Distribution of the Freshwater Prawns (*Macrobrachium* Bate, 1868) in Taiwan in Relation to Their Biogeographic Origins

台灣島上淡水沼蝦屬分布與其生物地理起源之關係

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Abstract

Using data collected from the freshwater prawn inventory survey of 2000-2008 and historical data obtained from literature prior to 2000, distribution patterns of 15 species of the *Macrobrachium* prawns in Taiwan were examined. They were able to divide into two groups: the east-coast group and the island-wide group. The east-coast group contained 11 amphidromous species: *M. equidens*, *M. mammillodactylus*, *M. latidactylus*, *M. gracilirostre*, *M. lepidactyloides*, *M. lar*, *M. placidulum*, *M. jaroense*, *M. esculentum*, *M. latimanus* and *M. australe*. They were found in the east coast, some of them in its adjacent northern and southern regions. They were the Southeast Asia origins and dispersed to Taiwan mainly through the Philippines, and showed close association with the Kuroshio Current in the dispersion. The island-wide group contained 4 species: *M. japonicum*, *M. formosense*, *M. asperulum* and *M. nipponense*. The former species was postulated to have evolved within the island of Taiwan, while the latter three species were originated from the China mainland. They were common in streams around the island. *M. japonicum* and

M. formosense that have been considered to be amphidromous showed the distribution patterns fairly similar to that of non-obligatory amphidromous *M. nipponense* and even to that of landlocked *M. asperulum*, rather than to those of the amphidromous species of the east-coast group. The evidences suggest that these two species might not be the amphidromous but the non-obligatory amphidromous, but a further study is needed for the confirmation. The distribution patterns of the *Macrobrachium* prawns in Taiwan are resulted from their life cycle modes, adaptability to local environments at present and biogeographic origins and dispersal routes in the past evolutionary history.

摘　要

台灣 15 種淡水沼蝦在島上的分布範圍，可區分爲東岸型及全島型等 2 種分布類型。東岸型均爲兩側洄游性物種，分別爲 *Macrobrachium equidens*、*M. mammillodactylus*、*M. latidactylus*、*M. gracilirostre*、*M. lepidactyloides*、*M. lar*、*M. placidulum*、*M. jaroense*、*M. esculentum*、*M. latimanus* 及 *M. australe* 等 11 種，牠們分布在台灣的東部，部分物種亦分布在鄰接的北部及南部地區，其中 *M. australe* 則另分布在台灣的西北部。這些物種皆來自東南亞島嶼，並經由菲律賓來到台灣，其在島上的分布及擴散來台的途徑與黑潮關係密切。全島型包括 4 種，分別爲 *M. japonicum*、*M. formosense*、*M. asperulum* 及 *M. nipponense*，前者在台灣種化形成，後 3 種則源自於中國大陸。牠們廣泛分布於台灣的溪流，其中 *M. japonicum* 及 *M. formosense* 爲兩側洄游性，其在島上的分布型態與兼具兩側洄游的 *M. nipponense* 及陸封性的 *M. asperulum* 極爲相似，卻與同爲兩側洄游性的東岸型物種之分布極爲不同，顯示 *M. japonicum* 及 *M. formosense* 或許並非全然爲兩側洄游性，而是如 *M. nipponense* 爲兼具兩側洄游性的物種，此點需要進一步的研究證實。台灣淡水沼蝦在島上的分布型態，是演化過程中物種地理起源、擴散來台途徑及其對環境適應能力等因素所造成。

Key words: biogeography, distribution pattern, *Macrobrachium*, Taiwan

關鍵詞：生物地理、分布型態、沼蝦屬、台灣

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Introduction

Freshwater prawns (*Macrobrachium* Bate, 1868) of Taiwan are highly diverse, rich in amphidromous forms, but poor in endemic and land-locked forms (Hwang and Yu 1982; Shy and

Yu 1998; Cai and Jeng 2001; Cai and Shokita 2006; Chen *et al*. 2009). The fauna is a mixture of the species of various biogeographic origins and more similar to those of the Philippines Islands and the Ryukyu Islands than that of the China mainland (Chen *et al*. 2009).

