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Mishima, Misako
The Kyushu University Museum

Yukawa, Junichi
Kyushu University

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Dimorphism of Leaf Galls Induced by *Pseudasphondylia neolitseae* (Diptera: Cecidomyiidae) on *Neolitsea sericea* (Lauraceae) and Their Distributional Patterns in Kyushu, Japan

Misako MISHIMA* and Junichi YUKAWA*†

*The Kyushu University Museum, 6-10-1 Hakozaki, Fukuoka 812-8581, Japan
†Kyushu University, 6-10-1 Hakozaki, Fukuoka 812-8581, Japan

Abstract *Pseudasphondylia neolitseae* (Diptera: Cecidomyiidae) induces two different types of gall (upper and lower types) on the leaves of *Neolitsea sericea* (Lauraceae). In the upper type, the adaxial side of the gall projects more prominently than the abaxial side, and *vice versa* in the lower type. The lower type galls were found mainly in northwestern and northern Kyushu, while the upper type were found mainly in southwestern and southern Kyushu and their distributional patterns were parapatric with a little overlapping. The coexistence of both types on a single host tree was relatively rare. Whenever they coexisted on a single tree, they always appeared together on the same leaf, although the relative abundance of one type to another was biased toward one side. The ploidy level of host plants was not related to the gall types, because almost all host trees examined were diploid. Therefore, the gall types are not determined by the differentiation of ploidy level of host plant, and possibly determined by the gall midge. The parapatric distribution pattern of the two gall types may suggest that *P. neolitseae* is now entering into the initial stage of speciation, if gall dimorphism leads to reproductive isolation.

Keywords: Cecidomyiidae, distribution pattern, gall dimorphism, Lauraceae, *Neolitsea sericea, Pseudasphondylia neolitseae.*

Introduction

Galls have been defined as all manifestations of growth, whether positive or negative, and of abnormal differentiation induced on a plant by animal or plant parasites (Meyer, 1987). Cecidomyiidae (Diptera) includes the largest number of gall-inducing species among arthropod taxa containing gall inducers, and many gall-inducing cecidomyiids are monophagous or oligophagous within one or a few plant genera (e.g. Yukawa and Rohfritsch, 2005). Cecidomyiid galls are diverse as a whole in shape and galling position, but the appearance and structure of each cecidomyiid gall is specific to a gall midge species in many instances (e.g. Yukawa and Rohfritsch, 2005). In contrast, a few cecidomyiid species, such as *Masakimyia pustulae* Yukawa and Sunose (Sunose 1985), *Hartigiola faggalli* (Monzen) (Sato and Yukawa 2004), and *Pseudasphondylia elaeocarpini* Tokuda and Yukawa (Tokuda and Yukawa 2005), have been known to exhibit gall dimorphism (Yukawa and Masuda, 1996). *Pseudasphondylia neolitseae* Yukawa (Diptera: Cecidomyiidae: Asphondyliini) (Yukawa, 1974) is also known to induce two different types of gall (upper and lower types) on the leaves of *Neolitsea sericea* (Bl.) Koidz. (Lauraceae) (Yukawa and Masuda, 1996). In the upper type, the adaxial side of the gall projects more prominently than the abaxial side, and *vice versa* in the lower type (Fig. 1). Yukawa and Masuda (1996) briefly mentioned that the upper and lower types could be seen, respectively, in southern and northern parts of Kyushu, Japan.

We have been considering that the gall dimorphism is worth being paid attention as it may be a good model to

Correspondence : M. Mishima.
FAX : +81-92-642-4299
E-mail address: mishima@museum.kyushu-u.ac.jp

understand the significance of gall shape diversification in the process of gall midge speciation. As the first step, we tried to gather further information on distributional patterns of the two gall types induced by *P. neolitseae* in Kyushu and to examine whether or not host plant traits, such as the ploidy level, are related to the determination of gall types.

