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Passive Long-Distance Migration of Apterous Dryinid Wasps Parasitizing Rice Planthoppers

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1. Introduction

The wasp family Dryinidae comprises predator and parasitoid wasps of leaf- and planthoppers (Hemiptera: Auchenorrhyncha). This family is morphologically distinct from other wasps. Females in most subfamilies of Dryinidae have forelegs that are modified into a chela, with an enlarged claw (Fig. 1: green) and 5th tarsomere (Fig. 1: red) that aid in grasping the host insect. The enlarged claw moves widely when the chela opens. Such foreleg morphology is not always the case, such as for females of the subfamily Aphelopinae R.C.L. Perkins and Erwiniinae Olmi & Guglielmino (Olmi & Guglielmino, 2010) that have simple forelegs. Dryinid wasps often show distinctive sexual dimorphism, such as the presence or absence of chela. The subfamily Gonatopodinae Kieffer is one of the extreme cases of sexual dimorphism, but in this case it is because females of most of the species are apterous. The pterothorax becomes so slender in the apterous form (Fig. 2: A, C) that they look like ants. In contrast, males have well developed wings and a pterothorax (Fig. 1: B).

Since apterous females cannot disperse very far by themselves, the current distribution of these wasps should have been caused by historical events, such as terrestrial immigration and local extinction. Immigration over large distances, especially across geographical barriers (e.g. open water) seems unlikely. Recent studies revealed the annual long-distance migration of rice planthoppers, which are host to apterous dryinids**.** If rice planthoppers carry dryinid larvae to distant locations, immigrant individuals of the Dryinidae should be recognizable from the destination locality. This behavior can be viewed as passive long-distance migration. Confirming the presence or absence of such behavior and determining the degree of influence that this has on a population at the destination locality will broaden our understanding on the current biogeographical distribution of the Dryinidae. In this chapter, we introduce a brief summary about apterous species of *Haplogonatopous* R.C.L. Perkins, which are common in Asian rice paddies. We then describe the life cycle of one of these species that inhabits other vegetation, discuss the possible mechanism for settling in a new environment, and show an important insight indicated from our recent phylogeographical approach using two species of *Haplogonatopus*.

2. Common species of *Haplogonatopus* in Asian rice paddies

This section briefly summarizes previous studies about *Haplogonatopus* species that parasitize rice planthoppers in monsoon Asia. There are two common species in rice paddies. The present understanding of the morphological differences, host ranges, and distribution of the two species are described.

2.1 Taxonomy

Like many other taxa of the subfamily Gonatopodinae, females of *Haplogonatopus* are wingless. The small palpal formula, 2/1 is one of the most distinctive apomorphies of this genus. The presence of "rhinarium" on the antennae, the large subapical tooth and a single row of lamellae on the enlarged claw, and a single spur on the hind tibia are also diagnostic characters for the female (Olmi, 1984, 1999). However, the combination of those latter character states also occurs within *Gonatopus* Ljungh. Among the four species of *Haplogonatopus* distributed in the Palaearctic and Oriental regions, *H. apicalis* R.C.L. Perkins, 1905 and *H. oratrius* (Westwood, 1833) are common in Asian rice paddies. Their appearance is very similar to each other, but they are morphologically distinguishable by the female coloration and male genitalia (Fig. 2).

Fig. 1. Life cycle of *Haplogonatopus oratrius*.

2.2 Biology

Although the biology of most dryinid species is not well studied, species parasitizing rice planthopper are relatively well understood. *H. apicalis* attacks the white-backed planthopper,

Sogatella furcifera (Horváth, 1899), and *H. oratrius* attacks the small brown planthopper, *Laodelphax striatellus* (Fallén, 1826) (Fig. 1). The host preference shows an important contrast. *H. apicalis* only parasitizes *S. furcifera* under natural conditions; although there are other host records (Guglielmino & Olmi, 1997), they are apparently exceptional. *H. oratrius* parasitizes many species (Guglielmino & Olmi, 1997), although the dominant host species in Asia is *L. striatellus*. The large biomass of *L. striatellus* could be advantageous for *H. oratrius*, as the wasp hibernates as a larva in the nymphs of this planthopper (Nishioka, 1980; Kitamura, 1987). Nishioka (1980) reported that a female *H. apicalis* was reared from an overwintering nymph of *L. striatellus* in Kochi Prefecture, southern Shikoku. However, despite an intensive field survey, parasitism of *H. apicalis* on *L. striatellus* has not been observed in Shimane, western Honshu (Kitamura, 1987, 1989; Kitamura & Nishikata, 1987). In view of the above, the hibernation of *H. apicalis* in *L. striatellus* is unlikely to be common in the temperate region.