In the previous study (Chen *et al*. 2009), we examined the distribution patterns of 15 known species of *Macrobrachium* of Taiwan in the Indo-Pacific region and their relationships based on the phylogenies reconstructed from the nuclear 28S rDNA gene. For the 13 amphidromous species, their biogeographic origins and dispersion routes to Taiwan were hypothesized to be: 1) in the eastern region of southeast Asia islands through the Philippines for *M. australe*, *M. lar*, *M. latimanus*, *M. gracilirostre*, *M. jaroense*, *M. esculentum*, *M. lepidactyloides* and *M. placidulum*; 2) in the western region of southeast Asia islands through the Philippines and/or China mainland for *M. equidens*, *M. latidactylus* and *M. mammillodactylus*; 3) in China mainland for *M. formosense*, and 4) on the island of Taiwan for *M. japonicum*. For the remaining two species, *M. asperulum*, a land-locked prawn, and *M. nipponense*, a non-obligatory amphidromous prawn, were originated from China mainland.

This study continued the previous study (Chen *et al*. 2009) to examine the distribution of the *Macrobrachium* prawns on the island of Taiwan and to determine whether there are relationships between the distribution and their biogeographic origins and past dispersion routes.

Material and Methods

During the period from 2000 to 2008, we made an inventory survey of freshwater prawns in inland waters of Taiwan. A 8-volt backpack electrofishing gear (Yeh *et al*. 2000), 30 cm x 10 cm baited shrimp traps (Chen *et al*. 2003), and various types of hand nets (Short 2000) were used. A total of 3,382 individuals belonging to 15 species of *Macrobrachium* were collected at 662 sites. An exception was *M. shaoi* that was extremely rare and found only in a tributary of Shuangchi River in the northern Taiwan (Cai and Jeng 2001) was not collected in this study. Most of the prawns were collected by the shrimp traps, but a lot of large individuals were captured by electrofishing. Most of the collections were fixed in 15% formalin water solution, preserved in 75% ethyl-alcohol water solution, and deposited at the Endemic Species Research Institute, Jiji, Nantou, Taiwan. The data were stored in Microsoft office Access 2003 for database setting. Also, distribution data of the prawns prior to 2000 were obtained from literatures (Hwang and Yu 1982; Shy 1994; Shy *et al*. 1996) and compared to those from our 2000-2008 survey. The distribution map of each species of the prawns was constructed with SuperGIS version 2.2.

Results

Based on field data collected from our 2000-2008 survey and distribution data obtained from literature (Hwang and Yu 1982; Shy 1994; Shy *et al*. 1996), the distribution patterns of 15 species of the *Macrobrachium* prawns in Taiwan were plotted in Figs. 1-4. They were divided into two groups: 1) the east-coast group and 2) the island-wide group:

The east-coast group

The east-coast group contained 11 amphidromous

species. They were distributed in the east coast with some in adjacent northern and/or southern regions and absent in the western region (Figs. 1-3). They corresponded to the species of three groups with different biogeographical origins and dispersion routes hypothesized by Chen *et al*. (2009). They were the Eastern Southeast Asia group (*M. esculentum*, *M. gracilirostre*, *M. jaroense*, *M. lepidactyloides* and *M. placidulum*), the Indo-West Pacific group (*M. australe*, *M. lar* and *M. latimanus*), and the Western Southeast Asia group (*M. equidens*, *M. latidactylus* and *M. mammillodactylus*). The former two groups were found in the Philippines but not in China mainland, and thus, they were postulated to originate from the eastern region of Southeast Asia islands and dispersed to Taiwan through the Philippines. The latter group was found in both the Philippines and China mainland and assumed to originate from the western region of Southeast Asia islands and dispersed to Taiwan through the Philippines and/or China mainland (Chen *et al*. 2009).