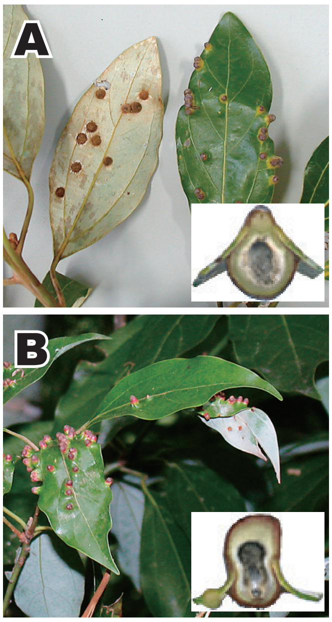

Fig. 1. Two gall types induced by *Pseudasphondylia neolitseae*. A: Lower type. B: Upper type.

Materials and Methods

Insect and plant materials

The host plant, *Neolitsea sericea*, is an evergreen tree of Lauraceae and widely distributed in Japan (Honshu, Shikoku, Kyushu, and the Ryukyus), southern Korea, and Taiwan (Momiyama, 1989). In Kyushu, *N. sericea* is commonly seen everywhere except for higher mountains. *Pseudasphondylia neolitseae* is fundamentally univoltine and distributed in Honshu, Shikoku, Kyushu, and the Ryukyus, Japan (Yukawa, 1974; Tokuda and Yukawa, 2005). In spring, the females lay their eggs in the host buds one by one with the aciculate ovipositor. The first instars hatch several days after oviposition. The first signs of attack are small reddish spots on the upper surface of the fresh leaves. Later, apically rounded subconical swellings appear on the surface of the leaves accompanied by hemispherical swellings on the lower surface. The galls mature in early summer and each gall contains one midge larva (Yukawa, 1974; Yukawa and Akimoto, 2006).

Table 1. Localities from which *P. neolitseae* galls were collected, gall type, the ploidy level of *N. sericea*, and the number of host plants surveyed.

Number	Locality		North latitude	East longitude	Gall type	Ploidy level of host plant	Number of host plants surveyed
1	Fukuoka Pref.:	Shikano-shima	33° 40' 00"	130° 18' 24"	Lower	no data	1
2		Ino 1	33° 40' 27"	130° 31' 12"	Lower	2x	1
3		Ino 2	33° 40' 41"	130° 32' 00"	Lower	2x	1
4		Motooka	33° 35' 55"	130° 12' 51"	Lower	no data	1
5		Kurômaru	33° 34' 16"	130° 40' 37"	Lower	no data	6
6		Nijo	33° 32' 14"	130° 10' 01"	Lower	no data	1
7		Raizan	33° 28' 43"	130° 13' 24"	Lower	no data	1
8	Saga Pref.:	Niri	33° 15' 35"	129° 50' 22"	?	2x	1
9		Hadatsu	33° 23' 39"	129° 52' 57"	Lower	no data	2
10		Yamauchi	33° 11' 53"	129° 56' 40"	?	2x	1
11		Kashima	33° 05' 14"	130° 07' 10"	Lower	2x	1
12		Kanzaki	33° 20' 45"	130° 22' 57"	Lower	no data	3
13		Taku 1	33° 17' 23"	130° 08' 11"	Lower	no data	2
14		Taku 2	33° 17' 29"	130° 08' 21"	Lower	no data	1
15		Kagami	33° 25' 57"	130° 00' 34"	Lower	2x	1
16		Takekoba	33° 25' 36"	129° 55' 29"	Lower	2x	2
17		Karakawa	33° 24' 53"	129° 54' 40"	Lower	2x	1
18		Ureshino	33° 04' 40"	129° 58' 49"	Lower	no data	3
19	Oita Pref.:	Usa 1	33° 17' 38"	131° 27' 30"	Lower	2x	1

