日本列島におけるクロショウジョウバエ区の地理分布

Geographic Distributions of the *Drosophila virilis* section (Diptera, Drosophilidae) in the Japanese Islands

WATABE Hideaki and TAKAHASHI Masafumi*

Biological Laboratory, Sapporo Campus, Hokkaido University of Education, Sapporo 002-8502

*Tsubetsu Junior High school, Tsubetsu, 092-0224

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渡部　英昭・高橋　将史*

北海道教育大学札幌校生物学教室

*北海道津別中学校

ABSTRACT

The collection records on the geographic distribution of the *Drosophila (Siphlodora) virilis* section were complied, based on the field surveys covering various climatic zones from subtropical to cool temperate districts in the islands of Japan. All of the six species groups of the *virilis* section were found, indicating a high biodiversity for this taxonomic group in Japan. The species groups showed different patterns of the distribution range. The *angor* species group, which included three members, *Drosophila angor* Lin & Ting, 1971, "*D. angor* A" (originally found from southwestern China) and "*Drosophila* species 1" (probably a new member), inhabited the subtropical zone in the Nansei (southwestern) Islands from Iriomote to Amami. The northern border for the distribution of this group is considered to lie between Amami and Yakushima, where the Watase Line runs, dividing the Oriental Region and the Palearctic Region in the zoogeography. The *polychaeta* group, *Drosophila latifshahi* Gupta & Ray-Chaudhuri, 1970 and *Drosophila daruma* Okada, 1956, preferred warm climates, and the former species was distributed from Iriomote to the Okinawa mainland and the latter from Iriomote to the Izu Peninsula in central Honshu, along the evergreen forest belt. On the other hand, the remaining four species groups of the *virilis* section, the *melanica*, the *quadrisetata*, the *robusta* and the *virilis* groups, had the range of distribution from Hokkaido to Kyushu, including adjacent islands. The *virilis* group and *Drosophila moriwakii* Okada & Kurokawa, 1957 of the *melanica* group were abundant in deciduous broad-leaved forests mixed with conifers in the cool temperate zone of Hokkaido. The ranges of distribution differed from species to species within the *robusta* species group.

Drosophila gani Watabe, Liang & Zhang, 1990 was common in riparian drosophilid communities from Honshu to Kyushu, whereas *Drosophila okadai* Takada, 1959 was common in those of Hokkaido. The northern border of *Drosophila gani* was the Tsugaru Strait between Honshu and Hokkaido, where the Blackiston Line lies, splitting the Palearctic Region into sub-regions.

Key words: biogeography, Watase Line, Blakiston Line, Oriental Region, Palearctic Region

1. INTRODUCTION

The fruit fly *Drosophila* is one of the model organisms, having been used in various research fields of biology, especially in genetics. The most famous species is *Drosophila melanogaster* Meigen, 1830. This species is a cosmopolitan domestic species occurring in houses and breweries, and its wide range of distribution is due to artificial transportations. Excepting several domestic species such as *Drosophila melanogaster*, all species of wild drosophilid flies possess their own distribution ranges.

Drosophila virilis Sturtevant, 1916 and its closely related members are distributed abundantly in temperate forests of North America, northern Europe and East Asia, and have been extensively studied from the evolutionary point of view by North American researchers, since the early 1940's (Sturtevant, 1942; Patterson et al., 1940; Patterson and Wheeler, 1942).

Hsu (1949) established the *Drosophila virilis* section including the *virilis* species group and its related *robusta* and *melanica* species groups in the subgenus *Drosophila*, based mainly on the morphological characters of the male genitalia. Further, Throckmorton (1975) hypothesized the *virilis-repleta* radiation in the evolution of the subgenus *Drosophila*, in which many members of this taxon might have emerged in different areas of the northern Hemisphere. Since then, the evolutionary process on the *robusta* group and the *melanica* group have been intensively studied (Narayanan, 1973; Levitan, 1982; Throckmorton, 1982). Yassin (2013) has recently transferred the *virilis* section groups from the subgenus *Drosophila* to the subgenus *Siphlodora*, based mainly on the molecular data.