The general life cycle of *Haplogonatopus* can be summarized as follows (Fig. 1). An adult female captures a host using its chela (= distal apex of modified foreleg) and oviposits an egg into the posterior part of abdomen. The larva develops in the abdomen of the host. The mature larva consumes the entire content of the host, and then emerges from the host's body. The larva spins a cocoon on plant tissue.

Fig. 2. General habitus and male genital organs of *Haplogonatopus* that are common in rice paddies. A *H. oratrius*, female; B ditto, male; C *H. apicalis*, female; D male genitalia, *H. oratrius* (left), *H. apicalis* (right). Scale = 1.0 mm (A–C), 0.1 mm (D).

2.3 Distribution

The distribution of the two *Haplogonatopus* species overlaps with the main distribution of their dominant hosts. *H. oratrius* is common from Europe to the temperate region of Asia, including Taiwan. Although there is no record from South East Asia, they have been recognized from the Mariana Islands (Olmi, 1999). Recently, they were found in the oceanic and tropical Bonin Islands (Mita, unpublished data). Many organisms have been accidentally introduced to new regions by human activity, and the distribution of *H. oratrius* needs additional evaluation. *H. apicalis* was originally described from Northern Australia. However, it is rather common in Monsoon Asia. There is no record from oceanic islands, but its host, *S. furcifera*, is distributed in Fiji, Micronesia and New Hebrides (Asche & Wilson, 1990).

3. Seasonal host shift of *Haplogonatopus oratrius*

Adult *L. striatellus* often moves a short distance from a rice paddy, but the destination locality may not be always suitable. This section will show recent results of field research conducted on vegetation unsuitable for *L. striatellus*.

As it is too cold for winter rice cropping in Japan, *L. striatellus* needs to hibernate on other vegetation. They can be found at paddy-side levees occupied with grasses. They may also be found in dry river beds occupied by *Eragrostis curvula* (Schrad.) Nees in autumn. Another planthopper, *Hosunka hakonensis* (Matsumura, 1935) is the predominant species in the bush of *E. curvula*. They also successfully reproduce and thrive on *E. curvula*. However, *L. striatellus* do not appear to reproduce on this plant as nymphs are not found on it. Figure 3 shows the seasonal fluctuation of *H. hakonensis* collected from a colony of *E. curvula* at Sagami-gawa River (Kanagawa, Central Honshu) by net-sweeping. The field research was conducted four times a month from April to October on 2006. The sweeping-netting was undertaken for 20 minutes each sampling. Nymphs were collected from April to September but they were also found in winter (data not shown). Conversely, all collected individuals of *L. striatellus* collected from *E. curvula* were adults and nothing was collected from April to June (Fig. 4). *H. oratrius* and *Gonatopus dromedarius* (A. Costa, 1882) inhabit the same environment. When nymphs parasitized by Dryinidae were collected, they were kept in a plastic tube with a grass leaf until the dryinid larvae emerged. The identification of dryinid species was undertaken on adults or, when they did not become adults, by coloration of the larval sac. The two dryinid species are easily identified by the color of the larval sac: in *H. oratrius* it is ash gray (Fig. 1), whereas in *G. dromedarius* it is black. *H. hakonensis* were found to be parasitized by both dryinid species (Figs. 3, 5). The rate of parasitism was highest in June (Fig. 5), and most dryinid species parasitizing *H. hakonensis* in June were *G. dromedarius* (*H. hakonensis*: *L. striatus* = 34: 11). Because parasitism of overwintering nymphs by both dryinid species was observed in April, *H. hakonensis* is regarded as a winter host.

