	Os	Sh	Ao+Iw	Ka	Ok
Sa	—	++(0-2/3-4/56)	$++^{oo}$	$++^{o}$	$++^{oo}$
Os		$++^{ooo}$	$++^{o}$	$++^{o}$	$++^{o}$

Sh	+(1-4/5-6)	++(1-4/5-6; 1-5/6)	++(1-5/6)
Iw		—	++(1-5/6)
Ka			++(1-5/6)

(°: sighificant for every division; °°: ditto, except for 1/2-6; °°°: ditto, except for 1-5/6)

T_1

	Os	Sh	Ka	Ok
Sa	—	++°	++°	++(0-3/4-6; 0-4/5-6; 0-5/6)
Os		++°	++°	×
Sh		±(0-5/6)		×

(°: significant for every division, except for 0/1-6; ×: not applicable)

T_2

	Os	Sh	Ao+Iw	Ka	Ok
Sa	—	++(0-1/2-7; 0-2/3-7)	++(0-2/3-7; 0-3/4-7; 0-4/5-7; 0-5/6-7; 0-6/7)	++°	++°
Os		++(0-1/2-7; 0-2/3-7)	++°	++°	++°
Sh			++(0-3/4-7; 0-4/5-7; 0-5/6-7; 0-6/7)	++(0-3/4-7; 0-4/5-7; 0-5/6-7)	++(0-3/4-7; 0-4/5-7; 0-5/6-7; 0-6/7)
Iw				—	++(0-4/5-7; 0-5/6-7 0-6/7)
Ka					++(0-6/7)

(°: significant for every division)

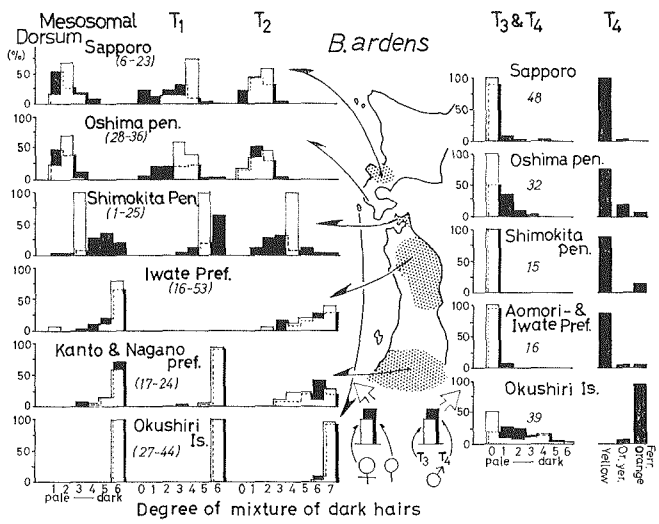

Fig. 13. Frequency distribution (in %) of color variation in diverse local populations of *B. ardens*. Cf. legend for Fig. 12

But, it is remarkable that Sh showed an intermediate condition between HOK and HON. DFD of mesosomal dorsum was significant (+ or ++) between Sh and other populations, while DFD in Sa/Os (HOK) or Iw/Ka (HON) was insignificant for all parts. Sh was also somewhat intermediate in T_1, less conspicuously. But, in general, Sh resembled more HON than

Table 2. Frequency distribution in diverse local populations of *B. ardens* Sm. (male); mixture of black hairs on T_3 and T_4, and coloration on T_4. Parenthetical numerals: percentage

T_3 degree of melanism	0	1	2	3	4	5	6	T
Sapporo and its vicinity (Sa)	48 (100)							48
Oshima Pen. (Os)	32 (100)							32
Shimokita Pen. (Sh)	15 (100)							15
Tohoku and mid- & southern Japan (Iw+Ka+SJ)	16 (100)							16
Okushiri Is. (Ok)	19 (50.0)	4 (10.5)	3 (7.9)	4 (10.5)	6 (15.8)	1 (2.6)	1 (2.6)	38