Our knowledges on the *virilis* section had been scanty in mainland China and East Siberia, until the early 1980's (Toda and Peng, 1989; Toda et al., 1996). China occupies an important position, when we consider the evolution of the *virilis* section, because its early adaptive radiation is considered to have occurred in low geographic latitudes of East Asia (Throckmorton, 1982). We have engaged in faunal surveys of drosophilid flies, since the 1980's in China and the 1990's in East Siberia. As the results of those faunal studies, two species groups, the *quadrisetata* group (Toda and Peng, 1989) and the *angor* group (Watabe and Peng, 1991), were newly established in the *virilis* section. At the same time, faunal studies on the *virilis* section re-started in Japans. In East Asia including Japan the green-belt spreads continuously from the tropics of Southeast Asia to the frigid zone of East Siberia. Drosophilid flies might have spread their distribution range northwards along the green belt, and some of them might have immigrated to North America via the Bering land-bridge between the Old and the New

Worlds (Wang et al., 2006b). Micro-habitats of the *virilis* section flies are quite biased to riparian environments such as streams or lakes, and it is rather difficult to collect the *virilis* section flies in comparison to other flies living in forests or grasslands. Thus, even in Japan, especially in Kyushu and the Nansei Islands, our knowledge on the *virilis* section was not enough to trace its evolutionary process.

We obtained distinct geographic borders for the range expansion of the species and the distribution record new to Japan. The present article shows geographic distributions of the *virilis* section in Japan, having been accumulated since the mid 1990's, and we discuss the different patterns of distribution in relation to vegetation and climates in different districts of Japans.

2. AREAS SURVEYED AND COLLECTION METHODS

Climate and vegetation of collection localities: Field surveys were made in various climatic or vegetation zones from Hokkaido, the most northern district of Japan, to Iriomote and Ishigaki, the most southern one in the Nansei Islands, extending from Kyushu to Taiwan (Fig. 1). Hokkaido is in the cool temperate zone, and deciduous broad-leaved trees are dominant in forests of its southern districts and conifers are so in those of its northern and eastern districts. The winter of Hokkaido is severe with low temperatures and deep snow (Table 1). In the Tohoku district of northern Honshu, deciduous trees are dominant in forests. The lucidophyllous (=evergreen broad-leaf) forests spread from Kyushu to areas of the Pacific side in the Kanto district of mid-Honshu (Hotta, 1974; Hukushima and Iwase, 2005). There is much snow in the

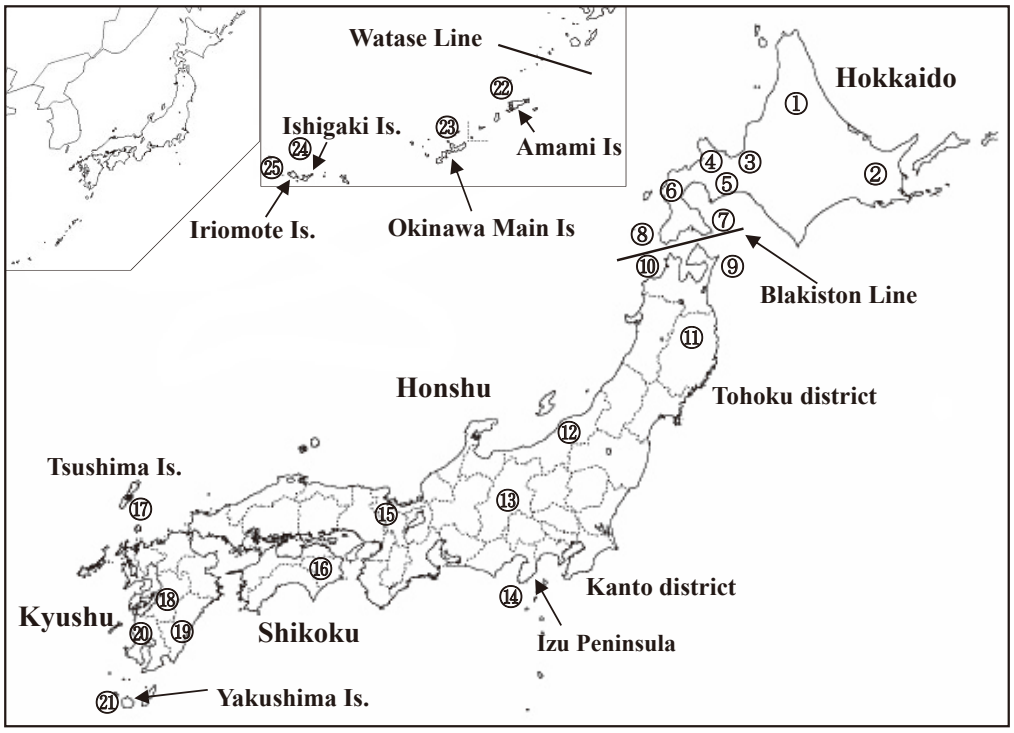

Figure 1. Map of the Japanese Islands shows collection places of the *Drosophila virilis* section. Locality number is explained in the text.

areas of the Sea of Japan side during the winter (see, the climatic data of Niigata Prefecture in Table 1). Both Iriomote and Ishigaki are in the subtropical zone, where the subtropical rainforest well develops and the average temperature of January (the coldest month) is about 18℃.