Table 1. Continued

Number	Locality		North latitude	East longitude	Gall type	Ploidy level of host plant	Number of host plants surveyed
20		Usa 2	33° 30' 25"	131° 19' 59"	Lower	no data	1
21		Hatake	33° 09' 39"	131° 46' 37"	Lower	2x	1
22		Usuki	33° 05' 09"	131° 43' 49"	Upper	2x	2
23		Kokonoe	33° 13' 42"	131° 12' 40"	Lower	2x	1
24		Nozuhara	33° 10' 28"	131° 32' 39"	Lower	no data	1
25		Oita	33° 13' 16"	131° 45' 18"	Lower	no data	5
26		Mie	32° 59' 06"	131° 36' 04"	Upper	no data	5
27		Ohara	32° 56' 40"	131° 35' 18"	Upper	2x	1
28		Asaji	33° 00' 33"	131° 28' 52"	Upper	2x	1
29		Moriya	32° 59' 08"	131° 25' 40"	Upper	no data	1
30		Oritate	33° 00' 40"	131° 21' 35"	Upper	no data	1
31		Yonai	32° 59' 17"	131° 22' 35"	Upper	no data	2
32		Matsutani	32° 56' 40"	131° 35' 28"	Upper	2x	5
33		Nagayu	33° 02' 17"	131° 21' 38"	Upper	no data	1
34		Nagano	33° 03' 40"	131° 21' 42"	Upper	2x	1
35		Kuju	33° 13' 42"	131° 12' 40"	Upper	2x	1
36		Yoake	33° 19' 20"	130° 51' 54"	Lower	2x	3
37		Hita	33° 19' 56"	130° 53' 38"	Lower	no data	1
38		Beppu	33° 17' 38"	131° 27' 30"	Upper	2x	2
39	Kumamoto Pref.:	Kugino	32° 49' 25"	131° 01' 34"	Lower	2x	2
40		Ueshikimi	32° 51' 25"	131° 09' 50"	Upper	no data	1
41		Takamori naka	32° 49' 00"	131° 07' 24"	Upper	2x	1
42		Takamori soto	32° 49' 00"	131° 07' 24"	Lower	3x	1
43		Naganohara	32° 47' 22"	131° 13' 16"	Upper	2x	2
44		Nagano	32° 53' 32"	131° 01' 09"	Upper	2x	1
45		Kawayou	32° 52' 25"	131° 00' 14"	Lower	2x	1
46		Minamioguni	33° 05' 42"	131° 04' 42"	Upper	2x	1
47		Sihrakawa	32° 49' 29"	131° 05' 40"	Upper	2x	1
48		Ohgouchi	32° 14' 48"	130° 29' 34"	Upper	no data	1
49		Tobase	32° 35' 48"	130° 29' 32"	?	no data	1
50		Misumi	32° 36' 57"	130° 30' 22"	Lower	no data	1
51		Tsubaki	32° 35' 44"	130° 48' 55"	Upper	no data	1
52		Toyono 1	32° 37' 58"	130° 44' 13"	Lower	2x	1
53		Toyono 2	32° 37' 37"	130° 44' 14"	?	2x	1
54		Shabagami-toge	32° 37' 21"	130° 44' 06"	Upper	2x	2
55		Haizuka	32° 51' 54"	130° 51' 34"	Lower	2x	1
56		Takaono	32° 53' 31"	130° 54' 24"	Lower	2x	1
57		Hitoyoshi	32° 13' 52"	130° 46' 04"	Upper	2x	2
58		Nankan	33° 04' 13"	130° 32' 46"	Lower	2x	1
59		Togigawa	32° 45' 33"	130° 48' 59"	Lower	2x	2
60		Takigawa	32° 44' 33"	130° 47' 07"	Lower	no data	1
61		Mifune	32° 45' 19"	130° 54' 49"	Upper	2x	1
62		Yabe	32° 40' 27"	130° 58' 53"	Upper	no data	1
63		Ego	32° 33' 48"	130° 24' 38"	Lower	no data	1
64		Fukuro	32° 09' 49"	130° 22' 31"	Upper	no data	2
65		Sushi	32° 30' 41"	130° 19' 55"	Lower	no data	2
66		Sakamoto	32° 24' 24"	130° 37' 27"	Upper	2x	1
67		Miyanjo	32° 29' 47"	130° 38' 21"	Upper	no data	1
68		Yatsushiro	32° 31' 24"	130° 39' 39"	Upper	no data	1
69		Kimigafuchi	32° 24' 27"	130° 33' 18"	Upper	2x	2
70		Shiranui	32° 39' 04"	130° 39' 38"	Lower	no data	1
71		Hondo	32° 27' 43"	130° 10' 57"	Upper	no data	1
72	Nagasaki Pref.:	Iki	33° 44' 38"	129° 46' 37"	Lower	no data	1