For the Eastern Southeast Asia group, *M. esculentum*, *M. jaroense* and *M. placidulum* were found to be rare and occurred only in streams along the east coast (Fig. 1), whereas *M. gracilirostre* and *M. lepidactyloides* were common and found not only in the east coast but also in the southwestern region (Fig. 2A-B). The Indo-West Pacific group, *M. lar* and *M. australe* were common and found in the east coast, southwestern and northwestern region of the island (Fig. 2C-D), while *M. latimanus* was rare and occurred in streams of southwestern region and some in the east coast (Fig. 1). For the Western Southeast Asia group, *M. equidens* was common and occurred in the east coast and also in both southwestern and northwestern regions of the island, while *M. latidactylus* and *M. mammillodactylus* were rare and occurred only in the east coast (Fig. 3).

The island-wide group

The island-wide group contained four species: *M. asperulum*, *M. nipponens*, *M. formosense* and *M. japonicum*. They occurred in streams around the island (Fig. 4), differing from those of the east coast group (Fig. 1-3). The former three species are postulated to originate from the China mainland, while the latter species is an autochthonous prawn that was evolved within the island of Taiwan (Chen *et al*. 2009). The four species have been considered to have different life cycle modes: *M. asperulum* as a landlocked prawn (Shokita 1977; Lin *et al*. 1988; Shy 1994; Shy *et al*. 1996; Liu *et al*. 2007; Mashiko and Shy 2008), *M. nipponense* as a non-obligatory amphidromous prawn (Shy *et al*. 1987; Shy 1994; Shy *et al*. 1996; Mashiko and Shy 2008), and *M. formosense* and *M. japonicum* as the amphidromous prawns (Shy *et al*. 1990; Shy 1994; Shy *et al*. 1996; Suzuki and Kusamura 1997; Liu *et al*. 2007; Mashiko and Shy 2008).

Distributions of the freshwater prawns in Taiwan are closed related to their biogeographical origins and modes of their life cycles. The east coast group contained amphidromous prawns of the tropical Southeast Asia islands origins, whereas the island-wide group contained land-locked, non-obligatory amphidromous, and amphidromous prawns of the East Asia origins (Taiwan or China mainland).

Discussion

The east-coast group

Although 11 amphidromous prawns of the east-coast group came from three different