Collection methods: Most of the *virilis* section flies are strongly restricted to streams, and cannot be captured at all at a trap site distant which is half a meter away from the stream-edge or the water surface. The fly collections were made by two methods, net sweepings and fruit bait-traps. The *virilis* section flies used ridges, gaps or undersides of rocks as the resting site during the daytime, and we used insect nets for collections from such places (Fig. 2A). In the morning and evening, adult flies become active for feedings, and we used fermenting bananas and put them on timber piles laid just above the water surface (Fig. 2B). Most of flies stayed on the undersides of piles (Fig. 2C). Two species of the *robusta* subgroup of the *robusta* species group (*Drosophila sordidula* Kikkawa & Peng, 1938 and *Drosophila pseudosordidula* Kaneko, Tokumitsu & Takada, 1964) and two species of the *melanica* species group (*Drosophila tsigana* Burla & Gloor, 1952 and *Drosophila pengi* Okada & Kurokawa, 1957) dwell in natural forests. We obtained these four species in the present field surveys, but we excluded them from the present discussion on the distribution and abundance of the *virilis* section, due to the limiting number of specimens obtained near watersides. The collection date

Table 1. Temperature and snowfall in 8 localities from Hokkaido to Okinawa Prefecture in Japan.

Prefecture	Annual mean temperature (℃)	Mean of the highest temperatures (℃)[1)]	Mean of the lowest temperatures (℃)[2)]	Days with snowfall per year
Hokkaido	9.8	29.1	−6.3	129
Aomori	11.1	31.4	−5.2	107
Niigata	14.4	33.3	0.3	63
Shizuoka	17.2	32.1	1.7	12
Kyoto	16.4	35.2	0.9	17
Tokushima	17.0	33.8	1.7	10
Kagoshima	18.9	33.4	4.3	5
Okinawa	23.1	31.6	14.1	0

The meteorological data were provided from the Statistic Bureau, Ministry of Internal Affairs and Communications of Japan. [1)] Mean of daily highest temperatures in the warmest month. [2)] Mean of daily lowest temperatures in the coldest month.

Figure 2. Collection sites of the *Drosophila virilis* section species in streams. Adult flies were collected under or between rocks (marked with red circles) in streams by insect nets (A). Fermenting bananas were put on piles laid just above the water surface (arrows in B). Adult flies were gathered mostly on the underside of piles (arrows in C).

and locations are shown below, with the mark of numeric characters in the map of Figure 1.

[Hokkaido]

① Northern Hokkaido: River Sanrugawa, Shimokawa, Nayoro. 17–18. vii. 2005.

② Eastern Hokkaido: R. Churuigawa, Kanaya, Sibetsu. 2–3. viii. 2006.

③ R. Ichibangawa, Aoyama, Tobetsu. 3. vi. –19. vii. 2004.

④ R. Furubiragawa, Takinosawa, Furubira. 18–19. vii. 2004.

⑤ Central Hokkaido: R. Toyohiragawa, Usubetsu, Jozankei, Sapporo. 11. vii. –16. viii. 2004.

⑥ R. Kuromatsunaigawa, Mt. Kuromatsunai, 18–19. vii. 2004, 22–24. vii. 2011.

⑦ Kameda Peninsula: R. Shiodomarigawa, R. Nisimatagawa, Yabetsu Dam, Hakodate, 10–11. vii. 2004, 28–30. x. 2007, 5–6. x. 2010; R. Matsukuragawa and R. Shiodomarigawa, 2–3. viii. 2014.

⑧ Matsumae Peninsula: R. Oibegawa, Matsumae, Oshima, 23–24. vii. 2005.

[Honshu]

⑨ Aomori Prefecture, Shimokita Peninsula: R. Metokigawa, Kazamaturimura, R. Ikokumagawa, Ikokuma, Ohhatagawa, Komokunazawa, Ohhata, 13–14. ix. 2004, 1–2. ix. 2015.

⑩ Aomori Prefect, Tsugaru Peninsula: R. Masukawagawa, Mt. Masukawa, Mimmaya, 11–12. ix. 2004.

⑪ Iwate Prefecture: R. Chikugawa, Ohshida, Morioka. 12–13. vi. 1995.

⑫ Niigata Prefecture: R. Annogawa, Mt. Gotouzan, Hatae, Aganogawa, 5–6. ix. 2006.

⑬ Nagano Prefecture: R. Azusagawa, Shimasimatani, Azumino, 19. x. 1998.

⑭ Shizuoka Prefecture: R. Motodanigawa, Namerikawa, Amagi Pass, Izu Peninsula. 28–30. x. 2007, 30. x. – 1. xi. 2011.

⑮ Kyoto Prefecture: R. Yuragawa, Ashu Experimental Forest of Kyoto University, Miyama, 5–6. ix. 2005.