The seasonal fluctuation of *L. striatellus* at Sagami-gawa River is similar to that of a paddy-side levee (Figs. 4, 6), except that the latter contains adults and nymphs (data not shown). At Sagami-gawa River, parasitism was observed in September (Fig. 5). All of the dyrinids were *H. oratrius* except for one female *G. dromedarius* (*L. striatus*: *H. hakonensis* = 23: 1). The parasitism of *G. dromedarius* toward *L. striatellus* appeared to be highly restricted. In a paddy-side levee at Atsugi, *L. striatellus* was not collected from April through May (Fig. 6). However, this result may have resulted from low density. Kitamura (1989) reported the presence of overwintering nymphs and a relatively high ratio of parasitism (9–34%) by *H. oratrius* in a similar environment from winter to spring in Shimane.
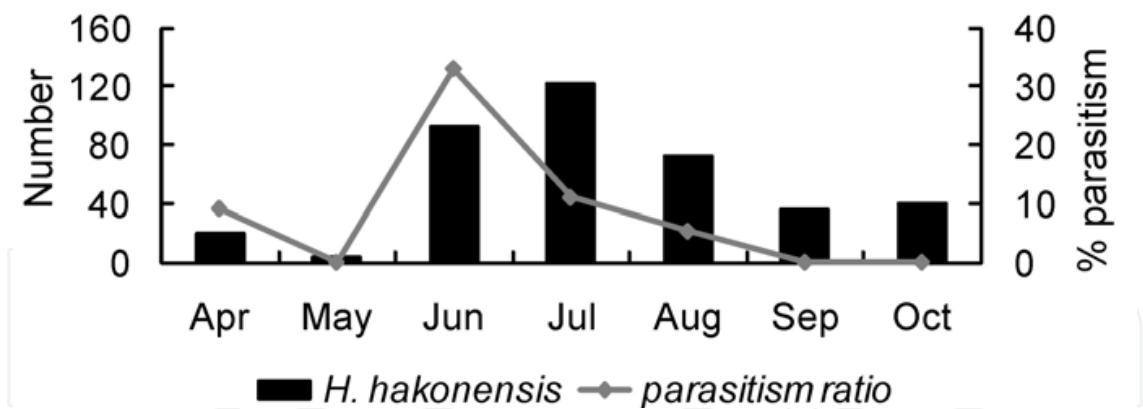
Fig. 3. Seasonal fluctuation of *Hosunka hakonensis* and parasitism by Dryinidae at Sagami-gawa River in 2006.
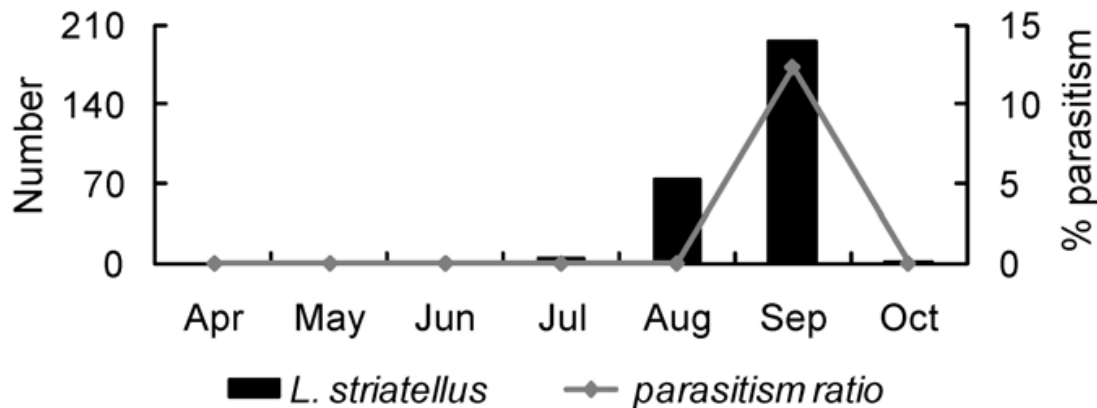