T_4 degree of melanism	0	1	2	3	4	5	6	T
Sapporo and its vicinity (Sa)	42 (87.5)	4 (8.3)	1 (2.1)		1 (2.1)			48
Oshima Pen. (Os)	16 (50.0)	11 (34.4)	3 (9.4)	1 (3.1)			1 (3.1)	32
Shimokita Pen. (Sh)	15 (100.0)							15
Tohoku and mid- & southern Japan (Iw+Ka+SJ)	15 (93.8)	1 (6.3)						16
Okushiri Is. (Ok)	7 (17.9)	10 (25.6)	9 (23.1)	5 (12.8)	6 (15.4)	2 (5.1)		39

T_4	yellow	intermediate	ferruginous Orange	T
Sapporo and its vicinity (Sa)	47 (97.9)	1 (2.1)		48
Oshima Pen. (Os)	24 (75.0)	6 (18.8)	2 (6.3)	32
Shimokita Pen. (Sh)	13 (86.7)		2 (13.3)	15
Tohoku and mid- & southern Japan (Iw+Ka+SJ)	14 (87.5)	1 (6.3)	1 (6.3)	16
Okushiri Is. (Ok)		2 (5.1)	37 (94.9)	39

HOK, because e. g. DFD in Sh/Ka was more or less significant for T_1, while that between Sh and HOK was highly significant for all parts.

Male The results (Fig. 13, right), again stress the peculiarity of Ok, as observed in females. About a half of males in Ok had dark hairs on T_3 while no such male was found in any other populations. In about 80% of individuals of Ok T_4 had some dark hairs, while percentage of such males was very low in other populations except Os (50%). Peculiarity of Ok is more conspicuous in the coloration of T_3. In this species, males normally have yellow $T_{1\sim4}$ and ferruginous orange $T_{5\sim7}$, and very rarely ferruginous oragne T_4. The result obtained (Table 2, Fig. 13, right) revealed that nearly all Ok males possessed ferruginous T_4, markedly contrasting any other populations. Again, Os has rather high percentage of this type indicating again slight resemblance between them.

The results are summarized: 1) In the mainland of Hokkaido, the coloration is very stable or only weekly variable among local populations, in general much paler than in Honshu. 2) In Honshu, a gradual southward melanism is recognized. 3) Among the populations of Honshu, Sh is characteristic with its variability intermediate between HOK and HON, but resembles more HON than HOK. 4) Difference in HOK/HON is obvious except for Sh. Therefore two subspecies should be retained as valid until the variability in Sh is fully examined with sufficient materials. 5) Ok is conspicuous. Females never exhibit pale-haired forms, resembling those from southern Japan. Males usually have some black hairs on T_3 and/or T_4, and nearly always have T_4 covered with ferruginous orange hairs. This specificity for all castes suggests lasting isolation of this population. The taxonomic status of this peculiar population will be given later after the accumulation of further information.

B. diversus: The differences so far mentioned between HON (*diversus*) and HOK (*tersatus*) are that pilosity on meso- and metasomal dorsum is deeper and $T_{2\sim5}$ has more dark hairs in the former (8, 12). As the first character is difficult to quantify, the variability of $T_{2\sim5}$ ($T_{3\sim6}$ for males) was studied. Stages for the degree of mixture of black hairs are shown in Fig. 11.

Queen The results on T_2 and T_3 confirmed the difference of the two subspecies, without showing obvious difference between local populations within each subspecies (Fig. 14, left, blank column). χ^2-test for each pair of populations showed:

T_3

	Sa	Os	Iw
EH	×	×	++(0-1/2-4; 0-2/3-4)
Sa		—	++(0-1/2-4; 0-2/3-4)
Os			++(0/1-4; 0-1/2-4; 0-2/3-4)

(× : not applicable)

T_4

	Sa	Os	Iw
EH	—	+(0–2/3–7) −(0–3/4–7)	++(0–5/6–7; 0–6/7)
Sa		++(0–2/3–7) −(0–3/4–7)	++(0–5/6–7; 0–6/7)
Os			++(0–5/6–7; 0–6/7)

T_5

	Sa	Os	Iw
EH	±(0–6/7) −(0–5/6–7)	++(0–6/7)	++(0–6/7)
Sa		±(0–6/7)	++(0–6/7)

DFD between Iw and any HOK was invariably highly significant for three terga examined. Within HOK DFD was highly significant for T_5 between EH/Os, while DFD in other pairs was more or less significant, or insignificant at least in one of the two possible dividings. This suggests a mild southward melanism within Hokkaido. Here again, Sh showed an intermediate condition, although the statistical test was not applicable.