[Shikoku]

⑯ Tokushima Prefecture: R. Futodanigawa, Koyadaira, 16–17. x. 2005.

[Tsushima Islands]

⑰ Nagasaki Prefecture: R. Sumogwa, Sumo, Mitsusimamachi, Tsushima, 27. ix. 1996.

[Kyushu]

⑱ Kumamoto Prefecture: R. Nigakobedanigawa, Gokanosho, Momiki, Yatsushiro, 15–18. vii. 1997.

⑲ Miyazaki Prefecture: R. Mitsyue, Ohkouchi, Shiiba, 19–20. vii. 1997; R. Itayagawa, Miyazaki Experimental Forest of Kyushu University, Shiiba, 27–28. ix. 2005.

⑳ Kagoshima Prefecture: R. Nigakobedanigawa, Jusso, Ohguchi, 29–30. ix. 1996.

[Nansei Islands]

㉑ Kagoshima Prefecture: R. Kuromi, Kurio, Yakushima Island, 2–3. x. 1996, R. Miyanoura, Miyanoura, Yakushima Island, 30. ix. – 1. x. 2005.

㉒ Kagoshima Prefecture: R. Yakukastu, Ukenmura, Amami, 11–13. iii. 2003.

㉓ Okinawa Prefecture: R. Yona, Experimental Forest of Ryukyu University, Kunigamison, Okinawa mainland, 9–11. xi. 2006.

㉔ Okinawa Prefecture: R. Tu-urogawa, Mt. Omoto, Ishigaki Island, 11–13. iii. 2004, 20–23. iii. 2015.

㉕ Okinawa Prefecture: R. Mahregara, R. Uranaigawa Funaura, Iriomote Island, 9–10. iii. 2004, 19–23. iii. 2008.

Table 2. Number of adult flies of the *Drosophila virilis* section, collected with fermenting bananas.

Localities	Iriomote	Ishigaki	Okinawa	Amami	Yakushima	Miyazaki	Tokushima	Kyoto	Izu	Niigata	Tsugaru	Shimaokita	Matsumae	Kameda
No. in Figure 1	㉕	㉔	㉓	㉒	㉑	⑲	⑯	⑮	⑭	⑫	⑩	⑨	⑧	⑦
D. okadai						4	22	1	7	16	17	20	164	217
D. neokadai					50	71	262	66	220	252	40	273	118	18
D. gani						45		9	68	118	21	53		
D. lacertosa					15	210	69	98	40	268	30	13	104	41
D. quadrisetata					8	252	32	6	19	131	9	17	7	23
D. flumeinicola				10		23	2	40	2					
D. ezoana						6				24	2	1	37	2
D. moriwakii						1				2	3		10	8
D. daruma	264	147	146	145	14	77	76	1	1					
D. latifshahi	16	7												
D. fluvialis	10		15	24										
D. angor	5	3	58	75										
Total	295	157	219	254	87	689	463	221	357	811	122	377	440	309

Localities	Kuromatsunai	Jozankei	Furubira	Aoyama	Shibetsu	Nayoro	Total
No. in Figure 1	⑥	⑤	④	③	②	①	
D. okadai	180	250	150	55	113	159	1375
D. neokadai	48	215	116	37	18	30	1834
D. gani							314
D. lacertosa	116	198	46	18	12	33	1311
D. quadrisetata	20	78	3	1	162	455	1223
D. flumeinicola							77
D. ezoana	31	315	3	43	16	44	524
D. moriwakii	2	99	1	1	2		128
D. daruma							871
D. latifshahi							23
D. fluvialis							49
D. angor							141
Total	397	1155	319	155	323	721	7870

3. RESULTS AND DISCUSSION

A total of about 8000 specimens of 15 species including two questionable ones were obtained in the present study, which belong to 6 species groups. They are as follows:

The *angor* species group Watabe & Peng

Drosophila angor Ling & Ting, 1971: 31♂44♀ (㉒ in Fig. 1), 47♂37♀ (㉓), 18♂14♀ (㉔), 20♂28♀ (㉕).

"*D. angor* A", in Wang et al., (2006a, p.486): 1♀ (㉕).

"*Drosophila* sp. 1", like *Drosophila hei* Watabe & Peng, 1991: 1♂2♀ (㉒).

The *melanica* species group Sturtevant

Drosophila moriwakii Okada & Kurokawa, 1957: 1♂1♀ (②), 1♂ (③), 1♂ (④), 68♂31♀ (⑤), 2♂ (⑥), 9♂4♀ (⑦), 6♂4♀ (⑧), 1♂2♀ (⑩), 1♂ (⑱), 1♂ (⑲).