Fig. 4. Seasonal fluctuation of *Laodelphax striatellus* and parasitism by *Haplogonatopus oratrius* at Sagami-gawa River in 2006.
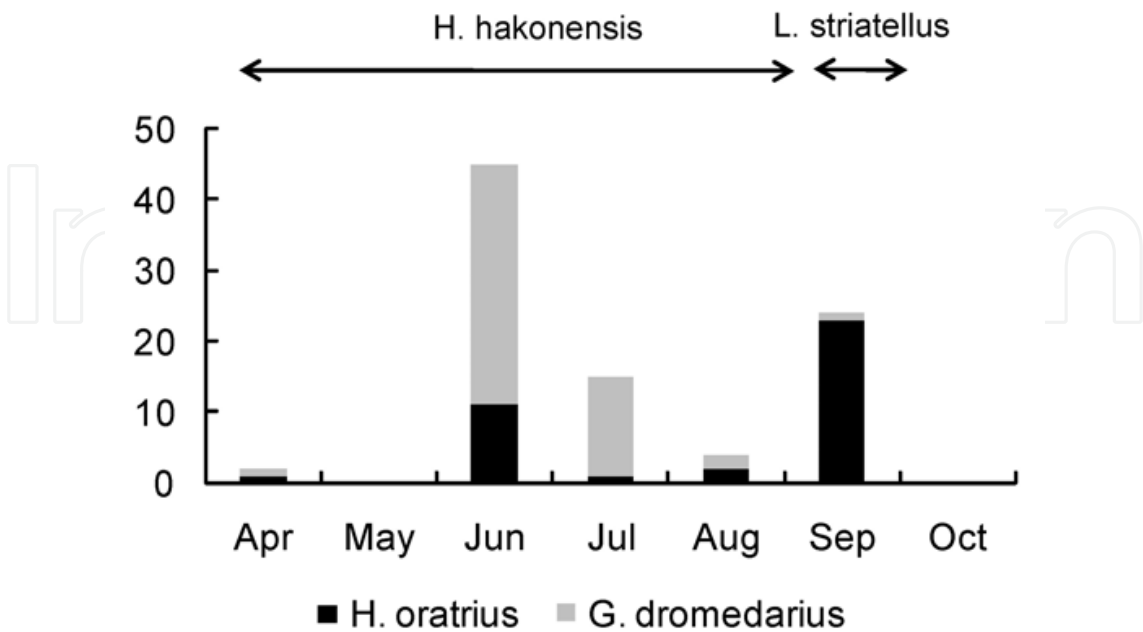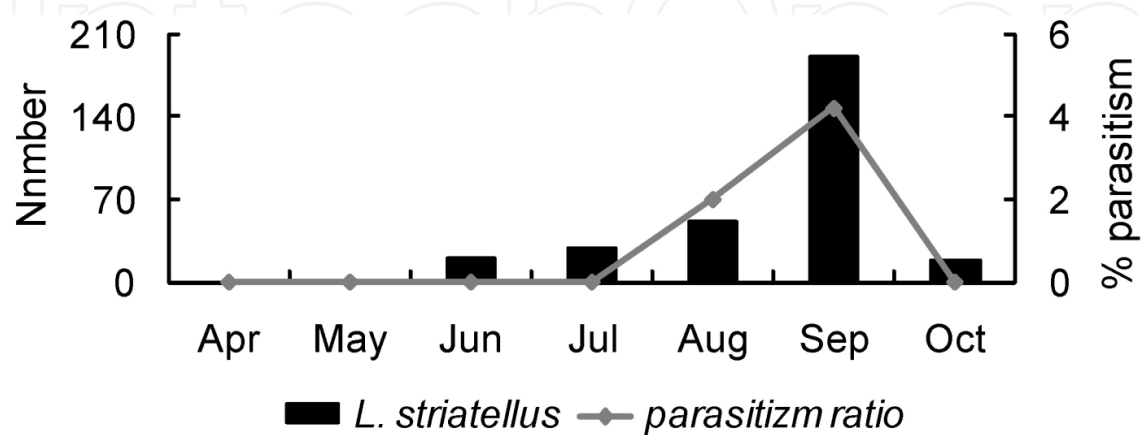

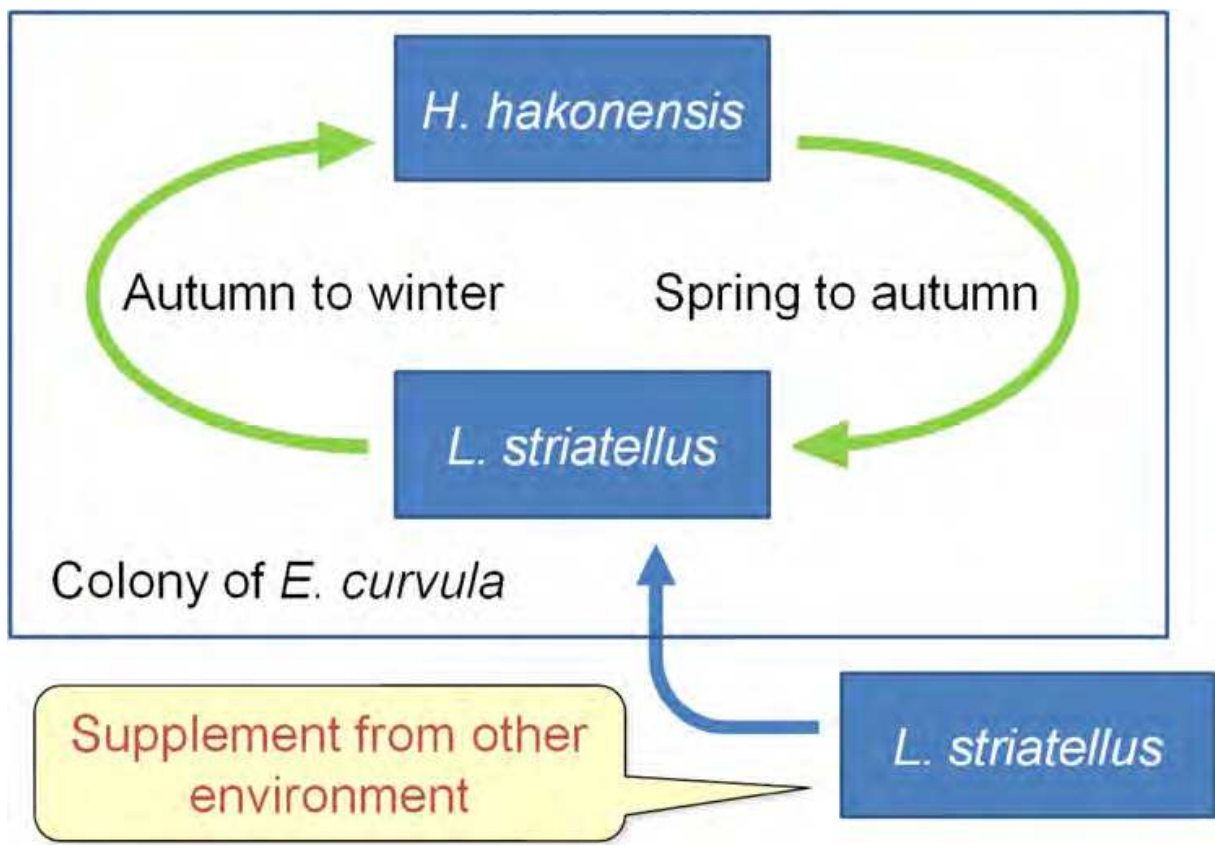Fig. 5. Seasonal fluctuation of dryinid wasps that emerged from *Hosunka hakonensis* and *Laodelphax striatellus* at Sagami-gawa River in 2006.