Table 1. Continued

Number	Locality		North latitude	East longitude	Gall type	Ploidy level of host plant	Number of host plants surveyed
73		Egami	33° 06' 14"	129° 46' 10"	Upper	2x	2
74		Sasebo	33° 11' 38"	129° 43' 16"	Upper	2x	2
75		Imafuku	33° 20' 45"	129° 47' 10"	Lower	2x	1
76		Nagasaki	32° 45' 17"	129° 52' 37"	Upper	no data	1
77		Mayuyama	32° 46' 09"	130° 20' 14"	Upper	no data	1
78		Higashisonogi	33° 02' 48"	129° 55' 40"	?	no data	1
79		Kushiyama	32° 39' 53"	130° 09' 01"	Upper	no data	1
80		Hirado	33° 22' 35"	129° 33' 15"	Lower	2x	1
81		Tanomoto1	33° 16' 35"	129° 41' 21"	Upper	2x	1
82		Tanomoto2	33° 16' 35"	129° 41' 21"	Lower	2x	2
83		Ikitsuki-shima	33° 23' 02"	129° 25' 03"	Lower	2x	1
84		Fukushima	33° 22' 59"	129° 50' 58"	Lower	no data	1
85		Konpira	32° 49' 24"	130° 05' 37"	Upper	no data	1
86		Matsuri	32° 45' 33"	129° 56' 39"	Upper	no data	1
87		Tsunaba	32° 45' 33"	129° 56' 39"	Upper	no data	1
88		Doisaki	32° 56' 49"	130° 12' 07"	Upper	no data	1
89	Miyazaki Pref.:	Kainohatake	32° 34' 08"	131° 35' 44"	Upper	no data	5
90		Kobayashi	31° 58' 52"	130° 56' 10"	Upper	2x	2
91		Takachiho	32° 46' 08"	131° 16' 54"	Upper	no data	2
92		Shiitani	32° 41' 32"	131° 19' 33"	Upper	no data	3
93	Kagoshima Pref.:	Noma-dake	31° 24' 05"	130° 09' 31"	Upper	no data	1
94		Sata	31° 01' 29"	130° 40' 53"	Upper	no data	1
95		Miyanjo	32° 03' 73"	130° 24' 46"	Upper	no data	1
96		Ibusuki	31° 17' 10"	130° 36' 04"	Upper	no data	1
97		Nagashima 1	32° 07' 20"	130° 07' 54"	Upper	no data	1
98		Nagashima 2	32° 08' 34"	130° 07' 05"	Upper	no data	1
99		Ohkubo	32° 08' 30"	130° 07' 28"	Upper	no data	2
100		Takarabe	31° 40' 59"	130° 56' 21"	Upper	2x	2
101		Ichiki	31° 40' 14"	130° 19' 49"	Upper	2x	2
102		Hinokami	31° 15' 16"	130° 16' 30"	Upper	no data	1
103		Tanegashima	30° 37' 45"	130° 58' 47"	Upper	no data	1
104		Yakushima	30° 18' 53"	130° 35' 99"	Upper	no data	1

Field survey and specimen acquisition

We searched for *N. sericea* trees that bore galled leaves at various localities in Kyushu in 2003, 2004, and 2005, and collected fully developed galls from a total of 104 localities during the season from October to April (Table 1). Each collection site is shown in Fig. 2 as a circle with a numeral that indicates the name of each locality in Table 1. We distinguished the two gall types from each other by their appearance. In some cases, galls exhibited an intermediate shape between the upper and lower type galls. We treated such galls as the intermediate type. The galls collected were fixed in FAA (5% formaldehyde, 5% acetic acid, and 60% ethanol) solution as voucher specimens. Plant voucher specimens were collected from the same plant individuals that bore the galls. All voucher specimens will be deposited to the Kyushu University Museum.