The *polychaeta* species group Sturtevant

Drosophila daruma Okada, 1956: 1♂ (⑭), 1♀ (⑮), 29♂47♀ (⑯), 2♂1♀ (⑰), 28♂49♀ (⑲), 1♂3♀ (⑳), 12♂12♀ (㉑), 74♂71♀ (㉒), 71♂75♀ (㉓) , 188♂199♀ (㉔) , 150♂164♀ (㉕).

Drosophila latifshahi Gupta & Ray-Chaudhuri, 1970: 3♂4♀ (㉔), 6♂10♀ (㉕).

The *quadrisetata* species group Toda & Peng

Drosophila quadrisetata Takada, Beppu & Toda, 1979: 226♂229♀(①), 80♂82♀(②), 1♂0♀(③), 2♂1♀(④), 148♂102♀(⑤), 75♂65♀(⑥), 120♂107♀(⑦), 37♂27♀(⑧), 108♂65♀(⑨), 26♂14♀(⑩), 63♂68♀(⑫), 1♂1♀(⑬), 11♂8♀(⑭), 35♂31♀(⑮), 14♂18♀(⑯), 1♂(⑰), 160♂103♀(⑱), 105♂66♀(⑲), 12♂13♀(⑳), 3♂5♀(㉑).

Drosophila flumenicola Watabe & Peng, 1991: 1♂2♀(⑭), 19♂21♀(⑮), 1♂1♀(⑯), 1♂6♀(⑰), 1♀(⑱), 14♂9♀(⑲), 47♂73♀(⑳), 1♂9♀(㉓).

The *robusta* species group Sturtevant

Drosophila okadai Takada, 1959: 80♂79♀(①), 73♂40♀(②), 43♂12♀(③), 67♂49♀(④), 106♂44♀(⑤), 115♂ ♀65(⑥), 128♂111♀(⑦), 137♂27♀(⑧), 20♂27♀(⑨), 7♂10♀(⑩), 118♂79♀⑪), 10♂6♀(⑫), 4♂3♀(⑭), 1 ♂(⑮), 9♂13♀(⑯), 25♂21♀(⑱), 7♂2♀(⑲).

Drosophila neokadai Kaneko & Takada, 1966: 18♂12♀(①), 14♂4♀(②), 23♂14♀(③), 106♂89♀(④), 148♂102♀(⑤), 115♂75♀(⑥), 33♂18♀(⑦), 90♂28♀(⑧), 208♂65♀(⑨), 26♂14♀(⑩), 38♂39♀(⑪), 159♂93♀(⑫), 3♂2♀(⑬), 86♂134♀(⑭), 35♂31♀(⑮), 144♂118♀(⑯), 1♂5♀(⑰), 91♂62♀(⑱), 120♂132♀(⑲), 70♂67♀(⑳), 34♂44♀(㉑).

Drosophila gani Watabe, Liang & Zhang, 1989: 37♂35♀(⑨), 15♂6♀(⑩), 1♂3♀⑪), 67♂51♀(⑫), 58♂29♀(⑭), 13♂4♀(⑮), 5♂4♀(⑱), 30♂15♀(⑲), 64♂65♀(⑳).

Drosophila lacertosa Okada, 1956: 17♂16♀(①), 10♂2♀(②), 13♂5♀(③), 32♂14♀(④), 126♂72♀(⑤), 81♂ ♀35(⑥), 63♂27♀(⑦), 73♂31♀(⑧), 7♂6♀(⑨), 18♂12♀(⑩), 11♂16♀⑪), 166♂102♀(⑫), 1♂2♀(⑬), 32♂18♀(⑭), 49♂49♀(⑮), 38♂31♀(⑯), 6♂4♀(⑰), 393♂269♀(⑱), 101♂109♀(⑲), 146♂128♀(⑳), 22♂15♀(㉑).

The *virilis* species group Sturtevant

Drosophila ezoana Takada & Okada, 1957: 29♂15♀(①), 7♂9♀(②), 25♂18♀(③), 3♂(④), 135♂177♀(⑤), 20♂11♀(⑥), 3♂6♀(⑦), 25♂12♀(⑧), 1♂(⑨), 1♂1♀(⑩), 1♂2♀(⑪), 20♂4♀(⑫), 1♂(⑱), 5♂1♀(⑲).

Drosophila kanekoi Watabe & Higuchi, 1979: 1♂1♀(③), 3♂5♀(⑤), 4♂3♀(⑧), 1♂1♀(⑫).

Ungrouped species in the *virilis* section

Drosophila fluvialis Toda & Peng, 1989: 16♂8♀(㉒), 10♂5♀(㉓), 3♂2♀(㉔), 6♂4♀(㉕).

Species probably belonging to the *virilis* section

Zaprionus flavofasciatus Takada, Beppu & Toda, 1979: 2♂2♀(①), 14♂13♀(⑦), 5♂1♀(⑧), 20♂11♀(⑨).