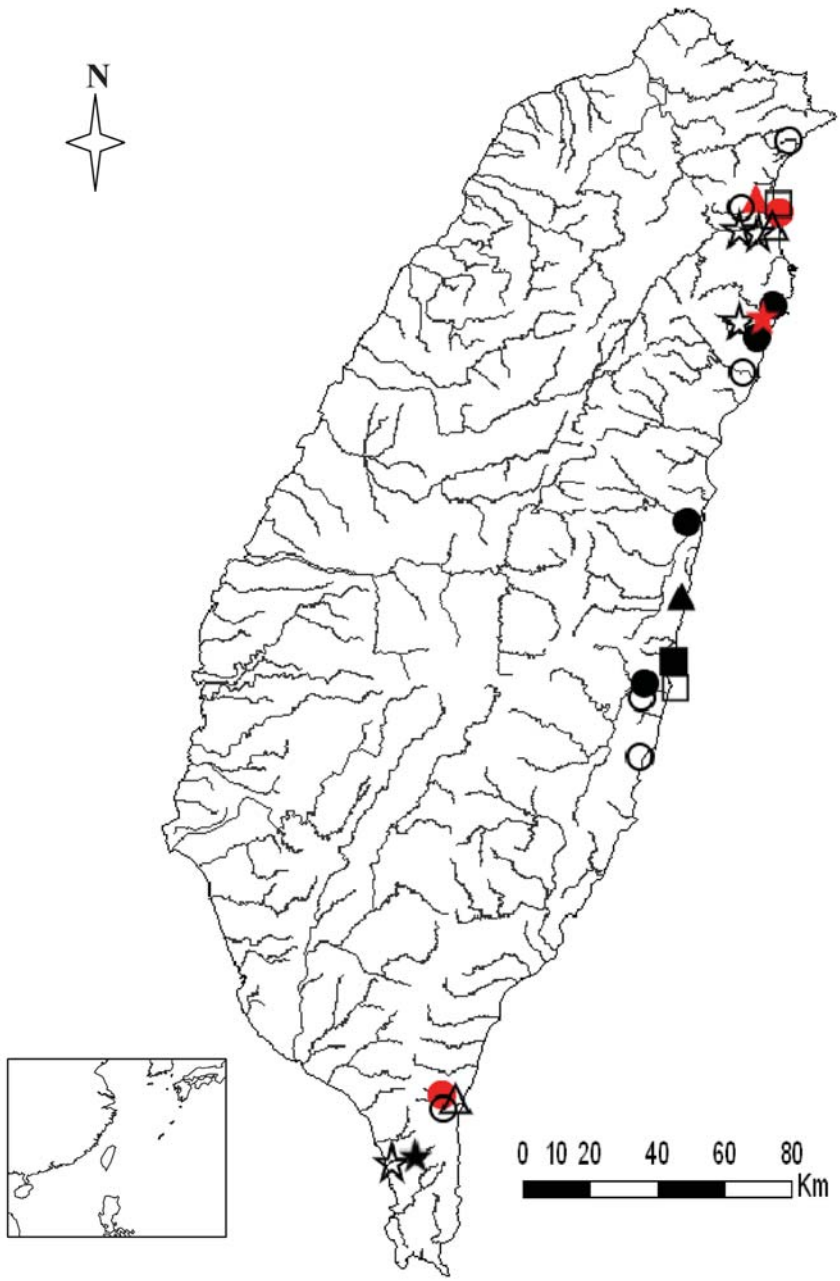

Fig. 1. Distributions of four rare species of the east coast group of *Macrobrachium* in Taiwan: *M. placidulum* (solid circles, 2000-2008 survey; open circles, Shy 1994; red solid circles, Hwang and Yu 1982); *M. jaroense* (solid triangles, 2000-2008 survey; open triangles, Shy 1994; red solid triangles, Hwang and Yu 1982); *M. esculentum* (solid squares, 2000-2008 survey; open squares, Shy 1994); and *M. latimanus* (solid stars, 2000-2008 survey; open stars, Shy 1994; red solid stars, Hwang and Yu 1982).