The abundance of parasitizing dryinid individuals indicates that *G. dromedarius* had one population peak in June in 2006. Although the host species was different from that of *G. dromedarius*, *H. oratrius* displays two population peaks, one each in June and September (Fig. 5). Kitamura's (1983) developmental model based on physiology and ambient temperature indicated that *H. oratrius* can have five generations a year in Matsue, Shimane Prefecture. As the climate in Kanagawa is similar to that of Shimane, the two observed population peaks are considered to be caused by a lack of host resource abundance (Figs. 3, 4).

Fig. 6. Seasonal fluctuation of *Laodelphax striatellus* and parasitism by *Haplogonatopus oratrius* at a paddy-side levee in Atsugi in 2006.

Fig. 7. Host-shift cycle of *Haplogonatopus oratrius* occurring on a colony of *Eragrostis curvula*. *Hosunka hakonensis* hibernates on *E. curvula* whereas *Laodelphax striatellus* dies in winter.

Adults of immigrant *L. striatellus* could be already parasitized by *H. oratrius*, as indicated in Fig. 6. Therefore, *H. oratrius* both the original inhabitants and immigrants, coexist in the same locality during autumn. In winter, overwintering nymphs of *H. hakonensis* are considered to be parasitized by both species. The seasonal host shift and life cycle of *H. oratrius* at Sagami-gawa River are summarized in Fig. 7. Although *H. oratrius* parasitizes only *L. striatellus* and *H. hakonensis* at Sagami-gawa River, many planthopper species can be parasitized by *H. oratrius* (Guglielmino & Olmi, 1997). We conclude that the relatively wide host range allows *H. oratrius* to settle in new environments when the parasitized hosts relocate.

4. Long-distance migration of rice planthoppers

S. furcifera and *L. striatellus*, together with the brown planthopper, *Nilaparvata lugens* (Stål, 1854) are the dominant planthopper pests of the rice plant in Asia. They are known as long-distance migrant insects (Kisimoto, 1975). Their migration ability in Asia has been demonstrated by temporal biotype changes (Sogawa, 1992, 1993) and migration analysis (Otuka et al., 2005a, 2005b, 2008, 2010).

S. furcifera is a tropical to subtropical species. Those found in Japan in the rainy season (June to July) originated from northern Vietnam via southern China (Sogawa, 1993; Otuka et al., 2008). As *S. furcifera* cannot hibernate in temperate regions, including Japan and Korea, it is thought that they immigrate from overseas each year. Conversely, *L. striatellus* is a temperate species. It is distributed mainly in the temperate to subarctic regions of Asia to Europe, but also in some subtropic or tropic regions (Taiwan, southern China, the high altitude areas of Southeast Asia). They hibernate as fourth instar nymphs (Kisimoto, 1957). Planthoppers captured at a weather ship on the East China Sea include many *L. striatellus* (Kisimoto, 1983), but this species is not distributed in the lower altitude areas of the tropic region, as are the other two planthoppers. Recently, a mass migration of *L. striatellus* from around Jiangsu Province of China to Kyushu, Japan, was strongly indicated by trap catches and source estimation using backward trajectory analysis (Otuka et al., 2010).

