

Pleistocene speciation of freshwater crabs (Crustacea: Potamidae: *Geothelphusa*) from northern Taiwan and southern Ryukyus, as revealed by phylogenetic relationships

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Received 9 May 2011; received in revised form 18 July 2011; accepted 20 July 2011

Corresponding editor: S. De Grave.

Abstract

The phylogenetic relationship among freshwater crab species of *Geothelphusa* from northern Taiwan and the Yaeyama Group of islands (including Iriomote and Ishigaki) in the southern Ryukyus was studied using the mitochondrial genes 16S rRNA and COI. Our results support the hypothesis that speciation of *Geothelphusa* among these islands was the result of cyclic glaciations and interglaciations during the Pleistocene. Two main clades, one the Taiwan Group (containing several clades, including most Taiwanese *Geothelphusa* species except *Geothelphusa miyazakii* but including *Geothelphusa minei* from Yaeyama), was estimated to be separated from its sister group, the southern Ryukyus-northern Taiwan (SRN) clade (including *G. miyazakii*, *Geothelphusa shokitai*, *Geothelphusa fulva* and *G. marginata* from northern Taiwan, the Pinnacle Islands [=Diaoyutai Islands or Senkaku Islands] and Yaeyama) at about 5.3 million years ago (mya). *G. shokitai* was separated from others within the SRN clade at 2.4 mya, but was probably derived from *G. miyazakii* in northern Taiwan. The ancestor of *G. miyazakii* is hypothesised to have dispersed from ancestors in Yaeyama and then isolated at 2.0 mya during the Pleistocene interglaciations. This is similar to the speciation of *G. minei* in Yaeyama at 1.5 mya, except that its ancestors originated from north-eastern Taiwan. Four clades of freshwater crabs are present in the Fushan Botanical Garden, located in the mountainous area of north-eastern Taiwan, which might be due to the historical rearrangements of the drainage and proximity of the various river origins.

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Keywords: 16S rRNA; Biogeography; COI; Freshwater crabs; *Geothelphusa*; Glaciations; Phylogeny

1. Introduction

The East Asian Arc is a chain of islands located east of continental Asia, stretching from the main islands of Japan to the Ryukyus and Taiwan. The biogeographical relationship of terrestrial vertebrates (especially amphibians and reptiles) between northern Taiwan and the southern Ryukyus (Yaeyama and Miyako Groups) has been relatively

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well studied (see Lue and Chen, 1997; Ota, 1998, 1999, 2000; Kimura, 2002), especially because many terrestrial organisms have dispersed between continental China and the islands during the various low sea levels of cyclic glaciations. However, almost no studies have been done on terrestrial or wholly freshwater invertebrates which may reveal other patterns.

The entire life cycle of freshwater crabs is spent within the freshwater environment. The fertilized eggs develop directly into juvenile crabs and females brood the early juveniles for periods of different lengths. Migratory abilities of freshwater crabs are also relatively weak. The reproductive biology of freshwater crabs, together with their intolerance of brackish or sea water for long periods means that seas and oceans are effective barriers against their dispersal, except during periods of glaciation when land masses and islands are connected by land bridges. As such, this makes them excellent biogeographical indicators (see Ng, 1988; Ng and Rodriguez, 1995; Cumberlidge and Ng, 2009; Shih and Ng, 2011). The phylogenetic and divergence patterns of freshwater crabs from Taiwan and the adjacent areas have been shown to be useful in understanding the island's geological history (Shih et al., 2004, 2005, 2006, 2007a,b, 2011).

Members of the genera *Geothelphusa* and *Candidiopotamon* are the dominant and endemic freshwater crabs of the East Asian islands. The species richness of *Geothelphusa* is the second highest among the East Asian freshwater crabs (Shih and Ng, 2011). Thirty-seven species have been reported from Taiwan itself, with another 14 from the Ryukyus, and two others from the main islands of Japan (Shy et al., 1994; Shy and Yu, 1999; Yoshigou, 1999; Ng et al., 2001; Kasai and Naruse, 2003; Shih and Ng, 2011). One additional species, *Geothelphusa shokitai*, was described by Shy and Ng (1998) from a small island group currently disputed by Taiwan, Japan and China; known as Diaoyutai in the Diaoyutai Islands by the Taiwanese, and Uotsurijima in the Senkaku Islands by the Japanese. This species is treated in this study but as there is political controversy over the islands' sovereignty, and this study has members from Taiwan and Japan, we have elected to use the old name for this group – the Pinnacle Islands, instead. The cladogenesis of the Ryukyuan freshwater crabs has been proposed to be the result of vicariance events separating them from other species on Asia (Shokita, 1996, 2002). This hypothesis has been supported by molecular and biogeographical analyses with more specific divergence times (Shih et al., 2009a; Shih and Ng, 2011).