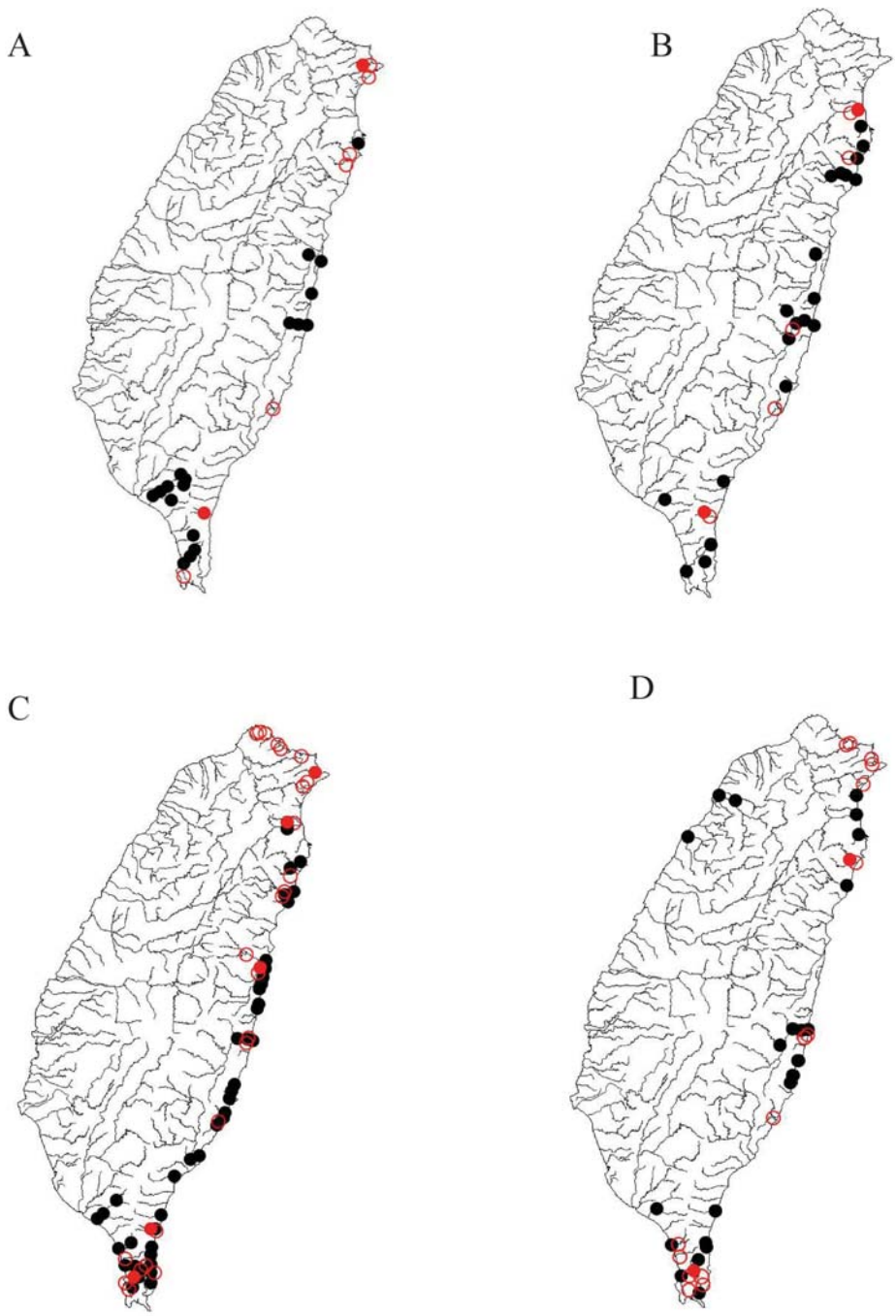

Fig. 2. Distributions of four common species of the east coast group of *Macrobrachium* in Taiwan: A. *M. gracilirostre*; B. *M. lepidactyloides*; C. *M. lar*; D. *M. australe* (solid circles, 2000-2008 survey; red open circles, Shy 1994; red solid circles, Hwang and Yu 1982).