Geographical information and map description

All localities were georeferenced by a handy GPS or map reading service provided by the Geographical Survey Institute of Japan (http://watchizu.gsi.go.jp/). Geographical Information System (GIS) was applied for all map description using ArcGIS (ESRI, Japan).

Flow cytometry

The ploidy level of individual host plants was determined with a flow cytometer as follows. Each fresh ungalled leaf of *N. sericea* removed from the respective plants was wiped with a sheet of wet paper. Then, leaf tip area with about 10mm×5mm was chopped up into small pieces with a razor blade in a 200μl solution A (Pertec) that was kept cool in a petri dish on ice. The solution, including extracted intact nuclei, was filtered through 30μm nylon mesh (Pertec) and then mixed with 1.5 ml of solution B (Pertec) including DAPI. The mixture was analyzed with PA (Pertec) and the ploidy level was determined by reading the peak position.

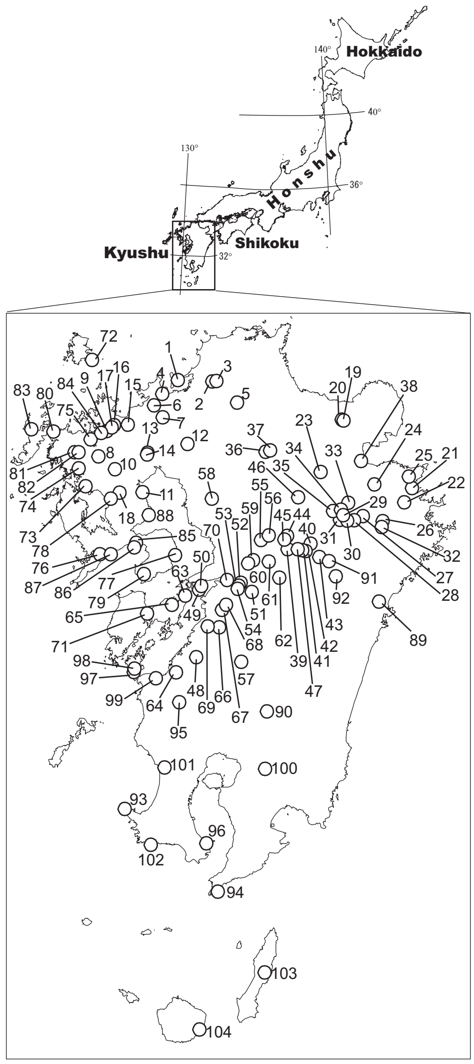

Fig. 2. Localities from which material was collected. Each locality is numbered for convenience of finding locations referred to in this paper (see also Table 1).

Results and Discussions

Distributional pattern of the two gall types

The lower type galls (Fig. 1-A) were found mainly in northwestern and northern Kyushu, while the upper type galls (Fig. 1-B) were found in southwestern and southern Kyushu (Fig. 3), as mentioned in Yukawa and Masuda (1996). In addition to the two gall types, we found the intermediate type of gall in three localities in northwestern Kyushu, and some inverted type of galls (Fig. 4-B) on a few occasions. As a whole, our data indicated that the two gall types were parapatrically distributed in Kyushu with a little overlapping.