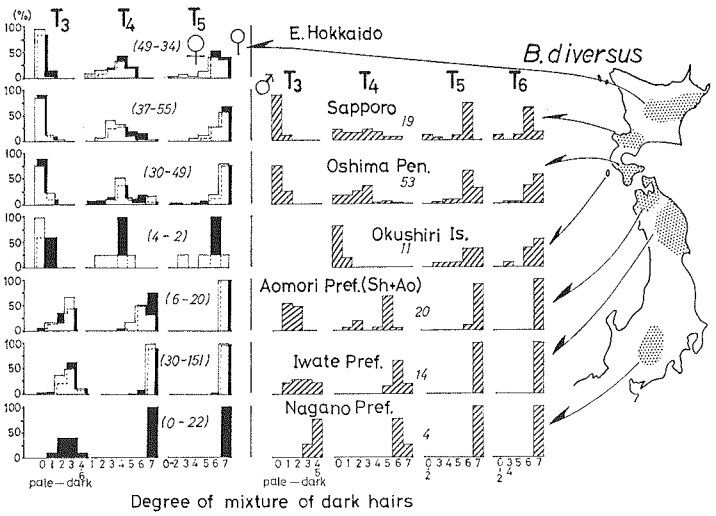

Fig. 14. Frequency distribution (in %) of color variation in diverse local populations of *B. diversus*. Cf. legend for Fig. 12

worker The results were nearly identical for all terga of workers too (Fig. 14, left, black column). The statistical results were:

T_3

	Sh+Ao	Iw	Na
EH	++(0/1–6; 0–1/2–6)	++(0/1–6; 0–1/2–6; 0–2/3–6)	++(0/1–4; 0–1/2–4)
Sa	++(0/1–6; 0–1/2–6)	++(0/1–6; 0–1/2–6; [0–2/3–6)	++(0/1–4; 0–1/2–4)

Os	++(0/1-6; 0-1/2-6)	++(0-2/3-6)	++(0/1-4; 0-1/2-4; 0-2/3-4)
Sh+Ao		+(0-2/3-6)	—
Iw			±(0-2/3-4)

T_4

	Sh+Ao	Iw	Na
EH	++(0/1-7; 0-1/2-7)	++(0/1-7; 0-1/2-7; 0-2/3-7)	++(0/1-7; 0-1/2-7)
Sa	++(0/1-7; 0-1/2-7)	++(0/1-7; 0-1/2-7; 0-2/3-7)	++(0/1-7; 0-1/2-7)
Os	++(0/1-7; 0-1/2-7)	++0-2/3-7)	++(0/1-7; 0-1/2-7; 0-2/3-7)
Sh+Ao		not applicable	++(0-6/7)
Iw			±(0-2/3-7)

(EH vs. Sa, EH vs. Os, Sa vs. Os: —)

T_5

	Sa	Os	Sh+Ao	Na
EH	±(0-6/7)	++(0-6/7)	++(0-6/7)	++(0-6/7)
Sa		—	++(0-6/7)	not applicable

DFD between any HOK and HON was quite obvious. Within HOK it was mostly insignificant (T_4) or χ^2-test was unapplicable (T_3), but for T_5 more or less significant (EH/Sa) or highly significant (EH/Os). While, within HON, significant (+ or ++) DFD was only in (Sh+Ao)/Na for T_4 and in (Sh+Ao)/Iw for T_3, respectively. These suggest the presence of a mild heterogeneity within both HOK and HON. But in HON, this might be caused by the peculiarity of Sh as in *B. ardens*, rather than a clinal variation.

Male In contrast to females, males showed a conspicuous southward melanism in all four examined terga (Fig. 14, right):

T_3

	Sh+Ao	Iw
Sa	++(0/1-5)	++(0/1-5)
Os	++(0/1-5)	++(0/1-5)
Sh+Ao		—

T_4

	Os	Ok	Sh+Ao	Iw
Sa	—	++(0-3/4-7) ±(0-2/3-7)	++(0-2/3-7; 0-3/4-7; 0-4/5-7)	++(0-2/3-7; 0-3/4-7; 0-4/5-7; 0-5/6-7)
Os		×	++(0-1/2-7; +(0-2/3-7)	++(0-2/3-7)
Ok			++(0-2/3-7; 0-3/4-7)	×
Ao+Sh				++(0-5/6-7)