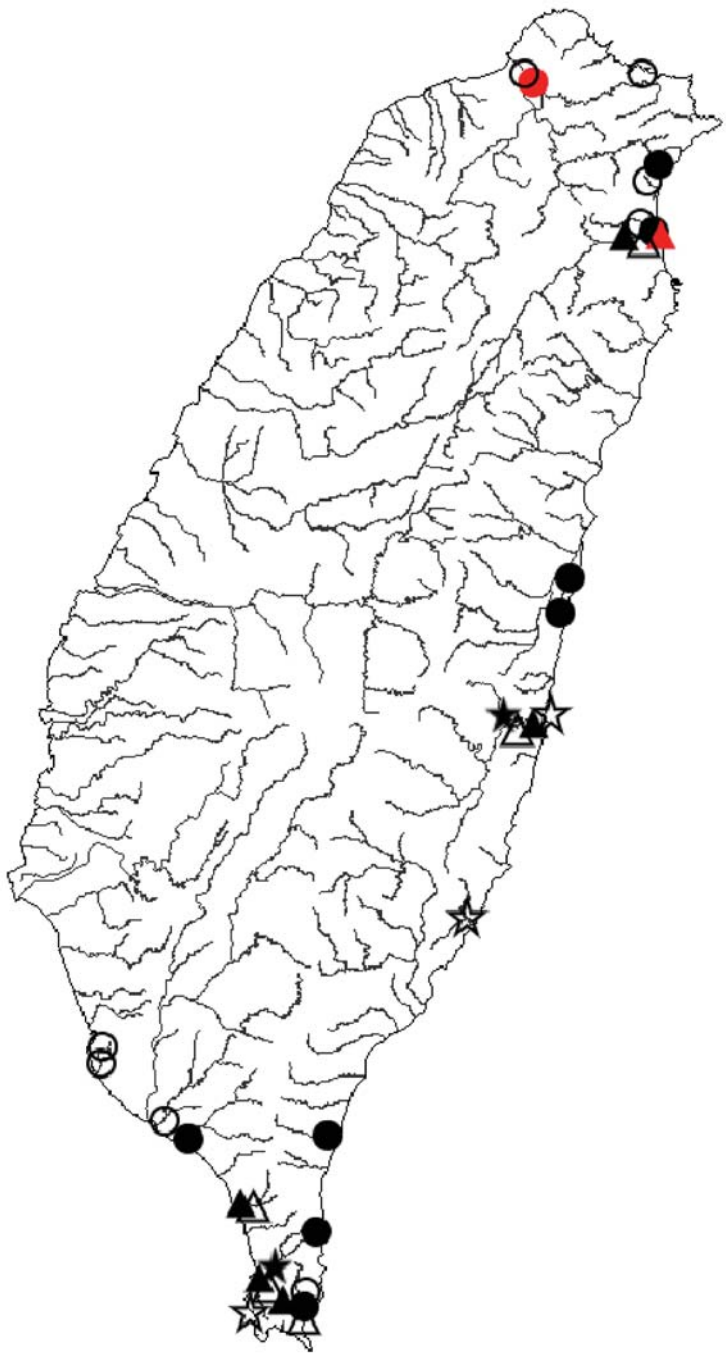

Fig. 3. Distributions of common *M. equidens* (solid circles, 2000-2008 survey; open circles, Shy 1994; red solid circles, Hwang and Yu 1982) and two rare species: *M. latidactylus* (solid triangles, 2000-2008 survey; open triangles, Shy 1994; red solid triangles, Hwang and Yu 1982); *M. mammillodactylus* (solid stars, 2000-2008 survey; open stars, Shy 1994) of the east-coast group in Taiwan.