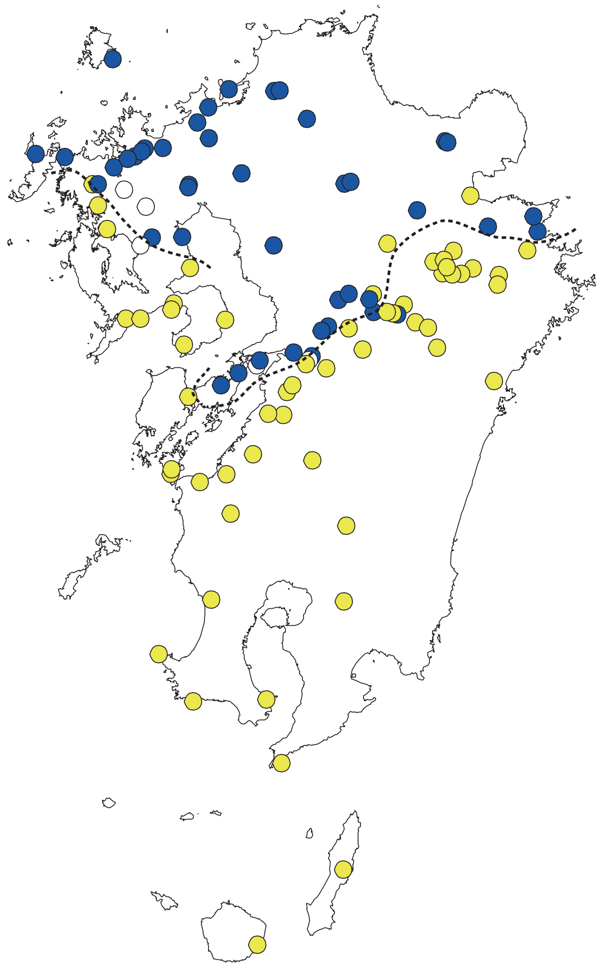

Fig. 3. Distribution map of two gall types induced by *Pseudasphondylia neolitseae* on the leaves of *Neolitsea sericea* in Kyushu. Yellow circle: upper type; Blue circle: lower type; White circle: intermediate type. Dotted lines show the rough borders of two gall types.

The two dividing lines could be drawn on the map to show the parapatric distribution pattern of the two gall types (Fig. 3). One line runs in northwestern Kyushu from the vicinity of Tanomoto (81, 82), Nagasaki Pref., through Ureshino (18), to Kashima (11), Saga Pref. Another line runs in central Kyushu from the Usuki (22), Oita Pref., through the southern foot of Mt. Aso (39-42, 47), to Toyono (52-54), Kumamoto Pref. At the western end of the latter line, the upper type galls replaced the lower type galls between Ue Island (65) and Shimo Island (71) of the Amakusa Islands.

Coexistence of the two gall types on a single tree

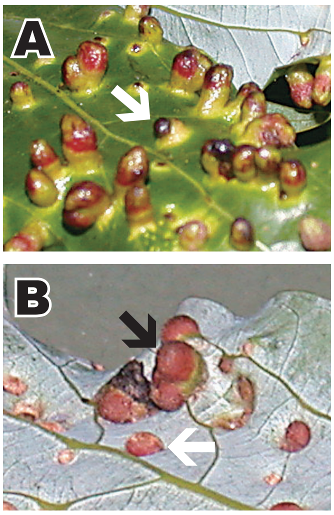

Fig. 4. Coexistence of two different gall types induced by *Pseudasphondylia neolitseae* on a leaf of *Neolitsea sericea*. A: Upper surface of the host leaf. White arrow points toward the upper part of a lower type gall that coexists with upper type galls. B: Under surface of the host leaf. White arrow points toward the lower part of a lower type gall that coexists with upper type galls. Black arrow points toward inverted type galls. The upper part of the inverted galls are projected to the under side of the leaf.

Usually the host trees bearing different gall types were growing several km apart from each other, but in a few cases they stood near by in Tanomoto (81 and 82) or within a distance of 20 m in Takamori (41 and 42). It might be possible for the females to fly for at least 20 m, but every host tree had either upper or lower type galls. The coexistence of both types on a single host tree was relatively rare. Whenever they coexisted on a single tree, the two types of gall always appeared together on the same leaf, although the relative abundance of one type to another was extremely biased toward one side (Fig. 4). Therefore, we have never seen any segregate utilization of leaves or shoots by the two different gall types. These observations may suggest that the coexistence of the two gall types on a single leaf would be derived from oviposition by a single female, as has been observed by Yukawa et al. (1976) and Yukawa and Akimoto (2005). The minor gall type might be caused by some kinds of behavioral mistake by the gall midge or by generic variation during the process of gall induction.