Drosophila calidata Takada, Beppu & Toda, 1979: 8♂2♀(⑦), 1♂1♀(⑧), 3♂2♀(⑨).

The species groups or species of the *virilis* section showed quite different patterns of geographic distribution with each other (Fig. 3). With regards to the *angor* species group, all members have been recorded from South Asia to southwestern China, Sri Lanka, India and China. *Drosophila angor* itself has been recorded from mainland China and Taiwan (Lin and Ting, 1971; Toda and Peng, 1989: Chen and Watabe, 1993), and in Japan it inhabits riparian environments from Iriomote to Amami of the Nansei Islands. Takada and Wakahama (1967) reported this species in the Okinawa mainland, although they did not describe it. We did not obtain any adult flies of *Drosophila angor* in Yakushima, and thus its northern range of geographic distribution is considered to lie between Amami and Yakushima. During our field survey, two questionable species of the *angor* group were captured in Iriomote and Amami, of which one species from Iriomote was considered to be conspecific to "*Drosophila*

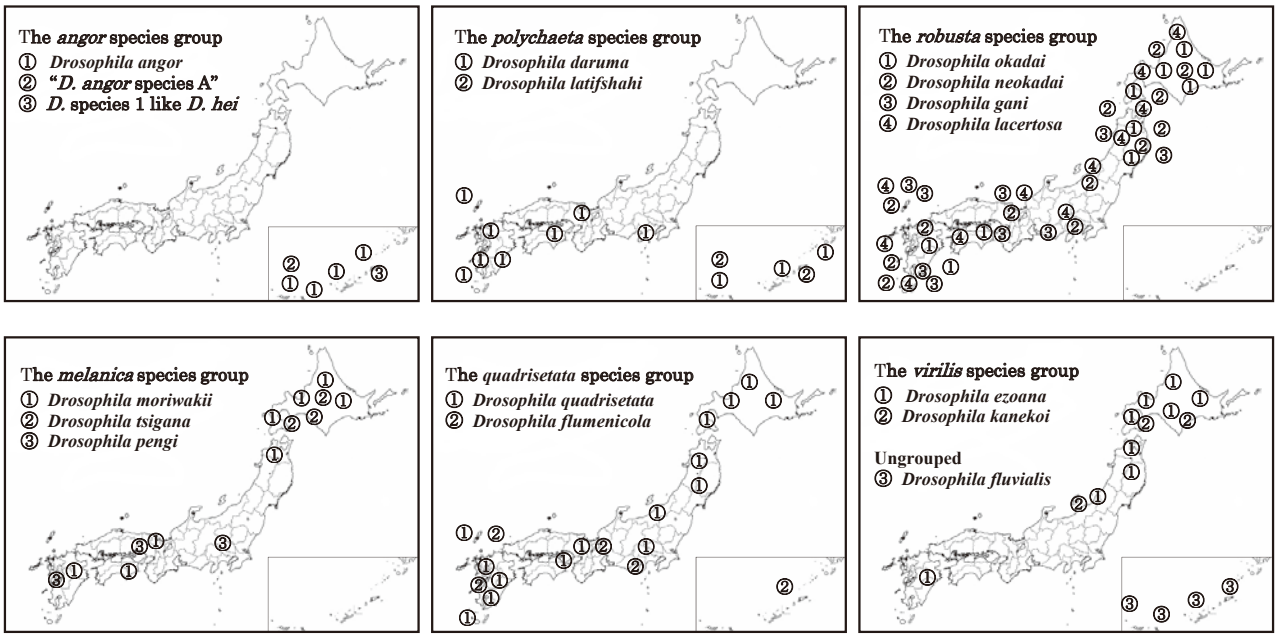

Figure 3. The distribution patterns of the *Drosophila virilis* section species in the Japanese Islands.

angor A" from southwestern China of Yunnan Province (Wang et al., 2006a) and the other from Amami to be closely related to *Drosophila hei* distributed from southwestern China, Guangdong Province. These two species will be published as new species in the near future.