T_5

	Sh-Ao	Iw
Sa	++(0-6/7)	++(0-6/7)

Os	++(0-6/7)	++(0-6/7)

T_6

	Os	Sh+Ao	Iw
Sa	++(0-6/7)	++(0-6/7)	++(0-6/7)
Os		++(0-6/7)	×

(× : not applicable)

Even within HOK, Sa/Os showed a highly significant difference at least for T_6. Three HON showed the same trend more evidently, especially for T_3 and T_4, although χ^2-test was not applicable for the most pairs. This gradual geographical change of melanism, however, seemed to be separated at the Tsugaru Strait. Because DFD in (Sh+Ao)/HOK was significant (+ or ++) for all examined terga, while that in HOK and in (Sh+Ao)/Iw was sometimes insignificant (for T_4 and T_3, respectively).

Melanism among local populations was also pairwise compared by Kendall's rank correlation and gave following results :

	T_4	T_5
T_3	$p<1.7\%$	$p<5\%$
T_4		$p<5\%$

Summarizing the results, 1) discrepancy of DFD between HOK and HON is obvious for females, although there might be a weak southward melanism within each of them ; 2) males showed more obviously a southward melanism in both HOK and HON. But the trend seemed to be disjuncted at the Tsugaru Strait, suggesting a mild isolation there. Thus, taxonomically the subspecies status should be retained, in spite of clinal melanism among populations. 3) Although not explained in detail, Ok seems different in T_5 of females and T_4 of males from other HOK.

Interestingly, this species exhibits an advanced melanism in Saghalin (11) and Is. Rishiri and Rebun, near the northernmost coast of Hokkaido (11). The populations will be analysed elsewhere.

B. hypocrita : Previous studies showed a segregation of HOK and HON, as to measosomal dorsum, T_1 and T_2 of queens (10). Besides these parts queen pleura and male T_2 and T_4 were examined in this study. Mesosomal dorsum varies mainly in the different development of yellow collaris which was expressed by the ratio of width of collaris (d_1) to the distance between posterior margin of scutum and the anterior margin of mesosoma (d_2) (Fig. 11).

Queen χ^2-test for DFD showed :

pleura

	Os	Iw
EH	—	++(1-3/4-5)
Sa	+(1-2/3-5) −(1-3/4-5)	—
Os		—

T_1

	Sa	Os
EH	—	—
Sa		—

T_2

	Os	Iw
EH	++(0-2/3-11)	++(0-3/4-11)
Sa	++(0-2/3-11)	++(0-3/4-11 ; 0-4/5-11)
Os		++(0-2/3-11 ; 0-3/4-11 ; 0-4/5-11)

Generally, the difference between HOK and HON was obvious in Fig. 15 (left, blank column), although χ^2-test was mostly unapplicable between them. DFD for T_1 and pleura was mostly insignificant within HOK. The results for T_2 showed highly significant DFD within HOK (EH/Os, Sa/Os). This seems to show north (east) ward melanism in HOK. But the tendency is subtle, and not evident from the figure. *B. hypocrita* in Hokkaido is rather chracterized by a stability of hair-coat judging from the narrow range of frequency distribution for T_2. Width of collaris also showed weakly a trend similar to that mentioned above (Table 3, left), i. e. the width was significantly (t-test) Os>EH or Sa :