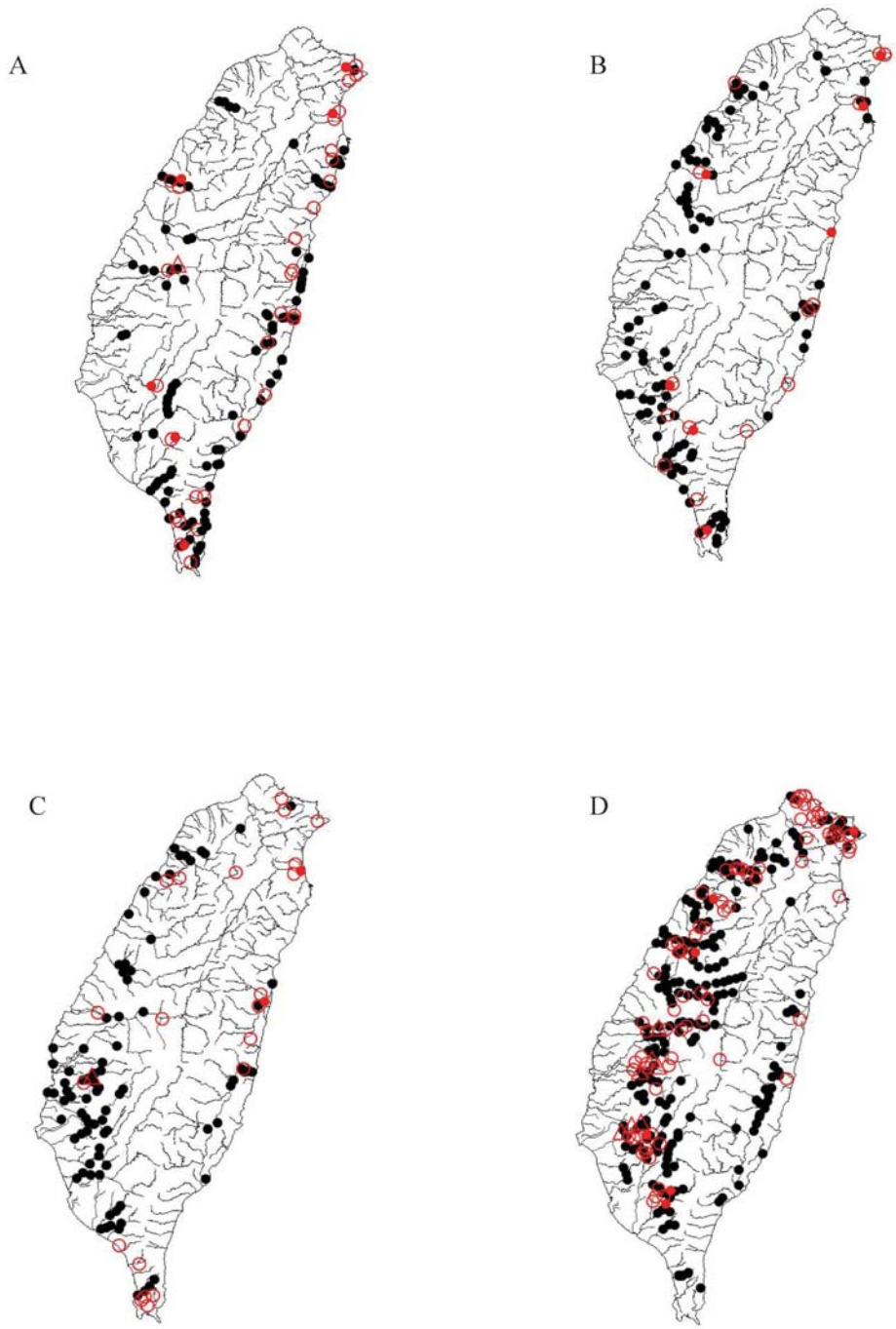

Fig. 4. Distributions of four species of the island-wide group of *Macrobrachium* in Taiwan: A. *M. japonicum*; B. *M. formosense*; C. *M. nipponense*; D. *M. asperulum* (solid circles, 2000-2008 survey; red open circles, Shy 1994; red solid circles, Hwang and Yu 1982; red open triangles, Shy *et al.* 1996).

phylogenetic lineages and biogeographic origins in the tropical Southeast Asia islands (Chen *et al*. 2009), they showed fairly similar distribution pattern in Taiwan. They were distributed in the downstream section of the rivers close to the mouths in the east coast (Figs. 1-3). Apparently, these prawns of Southeast Asia islands origins still shared fairly similar life cycle modes and habitat requirements in Taiwan.

Streams in the east coast of Taiwan have high gradients as the mountain ranges approach closely to the coast. The stream water flows directly into coastal waters, forming a small blackish water zone outside the stream mouth rather than within the mouth. Larval development of these amphidromous prawns must be completed in the coastal waters, suggesting that the larvae may require high salinity and be highly tolerant to it, even to sea water.

There is the warm Kuroshio Current flowing northwardly closely to the shore along the east coast of Taiwan. The larvae of these amphidromous prawns have a chance to be transported northwardly by the current. It seems that the Kuroshio Current might play a role in the northward dispersion of these amphidromous prawns from Southeast Asia islands to Taiwan, even to Japan. According to this line of the reduction, *M. equidens*, *M. latidactylus* and *M. mammillodactylus* of the Western Southeast Asia group that are considered to have dispersed to Taiwan through the Philippines and/or China mainland (Chen *et al*. 2009) might be more likely through the Philippines than through the China mainland.

When the Kuroshio Current hits the southern tip of Taiwan, its main stem flows along the east coast of the island and a small western branch enters the Taiwan Strait and flows along the southwestern coast of the island (Lin *et al*. 1992; Liang *et al*. 2003). This may explain the reason that these tropical prawns are often also found in the southwestern region.