With the Asian *polychaeta* group, *Drosophila latifshahi* was originally described from India as a new member of the genus *Scaptodrosophila* (Gupta and Ray-Chaudhuri, 1970), and thereafter it was found in southwestern China and its taxonomic position was transferred from the genus *Scaptodrosophila* to the *polychaeta* group of the genus *Drosophila*, based on the morphological characters of the male genitalia (Toda and Peng, 1989; Watabe et al., 1990b). In Japan, *Drosophila latifshahi* was found from the Sakishima Islands, Iriomote and Ishigaki, alone. Compared to *Drosophila latifshahi, Drosophila daruma* possessed a wide range of distribution from Iriomote to the Izu Peninsula in the Kanto district, central Honshu. *Drosophila daruma* was most abundant in riparian environments of the Sakishima Islands. Irrespective of our extensive faunal surveys, however, *Drosophila daruma* has not been obtained in Tohoku district of northern Honshu and Hokkaido, indicating that the northern border of this species is the Izu Peninsula. The previous record of *Drosophila daruma* from Hokkaido (Beppu et al., 1977; Okada, 1988) is probably due to miss-identification of *Drosophila calidata* and/or *Zaprionus flavofasciatus*, since they share the same body color (yellowish brown) and riparian habitat. The distribution pattern of *Drosophila daruma*, from India to southern Japan through Nepal and southwestern China nearly overlaps the green belt of lucidophyllous forests in Asia (Hotta, 1974). Thus, *Drosophila daruma* can be regarded as one of the Sino-Japanese elements in the biogeography of *Drosophila*.

Regarding to the *robusta* species group, both *Drosophila neokadai* and *Drosophila lacertosa* showed the same distribution pattern, ranging from Kyushu and its adjacent islands to Hokkaido. In mainland China, these two species have been widely recorded from its northeastern to southwestern districts (Watabe et al., 1990a;

Zhang et al., 1996; He et al., 2003). *Drosophila okadai* was collected from Kyushu to Hokkaido, but it was rare in occurrence in Kyushu. In Kyushu and Shikoku, this species inhabited highlands with cool climates. *Drosophila gani* was first discovered in Yunnan Province, and has been recorded in southwestern and eastern China (Watabe et al, 1990a; Chen and Watabe, 1993; Zhang et al., 1996). In Japan, the present species was distributed from Kyushu to Aomori Prefecture, the most northern district of Honshu. In order to study the northern border of *Drosophila gani*, we have carried out field collections in four localities in Hokkaido and Aomori Prefecture, all of which face to the Tsugaru Strait between Honshu and Hokkaido. In the Tsugaru and the Shimokita of Aomori Prefecture, *Drosophila gani* was collected as a common species in the riparian community of *Drosophila*, but it was not obtained at all in the Matsumae and the Kameda Peninsula of Hokkaido, clearly indicating the Tsugaru Strait is the northern border for the distribution range of *Drosophila gani* (Table 2; Fig. 3). The *robusta* species group is originally a temperate element for the biogeography of *Drosophila*. In lower geographic latitudes of southwestern China, many members of the *robusta* group inhabit highlands, with the elevation of more than 1000 m above sea level. The Ryukyu Islands from Amami to Iriomote lack such mountain areas, and the highest mountain is Mt. Omoto with the elevation of 525 m, in Ishigaki. The Nansei Islands and Taiwan are considered to have connected to the Asian continent during the glacial age of the Quaternary of the Cenozoic era (Lin, 1963; Kamei, 1981). Taiwan possesses high mountain ranges with an elevation of more than 3000 m, and many of the *robusta* group species, e.g., *Drosophila lacertosa, Drosophila gani* and *Drosophila yunnanensis*, inhabit there (Zhang et al., 1996). This suggests that the *robusta* group species might have been once lived on Nansei Island and thereafter disappeared there with global warming after the glacial age.

Two members of the *quadrisetata* species group were obtained. *Drosophila quadrisetata* is widely distributed from Hokkaido to Kyushu (Watabe and Takahashi, 2007), and D*rosophila flumenicola*, originally described from Guangdong Province, showed the Sino-Japanese distribution, like as that of *Drosophila daruma* (Suwito et al., 2013).

As for the *melanica* species group, only *Drosophila moriwakii* inhabits both stream-sides and forests, and was collected from Kyushu to Hokkaido. Its distribution pattern is similar to that of *Drosophila okadai*, sifting to northern areas. *Drosophila ezoana* and *Drosophila kanekoi*, both of which belong to the *virilis* species group, were found from Hokkaido to Kyushu or Honshu. *Drosophila ezoana* and *Drosophila kanekoi* are thought to prefer cool climates from their distribution and abundance.

Drosophila fluvialis was originally described from Guangdong Province, and is considered to belong to the *virilis* section (Toda and Peng, 1989; Wang et al., 2006a). The distribution pattern is nearly identical to that of *Drosophila angor*, ranging from Iriomote to Amami.