5. Parasitized rice planthoppers collected over the ocean

Several authors have reported that the parasitism of dryinid larval sacs and stylops on rice planthoppers was probably a direct result of migration from overseas. Kisimoto (1975) reported parasitized *S. furcifera* and *N. lugens* collected by a monitoring net trap for migrant insects. Kitamura & Nishikata (1987) reported the seasonal changes of parasitism ratio on leaf- and planthoppers probably migrated from China. The above two observations were conducted on land. The parasitizing dryinid larvae and stylops were also recognized from individuals collected over the ocean. In 1967 and 1968, a mass flight of *S. furcifera* and *N. lugens* was observed around the weather ship, "Ojika" in the Pacific Ocean (N29°, E135°) (Kisimoto, 1983; Kisimoto & Sogawa, 1995). Three females of *H. apicalis* were reared from *S. furcifera* collected from the ship in 1968. These species have also been found over the East China Sea. *S. furcifera* parasitized by stylops and dryinids were collected on the weather ship, "Keifu-maru", on the East China Sea (N31°, E126°) in 1984 (Noda, 1986). The stylops was identified as *Elenchus japonicus* (Esaki & Hashimoto, 1931) (Kifune & Maeta, 1986). The dryinid species was not identified, but was likely *H. apicalis*.

6. Genetic variation among East Asian populations

The phylogeographical analysis was conducted using the two species of *Haplogonatopus* based on 807-bp mitochondrial COI sequence data obtained from many localities in East Asia (Fig. 8). The monophyly of the species was strongly supported by cladistic analysis. In the parsimonious network of *H. oratrius*, a combination of three star-like core haplotype groups (Fig. 9, A–C) was indicated. The largest haplotype, group A, was composed from China, Taiwan and Kyushu elements. Haplotype group C was regarded as the Japanese endemic population. Haplotype group B was composed from mainly Japanese elements, but a few foreign elements were also included. The network structure was moderately equivalent to the geographical distribution. On the other hand, the network of *H. apicalis* is complicated. A single star-like structure and two circular structures were recognized. Most of the others show multimodal distribution and the structure is very different from the geographical distribution. Compared to *H. oratrius*, *H. apicalis* has high genetic variation over all localities sampled. However, they could not been isolated by geographical distribution. This could imply that all sampling sites should be regarded as the same population, which would be consistent with the annual long-distance migration of *S. furcifera*. However, *S. furcifera* showed no genetic variation among the East Asian populations sampled (Mun et al., 1999). Because the present study investigated the original and the secondary migration direction, the similar genetic structure of *H. apicalis* might be retrieved from the other localities in East
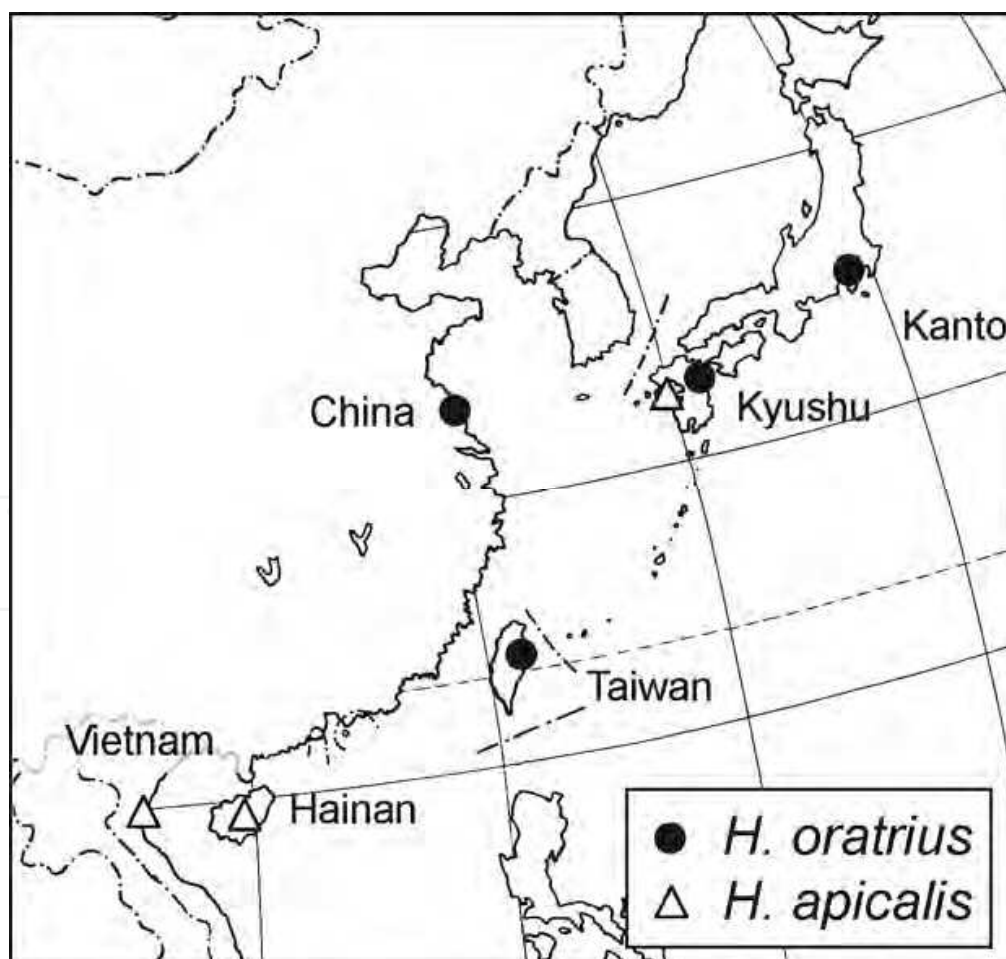