During the Pleistocene glaciation, the western region of Taiwan was connected to the China mainland with the land bridge. The region was undoubtedly inhabitable for amphidromous prawns that requires brackish waster for larval development. Since the last glaciation, the land bridge has been transformed into Taiwan Strait, but the western region has still remained inhabitable for these tropical amphidromous prawns. This may be due to the cold China mainland current that flows southwardly along the west coast from China mainland in winter.

The island-wide group

For the four species of the island-wide group, the distribution patterns of *M. japonicum* and *M. formosense* (Fig. 4A-B) that are considered to be amphidromous (Shy *et al*. 1990; Shy 1994; Shy *et al*. 1996; Suzuki and Kusamura 1997; Liu *et al*. 2007) differed greatly from those of the amphidromous species of the east-coast group (Fig. 1-3) but were fairly similar to that of *M. nipponense* that is non-obligatory amphidromous and *M. asperulum* that is landlocked (Fig. 4C-D).

The life cycles of *M. japonicum* and *M. formosense* are somewhat similar to that of *M. nipponense*. They have small eggs and general nine zoea stages (Ogasawara *et al*. 1979). In Japan the three species are found to spend their long pelagic zoeal stage in estuarine brackish waters, and then juveniles of *M. formosense* and *M. japonicum* migrate upstream to freshwater (Ogasawara *et al*. 1979; Shokita 1979; Shy *et al*. 1990), whereas individuals of *M. nipponense* remain in the estuaries (river mouths) to complete

their life cycle, but some populations are found in coastal or inland freshwater lakes, resulting from a recent shift in its habitat from estuaries to inland freshwaters (Mashiko 1990; Mashiko and Numachi 2000). Such shift to freshwater form from amphidromous form have been well documented for other freshwater shrimp *Paratya australiensis* Kemp, 1917 in Australia (Williams 1977; Hancock and Bunn 1977; Walsh and Mitchell 1995; Cook *et al*. 2006), and also many species of fishes and invertebrates (Lee and Bell 1999; Lee 1999; Taylor and McPhail 1999; Waters and Wallis 2001; Raeymaekers *et al*. 2005; Cook *et al*. 2006). The shift of amphydromy to freshwater form plays an important role in diversification of many freshwater fauna in evolution.

The above evidences may suggest that *M. japonicum* and *M. formosense* might not be amphidromous but non-obligatory amphidromous like *M. nipponense*. A further study is needed to confirm the life cycle modes of those two species.

Mashiko and Shy (2008) used molecular clock to estimate the time of speciation events and suggest that *M. shokitai* endemic to the Irimoto Island of the southern Ryukyu differentiated from *M. asperulum* of Taiwan approximately 1.0 million years ago, and *M. nipponense* from *M. formosense* 0.48 million years ago. According to Lee (2006) the uplift rate of Taiwan Central Range was initially slow at a rate of < 1 mm/year from 6 million years ago to 1 million years ago. Since then the rate has increased to 4-10 mm/year. The mountains started to build from the north toward the south at a rate of 60-90 km/million years.

M. asperulum of China mainland might arrive in the west coast of Taiwan before the time of the rapid uplift of the Central Mountain Range 1 million years ago at the time when the east coast remained in connection to the west coast with shallow valleys. This might enable the species to disperse across the island to the east coast. *M. nipponense* and *M. formosense* arrived in the west coast of Taiwan from China mainland apparently latter than that of *M. asperulum*, but still enable them to disperse to the east coast. The similar cases of cross island dispersions are reported for the freshwater fish *Varicorhinus barbatulus* and freshwater crab *Candidiopotamon rathbunae* (Wang *et al*. 2004; Shin *et al*. 2006).

The distribution patterns of the *Macrobrachium* prawns in Taiwan are related to their biogeographic origins and dispersal routes in the evolutionary history, their life cycle modes, and their adaptability to local climatic and environmental conditions at the present.

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