The freshwater crab fauna of the region of northern Taiwan and the southern Ryukyus (Fig. 1) has been well studied. A total of 12 species of *Geothelphusa* and *Candidiopotamon rathbunae* (De Man, 1914) have been reported from northern Taiwan, one *Geothelphusa* from the Pinnacle Islands, three *Geothelphusa* as well as *Ryukyum yaeyamense* (Minei, 1973) from the Yaeyama Group (Iriomote and Ishigaki), and one *Geothelphusa* from Miyako Island (cf. Table 1). However, the phylogenetic relationship of *Geothelphusa miyakoensis* Shokita, Naruse and Fujii, 2002 from Miyako is actually

closer to species from the central Ryukyus instead of those from the Yaeyama Group (Segawa, 2000).

The Pinnacle Islands are located in the southern Taiwan-Sinzi Folded Zone (TSFZ) of the Asian continental shelf that was part of the Taiwan Orogeny during the Pliocene (Chen and Juang, 1997; Hsiao et al., 1998), with the deep Okinawa Trough separating the Pinnacle Islands and the Ryukyu Islands (Fig. 1). The main island, Diaoyutai or Uotsurijima, has an area of $\sim 4 \text{ km}^2$, is mainly composed of sandstone, with several streams (Nohara, 1971; Yoshida et al., 1971; Ho, 1988; Chen and Juang, 1997). It has long been known that a species of freshwater crab exists on this island, variously referred to as *Geothelphusa candidiensis* Bott, 1967 or *Geothelphusa miyazakii* (Miyake and Chiu, 1965), taxa in common with Taiwan (Minei, 1973, 1981; Kasai and Naruse, 2003). Only recently was the taxon elevated to species status, as *G. shokitai* Shy and Ng, 1998 (Yoshigou, 1999; Kasai and Naruse, 2003; Naruse et al., 2004; Shih, 2008).

The extent of genetic diversity and the occurrence of regional endemism for the freshwater crabs around the area of northern Taiwan, the Pinnacle Islands and Yaeyama in the southern Ryukyus are here revealed by phylogenetic and geological evidence. We hypothesise that the speciation of these species was largely the result of cyclic glaciations and interglaciations affecting dispersal and isolation during the Pleistocene (2.6–0.01 mya). The mitochondrial 16S rRNA and cytochrome oxidase I (COI) genes for the *Geothelphusa* species from this area were analysed and discussed in the context of their phylogeny and the background geological events.

2. Materials and methods

Specimens of the genus *Geothelphusa* were collected from the streams of northern Taiwan, defined as the areas north of Dajia River (=R.) in western Taiwan and Heping R. in eastern Taiwan, including New Taipei City (formerly as Taipei County = Co.), Taipei City, Taoyuan Co., Hsinchu Co., Miaoli Co., northern part of Taichung City (formerly included old Taichung City and Taichung Co.) and Ilan Co.; the Pinnacle Islands; and Yaeyama (including Iriomote and Ishigaki islands) in the southern Ryukyus (Fig. 1). In total, 112 specimens belonging to 17 species or species-groups were collected from this region (Table 1). Specimens of congeneric *Geothelphusa amagui* Naruse and Shokita, 2009 (from the central Ryukyus) and *Geothelphusa dehaani* (White, 1847) (from the main islands of Japan), and *C. rathbunae*, a taxon close to *Geothelphusa* (Shih et al., 2009a; Shih and Ng, 2011), were used as outgroups (Table 1). All specimens were preserved in 75–95% ethanol after collection.

Genomic DNA was isolated from the muscle tissue of legs by using the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A region of ~ 550 base-pairs (=bp) of the 5'-end of the 16S gene was selected for amplification with polymerase chain reaction (PCR) using

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