Fig. 8. Sampling localities.

Asia. However, East Asia is only part of the distribution. The genetic structure in South East Asia and South Asia is disputed.

The haplotype network of *H. oratrius* moderately reflects geographical distances. This pattern is similar to *E. japonicus* (Matsumoto et al., 2011). The stylops can parasitize all three rice planthoppers and other species. Furthermore, host preference is considered to differ with region (Maeta et al., 2007; Chandra, 1980). Conversely, *H. oratrius* mostly relies on *L. striatellus* as a host resource, and thus the geographical difference in host preference, excluding *L. striatellus*, could be a minor effect. The genetic structure of the Kyushu population sampled was intermediate between the Kanto and Taiwan-China populations. Haplotypes are seemingly composed of two elements: the more-variable part directly connected with Kanto, and the less-variable part connected with Taiwan and China. The natural populations of Kyushu, Taiwan and China probably share many haplotype components. However, the dominant haplotypes among the three populations are observed in haplotype group A (Fig. 9). This indicates a current large gene flow caused by the migration of parasitized *L. striatellus*. The haplotype network of Taiwan and China is somewhat simpler than the Japanese populations. They are geographically distant, but genetically indistinguishable. The current migration of *L. striatellus* between Taiwan and China should be tested. Otherwise, it is possible that *H. oratrius* has experienced past fragmentation.
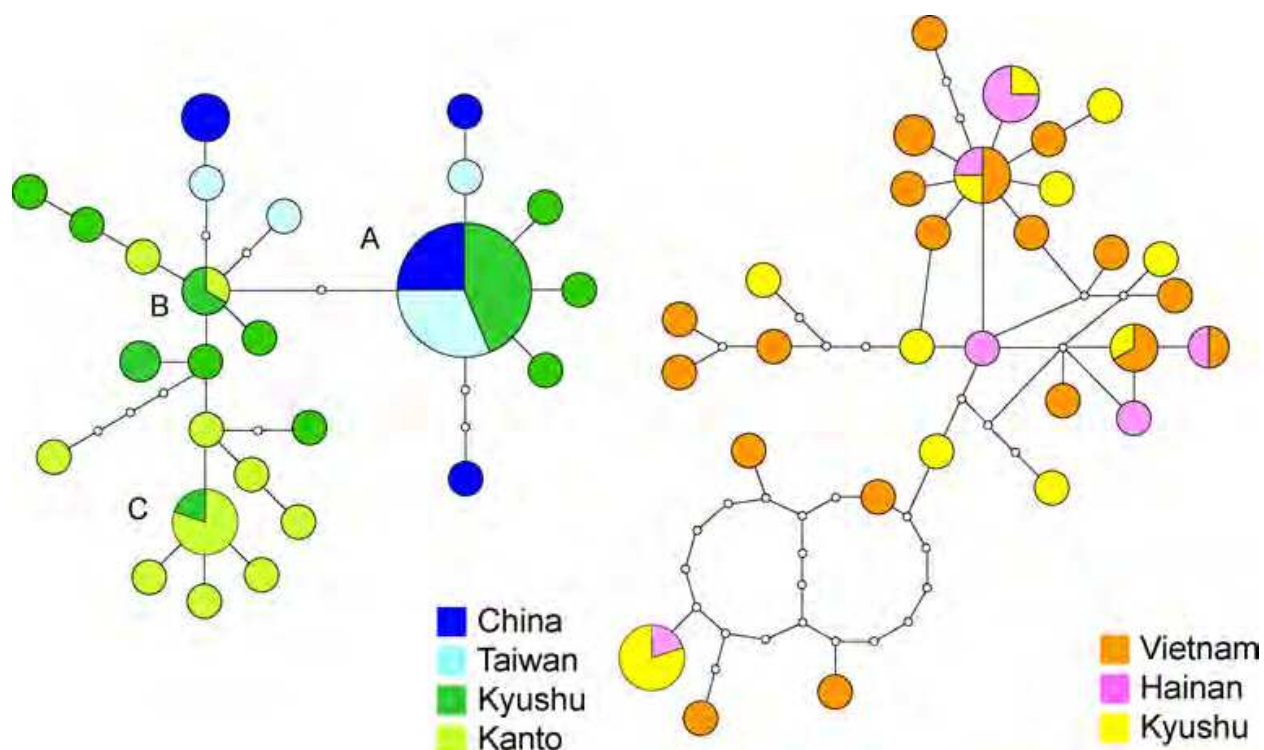