The distribution and abundance of the *virilis* section species are summarized in Figure 4, based on the collection data with banana traps (Table 2), since there were some differences in the species composition between net sweepings and bait-traps. For the *angor* group and *Drosophila fluvialis*, the northern border lies between Amami and Yakushima. This border line running between the two islands is known

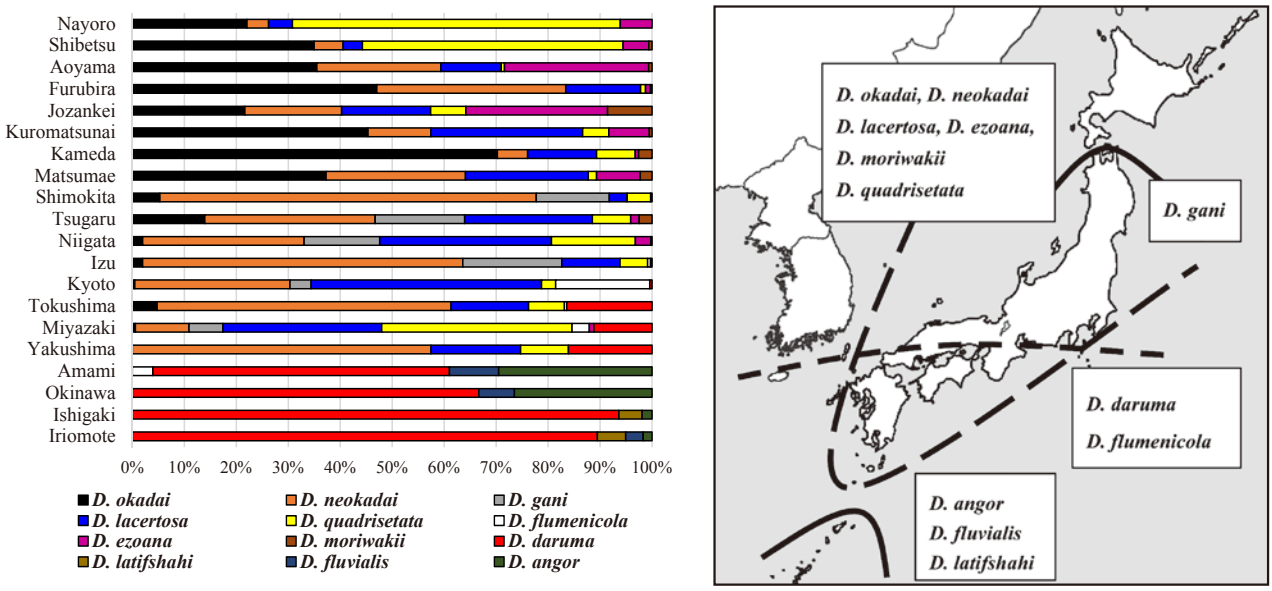

Figure 4. The distribution range (right) and abundance (left) of the *Drosophila virilis* section flies in the Japanese Islands, based on Table 2.

as the Watase Line in zoogeography, dividing the Palearctic Region and the Oriental region (Komai, 1974). In Japan, the northern border of *Drosophila gani* is the Tsugaru Strait. This channel is deep with about 150–450 m in the water-depth, and two Islands, Honshu and Hokkaido, might have not connected for the most part during the ice age, when the sea level decreased (Kamei, 1981). Therefore, it is considered to act a strong barrier for the range expansion of mammals during the ice age. The Tsugaru Strait is called as the Blakiston Line in zoogeography. In fact, the Tsugaru strait is the southern border for brown bear *Ursus arctos* Linnaeus, 1758 and red squirrel *Sciurus vulgaris orientis* Thomas, 1906, whereas it is the northern border for Japanese macaque *Macaca fuscata* Blyth, 1875 and Asian black bear *Ursus thibetanus japonicas* Schlegel, 1857 (Komai, 1974). The borderline of distribution range is quite obscure in many cases of *Drosophila*, and the remarkable northern border of *Drosophila gani* is noteworthy, when we consider the range expansion and adaptation of *Drosophila*. The percentage of *Drosophila okadai* rapidly decreases southwards from the Tsugaru Strait, also indicating the strong barrier for the range expansion of *Drosophila* (see, the black bar in Fig. 4).

As for sylvatic species, *Drosophila tsigana* was captured with banana traps in Hokkaido (①, ③, ⑤–⑦), and its related *Drosophila pengi* from tree saps of oaks in Musashi-murayama in the Kanto district, from the same tree species in Kyoto (⑮) and from timber piles in Miyazaki (⑲). *Drosophila pseudosordidula* was collected from cliff-shelters near a streamside in Kyoto (⑮), and from tree saps of Japanese beech *Fagus crenata* Blume in Iwate (⑪).

At last, distributions of *Zaprionus flavofasciatus* and *Drosophila calidata* were restricted to Hokkaido and northern Honshu (Aomori Prefecture), and their systematic positions remain uncertain (Takada et al., 1979). Some species related to *Zaprionus flavofasciatus* have recently been discovered in mountains of mainland China, and we have just started the phylogenetic study of these two species.

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（渡部　英昭　札幌校教授）
（高橋　将史　津別中学校教諭）