	Sa	Os	Sh-Ao	Iw
EH	—	+	++	++
Sa		+	++	++
Oo			++	++
Sh-oA				—

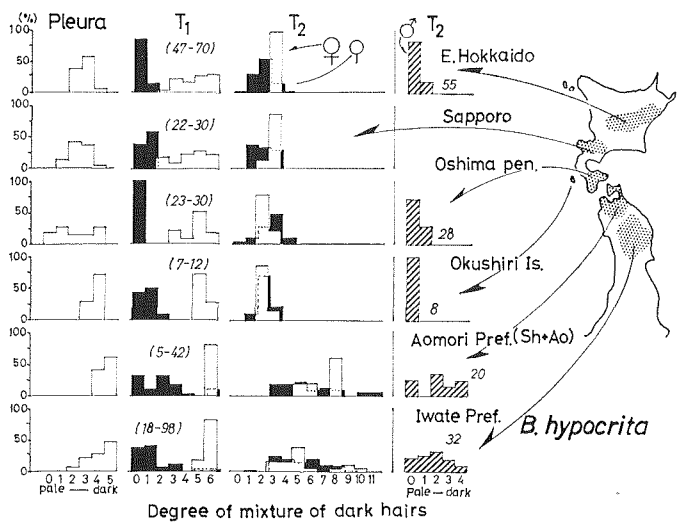

Fig. 15. Frequency distribution (in %) of color variation in diverse local populations of *B. hypocrita*. Cf. legend for Fig. 12

Table 3. The relative width of collaris ($100 \times d_1/d_2$) in diverse localities of *B. hypocrita* Pérez: (queen and worker)

	(queen)				(worker)		
	n	$\bar{x}$	σ_{n-1}		n	$\bar{x}$	σ_{n-1}
EH	25	39.8	2.57		67	34.7	4.02
Sa	25	39.3	4.09		31	37.8	4.22
Os	23	42.1	2.87		35	38.4	5.31
Ok	5	37.6	2.37		—	—	—
Sh+Ao	15	26.3	3.91	Sh Ao	27 28	32.7 30.4	5.38 5.26
Iw	7	37.6	4.69		69	27.2	60.0

Interestingly DFD within HON suggests also a northward melanism for all four characters (Fig. 15, Table 3), resulting in greater difference between Os and (Sh+Ao) than any other pairs between HOK and HON, although the statistical test was unapplicable for (Sh+Ao).

Worker The difference in HOK/HON was evident for T_1 and T_2 (Fig. 15, left, black column):

T_1

	Sa	Sh+Ao	Iw
EH	++(0-1/2-6)	++(0-1/2-6)	++(0-1/2-6)
Sa		++(0-1/2-6)	−
Os			+(0-1/2-6)

T_2

	Sa	Os	Sh+Ao	Iw
EH	—	—	++(0-1/2-11; 0-2/3-11; 0-3/4-11; 0-4/5-11)	++(0-1/2-11; 0-2/3-11; 0-3/4-11; 0-4/5-11; 0-5/6-11; 0-6/7-11)
Sa		±(0-1/2-11; 0-2/3-11)	++(0-2/3-11; 0-3/4-11; 0-4/5-11; 0-5/6-11)	++(0-3/4-11; 0-4/5-11; 0-5/6-11)
Os			++(0-3/4-11) ±(0-2/3-11)	++(0-3/4-11; 0-4/5-11; 0-5/6-11)
Sh+Ao				—

Difference within HOK is not obvious in the figure, although significant DFD was obtained in EH/Sa (T_1, ++) and in Sa/Os (T_2, +). This suggests a weak south (west) ward melanism, the reverse of that mentioned in queen. The width of collaris, however, showed mild north (east) ward melanism as in queen (Table 3, right), giving highly significant DFD in EH/Sa and EH/Os:

	Sa	Os	Sh	Ao	Iw
EH	++	++	+	++	++

Sa	−	++	++	++
Os		++	++	++
Sh			−	++
Ao				++

Within HON no evident difference was seen for T_1 and T_2. But, the collaris was rather developed in the northern populations, as Sh>Ao>Iw, showing significant DFD in Sh/Iw (++) and Ao/Iw (+). This trend of northward flavism in HON is the reverse of that mentioned in queen.

Male No significant difference was found on the variability of T_4 among local populations, although the variation range was quite ample (data not mentioned). In general, T_2 shows evidently advanced melanism in HON compared to HOK:

T_2

	Os	Sh+Ao	Iw
EH	—	++(0/1-4)	++(0/1-4; 0-1/2-4)
Os		++(0-1/2-4) +(0/1-4)	++(0/1-4; 0-1/2-4)
Sh+Ao			—

Summarizing the results, 1) difference of HOK and HON is evident in all castes, and HOK is characterized by the paler hair-coat and the narrower variation range at least for T_2, as suggested by previous work (10), 2) a northward melanism might occur in both HOK and HON, although the trend shows very complicated appearance, requiring more detailed studies.