Fig. 9. Parsimonious network of two species of *Haplogonatopus* (left: *H. oratrius*, right: *H. apicalis*). Each circle indicates a different haplotype. The frequency of a geographical population is indicated by a different color.

7. Discussion

Host range and hibernation ability contrasts between *H. apicalis* and *H. oratrius*. However, both species have long-distance passive migration ability in association with their hosts. The

hibernation ability of their main hosts and the host-shifting ability of dryinids at the destination locality may influence their genetic structure. According to the Palaearctic distribution of *L. striatellus* and their biology, *H. oratrius* could have been distributed widely without long-distance migration of the host. The overseas mass migration of *L. striatellus* demonstrated by Otuka et al. (2010) and genetic structure of *H. oratrius* suggests the presence of current gene flow among domestic populations of both species in China, Taiwan, and Kyushu. *H. apicalis* migrates into northern temperate regions as larvae parasitizing *S. furcifera*. This host probably becomes extinct each winter (Kitamura, 1987). Before the origin of rice culture in monsoonal Asia, heavy outbreaks of rice planthoppers should have occurred rarely. Gene flow within *H. apicalis* may have been accelerated by human activity. Another important dryinid species is *G. fluvifermur* (Esaki & Hashimoto, 1935). It parasitizes *N. lugens* in rice paddies. The observation of insecticide resistance and virulence to resistant rice varieties implies that the East Asian population of *N. lugens* has different traits from the South East Asia population (Sogawa, 1992, Matsumura et al., 2008, unpublished data). During field research at Sagami-gawa River, some females of *G. fluvifemur* were reared from other delphacid species collected on reed bush (*Phragmites australis* (Cav.) Trin. ex Steud.) habitat and grasslands in Kanto, central Honshu (Mita, unpublished data). Because few individuals of *N. lugens* reach there, these dryinids might be considered to adapt to other delphacids and establish in the new locality. It is important to compare many traits of different species for further discussion on the significance of passive migration (Mita et al., in preparation).

Dryinid wasps, including apterous taxa like *Haplogonatopus*, can be passively transported to distant localities by their hosts. This is similar to the dispersal capability of "aerial plankton" arthropods (Richter, 1970; Bowman et al., 1978; Mound, 1983). Insect migration is often considered to be an active behavior (Drake et al., 1995); however, passive aerial dispersal of minute apterous arthropods has been reported (Washburn & Washburn, 1984; Jung and Croft, 2001). Such species may actively launch themselves into air drafts, and are passively carried by the wind. On the other hand, the long-distance dispersal of dryinid wasps completely depends on hosts' activity. The long-distance migration of dryinid wasps together with stylops is an interesting example of passive behavior. The concept of "passive migration" is an important element in the historical biogeography of the Dryinidae. In this chapter, we reported the possibility of a local host shift by *H. oratrius* caused by the immigration of *L. striatellus* from elsewhere. So far, *H. apicalis* have not adapted to their planthopper host's destination localities. However, the expansion of the distribution caused by host dispersal is a highly probable event in certain taxa, perhaps together with host change. Consequently subsequent allopatric speciation and/or secondary contact might have occurred. The long-distance migration of their host has greatly influenced the distribution of the Dryinidae in monsoon Asia, not only in the past, but also as a progressive event.
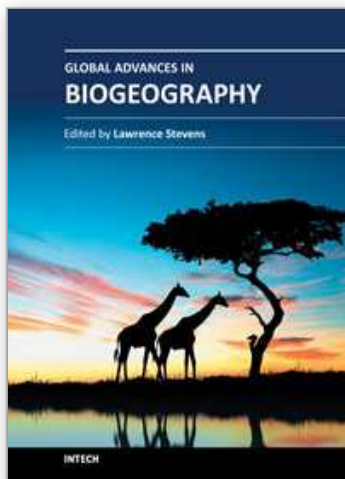
8. Acknowledgments

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