Ploidy of host plants

All host plants examined were diploid, except one triploid individual. This result indicates that the ploidy level of host plants was not related to the types of gall. The triploid individual (Fig. 5) was found in Takamori (42), Kumamoto Pref. and seems to be a natural polyploid. It bore lower type galls, but we cannot conclude that triploid individuals always have lower type galls, because triploid individuals are very rare among wild *N. sericea* trees. We will report elsewhere more about the cecidomyiid galls induced on the triploid individual.

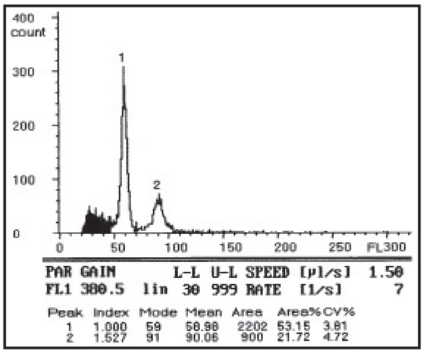

Fig. 5. Histograms showing DNA contents of diploid and triploid individuals of *Neolitsea sericea* that were analyzed with a flow cytometer. The numeral 1 indicates a peak of diploid and 2 indicates that of triploid.

Because the shape of galls is often specific to a gall-inducing species, the galls have been regarded as an extended phenotype of the gall inducers (e.g. Fukatsu et al., 1994; Stone & Schönrogge, 2003; Yukawa & Rohfritsch, 2005). Therefore, the parapatric distribution pattern of the two gall types may suggest that *P. neolitseae* is now entering into the initial stage of speciation, if gall dimorphism leads to reproductive isolation. In order to confirm such a hypothesis, we need to clarify the mechanism of gall shape differentiation. The mechanism is possibly related to behavioral traits of the gall midge, such as the position of egg-laying (upper or under surface of leaves that are folded in a host bud), the direction of the larval head to feed on upper or under surface of the leaves, and so on. In addition, intraspecific mating tests and comparison of DNA sequencing data are required between the two different populations. Then, we have to gather phenological data of gall midge emergence from different gall types to examine whether or not a chronological isolation mechanism is operating on the different populations.

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和文要旨

シロダモタマバエ(双翅目:タマバエ科)によってシロダモ(クスノキ科)の葉に形成されるゴール2型と九州におけるそれらの地理的分布様式

三島美佐子*・湯川淳一*†

*九州大学総合研究博物館
†九州大学
(〒812-8581福岡市東区箱崎6-10-1)

タマバエ科のシロダモタマバエは、クスノキ科の常緑樹であるシロダモの葉にゴールを形成する。ゴールには2型があり、一方は葉の表面側がより突出しており(表型)、他方は葉の裏面側がより肥大している(裏型)。我々は、九州におけるそれぞれのゴール型の詳しい分布パターンを調べた。それぞれのゴール型はやや重なる側所的な分布域を持ち、九州北西部と中央部に2つの分布境界を持っていた。通常、1個体の寄主植物上には、どちらか一方のゴール型しか出現しないが、2型が共存している場合もあった。その場合は、同一葉上に一方の型が多数存在するなかに、他方の型がわずかにみられるというものであった。同じ寄主植物上で、異なるシュートや葉を、どちらか一方の型のゴールが占めている状態で共存しているようなケースは、まったくなかった。調査したシロダモはほとんど2倍体で、1個体のみ3倍体であった。同じ倍数レベルのシロダモに、異なるゴール型が出現していることから、植物の倍数性は、これらのゴール型の決定には関与していないと結論づけられた。今回明らかになったゴール2型の側所的な分布様式は、タマバエの行動学的、生態学的、遺伝学的な違いが、2型の発現に何らかの形で関与した結果であると推察される。このことは、シロダモタマバエが種分化のきわめて初期の段階に移行しているという可能性を示唆しているかも知れない。