Discussion

Concerning distributional boundaries of the bumblebee species inhabiting Hokkaido and Honshu, the seven theoretical groups are conceivable, not all of which are represented by actual cases (Information is still incomplete for asterisked species). I. Found only in Hokkaido with the southern boundary north of the Tsugaru Strait: *hypnorum, schrencki, yezoensis.* II. Only in Hokkaido, with the southern boundary at the strait: no actual case. III. In both Hokkaido and Honshu, with subspecific differentiation between two islands: *ardens, beaticola, deuteronymus*, diversus, hypocrita.* IV. Ditto, with the subspecific boundary either north or south of the strait: no actual case. V. Ditto, without subspecific differentiation: *honshuensis, pseudobaicalensis.* VI. Only in Honshu, with the northern boundary at the strait: *ignitus.* VII. Only in Honshu, with northern boundary south of the strait: *consobrinus*, ussurensis*.*

At the present the Tsugaru Strait does not limit the distribution at species level, except for *B. ignitus.* Naturally, this does not preclude the significance of the strait in the past. Instead, it is likely that many if not all species now absent in southern Hokkaido and northernmost Honshu had

once passed the land bridge formed between two areas during the maximum Würm, about 20,000 year ago (4, 5). At that age mean air temperature in Japan was about 10°C lower and the northern boundary of forests was at or near Oshima Peninsula (1, 4, 5). This suggests a southward withdrawal of many species now found in or near the peninsula, leaving only a few species in Hokkaido.

B. ignitus, the unique representative of VI, is a China-Japan element (10, 12), and very likely of the mid-temperature origin. It would have been confined in the southernmost Japan during the maximum Würm, unless a less probable alternative, its postglacial invasion in Japan via Korea, is assumed. Its absence in Hokkaido is explained by the delayed start of postglacial northward expansion, arriving at northern Honshu after formation of the Tsugaru Strait.

All or most other species are, with possible exception of *B. ardens* and *B. diversus*, of the northern origin in the broad sense, and could recolonize Hokkaido post-glacially, or even Saghalin, with exception of group VII, referred to below. The species of I, III, V are those either having passed the strait before separation of Hokkaido and Honshu followed by postglacial recolonization or having survived in certain refuges in southern Hokkaido during the glacial period, or those colonized Hokkaido postglacially. Among them, group I involves the species more adapted to cooler climate as supported by the occurrence of *B. hypnorum* and *B. schrencki* in Saghalin. These might remain in Hokkaido even during the glacial period.

The species endemic to Japan are *B. ardns* and *B. beaticola* of group III and *B. honshuensis* of V. *B. diversus* of III might be considered also "sub-endemic", as it is found in Saghalin but not in the continent except a single dubious record (12). Altitudinal distribution shows that, except *B. beaticola*, these species are adapted to relatively warmer climate. During the Riss-Würm interglacial period, Japan Archipelago had suffered a lasting isolation under relatively warm climate (5). This should contribute to the formation of these endemics. *B. beaticola*, closely allied to *B. modestus* of Siberia and Saghalin, is the most alpine species in Japan. This species might be differentiated during Würm.

B. ussurensis of group VII inhabits the continent and Honshu, but absent in Saghalin and Hokkaido. The Korean population does not subspecifically differ from that isolated in the high mountains of Honshu (9, 12). This species would arrive recently in Japan possibly in the maximum Würm. Its absence in Hokkaido and Saghalin favors invasion via Korea, not via Saghalin and Hokkaido. The situation is complicated in *B. consobrinus*, particularly in relation to the consubgeneric species, *B. yezoensis*. The former is absent in Hokkaido and Korea but present in Central Honshu, Saghalin and the continent (9, 12). The latter is absent in Saghalin and Korea but present in Hokkaido and the continent (Ordos and northern China (9, 12)). According to Tkalců (personal communication to Prof. Sakagami),

these two species are sympatric in Ordos. But they are morphologically very close in spite of a conspicuous difference in coloration. Further critical studies are required on the relation of these two taxa.

As discussed above, the Tsugaru Strait have not well functioned for speciation after Würm. Concerning subspeciation, however, it has functioned to some degree. A north-south clinal change of melanism is confirmed in four species. But it is somewhat disjunctive between the both sides of the strait in *B. ardens*, *B. hypocrita* and *B. diversus*. No remarkable difference in climatic conditions is formed between southernmost Hokkaido and northernmost Honshu (2). This suggests the disjunction of hair-coat variability has genetical bases. Possibly gene flow is lowered there apparently due to the presence of the strait. But the isolation should not be too strong, as suggested by the intermediate conditions in the populations of Shimokita Peninsula.

Another strange situation is found in Okushiri Is. which is considered isolated from the mainland of Hokkaido even in the maximum Würm (5). Among three of four species found in the island *B. hypocrita* and *B. diversus* show little difference from the conspecific mainland populations (the monomorphic species, *B. pseudobaicalensis*, not studied), while the third species *B. ardens* exhibits a marked deviation in female coloration. Arrival of the pioneer immigrants of these species at the island is assusmed quite old. The pioneers of *B. ardens* might be genetically so homogeneous that their descendants retained the possibly ancestral melanic coloration. But *B. ardens* is rather adapted to warmer climate. Its persistence in the island during Würm is not persuasive. An alternative hypothesis, which should be applied to the other two species, too, is the recent immigration of *B. ardens* after the isolation of Okushiri. Males of *B. ardens* in Okushiri possess dark hairs on T_4, the condition being shared by many males from Oshima Peninsula. This favors the latter hypothesis. Both hypotheses have serious advantages like some other explanations given above. Accumulation of further information is required to solve various chorological problems given in the present paper.

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Literature Cited

1)* Fujioka, T. 1971 "Elements of Japanese butterfly fauna and their provenance." *Insects and Nature*, 6 (6) 2–7 ; (7) 10–17 ; (8) 5–11.

2)* Japan meteorological Agency 1972 Climatic atlas of Japan II.

3) Løken, A. 1973 Studies on Scandinavian bumblebees (Hymenoptera, Apidae) *Nor. Ent. Tids.*, 20 : 1–218.

4)* Minato, M. 1967 "Eustatic movement of sea level and paleogeography of the Japanese Islands since the late Pleistocene : *Jap. Soc. Syst. Zool. Circular*, 36 : 1–3.

5)* ——— 1974 "The Quaternary system in Japan" Tsukiji.

6) Munakata, M. and S. Yamane 1970 Social Vespid wasps from the southern part of the Oshima Peninsula and the Okushiri Island, northern Japan (Hymenoptera, Vespidae). *Kontyu*, 38 (4) : 281–291.

7)* Nakaya, M. and Y. Maeta 1979 Bumblebee fauna in Iwate Pref. *Iwate-Mushi-no-Kai. Kaiho*, 3 : 7–14.

8) Sakagami S. F. 1953 Ueber *Bombus* (*Diversobombus*) *diversus* Smith. (Systematic Studien der Hummeln IV.) *J. Fac. Sci. Hokkaido Univ.* VI. *Zool.*, 11 : 182–192.

9) ——— 1975 Some bumblebees from Korea with remarks on the Japanese fauna (Hymenoptera, Apidae). *Ann. Hist.-nat. Mus. Nat.* Hung., 67, 1976.

10) ——— and R. Ishikawa 1969 Note preliminaire sur la répartition géographique des bourdons japonais, avec descriptions et remarques sur quelques formes nouvelles ou peu connues. *J. Fac. Sci Hokkaido Univ.* VI. *Zool.*, 17 : 152–196.

11) ——— and ——— 1972 Notes supplémentaire sur la taxonomie et répartition géographique de quelques bourdons Japonais, avec la description d'une nouvelle sous-espèce. *Bull. Natn. Sci. Mus. Tokyo*, 15 (4) : 607–616.

12) Tkalcú, B. 1962–1966 Contribution à l'étude des bourdons du Japan, I. Bull. Soc. ent. Mulhouse Nov.-Dec. 1962 : 81–100 ; II. Ibid. Jan.-Fév.-Mars, 1965 : 1–14 ; III. Ibid. Mars-Avril, 1966 : 17–21.

13) ——— 1968 Neue Arten der Unterfamilie Bombidae der paläarktischen Region (Hymenoptera, Apidae). *Acta ent. bohemoslov.*, 65 : 21–51.

14)* Tokuda, M. 1969 "Biogeography" Tsukiji.

15)* Yoshioka, K. 1973 "Phytogeography" 85 pp. Kyoritsu.

* In Japanese