

# Phylogeography of Japanese water crowfoot based on chloroplast DNA haplotypes

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## Abstract

Water crowfoot, *Ranunculus* subgenus *Batrachium*, are submerged macrophytes in the Ranunculaceae. We aimed to infer the Quaternary history of these aquatic macrophytes in the Japanese archipelago. We studied 212 individuals of three perennial and one annual species from 46 populations covering the entire geographic range and found eight haplotypes based on approximately 1800 bp of four spacers in chloroplast DNA. The relationships among haplotypes were resolved using maximum parsimony and parsimony network analyses. To identify the zones of clear genetic boundaries, Monmonier's algorithm was used. The eight haplotypes were distinguished from adjacent haplotypes by one substitution or indel. Each of the 46 populations was fixed for a single haplotype. Inconsistency between cpDNA haplotypes and *Batrachium* taxa was found, except in one annual species. The distribution of the haplotypes in perennial species was highly geographically structured. An abrupt genetic change was detected between the Tohoku region and more southerly regions. Since the perennial *Batrachium* are cold-adapted, this genetic differentiation may be due to historical changes in their distributions caused by Quaternary climatic oscillations: interglacial retreats in colder refugia and glacial range expansions. The single haplotype composition of each population may have been shaped by founder effects during colonization and/or by genetic drift. The interglacial refugial populations must have been small enough to deplete haplotype diversity. Inconsistency between cpDNA haplotypes and *Batrachium* taxa may be due to incomplete lineage sorting of ancestral polymorphic haplotypes. © 2008 Elsevier B.V. All rights reserved.

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## 1. Introduction

The 30 species in the genus *Ranunculus* subgenus *Batrachium* (water crowfoot: Ranunculaceae) are aquatic macrophytes mainly distributed in the temperate to subfrigid zones of the Northern Hemisphere (Kadota, 1996). Four species inhabit the Japanese archipelago, located at the eastern edge of East Asia, in shallow streambeds in rivers, canals, or standing ponds. Three of the four species (*R. nipponicus* (Makino) Nakai, *R. yezoensis* Nakai, and *R. ashibetsuensis* Wiegleb) are endemic to Japan, perennial, and grow in clear, cold streams (<20 °C; Kimura and Kunii, 1998). *Ranunculus kadzusensis* Makino is polydemic in Japan and Korea and is an annual that can inhabit stagnant water (Kadono, 1994; Meguro and Takiguchi, 2002).

The most common species is *R. nipponicus*, which is widely distributed on the islands of Honshu and Hokkaido (see Fig. 1). This species is classified into three varieties based on vegetative characteristics, the presence or absence of a floating leaf, hair on the receptacles and achenes, and/or the length of the lamina and petiole (Appendix A): var. *submersus* Hara, var. *okayamensis* Wiegleb, and var. *nipponicus* (Kadono, 1994). Variety *okayamensis* is confined to several rivers in western Honshu and var. *nipponicus* is confined to a few rivers in midland Honshu (Chubu region) and Hokkaido. In contrast, var. *submersus* is widely distributed throughout Honshu and Hokkaido.

Other river perennial species, *R. yezoensis* and *R. ashibetsuensis*, are distinguished from *R. nipponicus* by glabrous receptacles (*R. yezoensis*: northern Honshu [Tohoku region] and Hokkaido) and larger flowers and internodes (*R. ashibetsuensis*: one location in eastern Hokkaido; see Appendix A). However, the classification among the three river perennial species is sometimes difficult, and the intra- and interspecific classification of the river perennial species based

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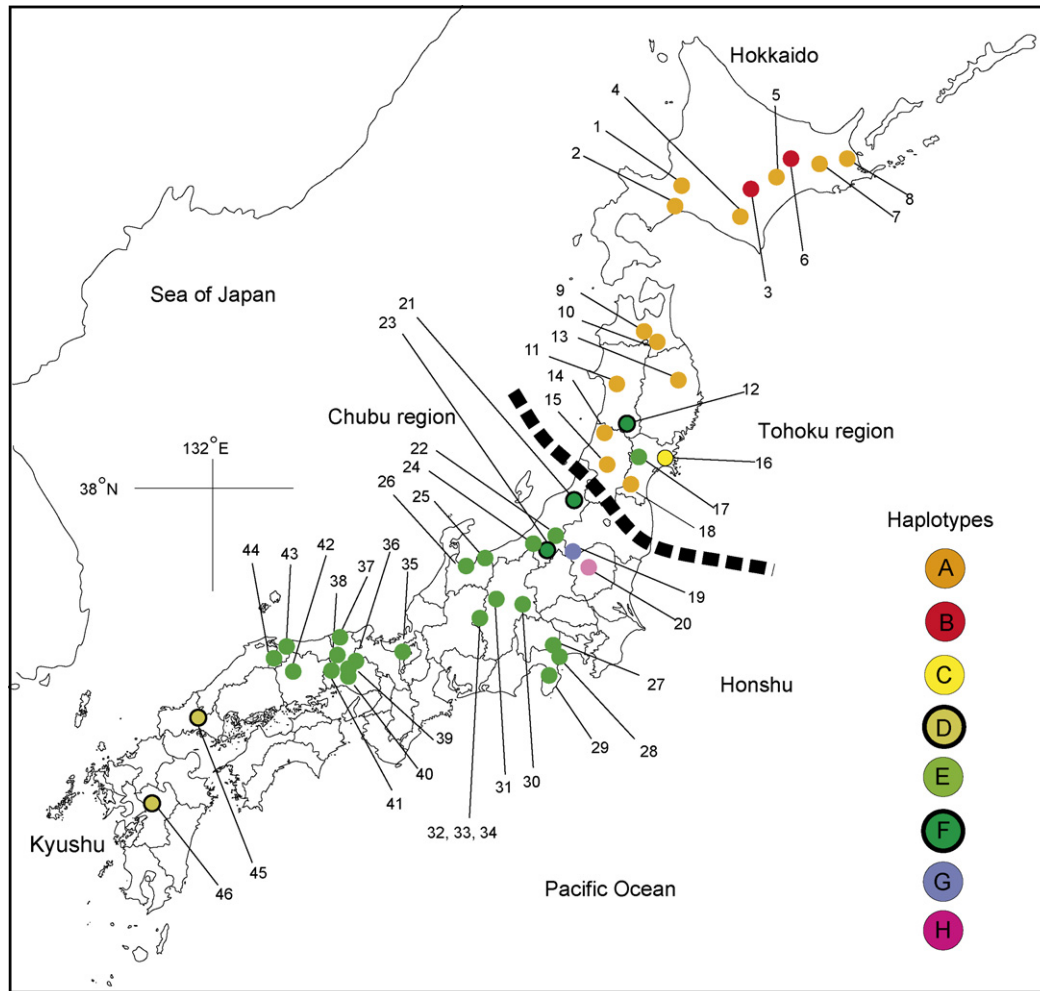


Fig. 1. Geographic distribution of cpDNA haplotypes detected in Japanese *Batrachium* species. The population numbers correspond to those detailed in Table 1. Each colour corresponds to a haplotype represented in the right column. Five individuals were sampled in most populations. Tohoku and Chubu are the regional names of the northern and middle portions of Honshu Island. The dashed line represents the first genetic boundary among 43 populations of perennial *Batrachium* taxa obtained with Monmonier's maximum difference algorithm based on Euclidian distances among populations.

on morphological characteristics has changed several times (Wiegand, 1988). This taxonomic confusion is attributable to plasticity and morphological polymorphism, which are common in aquatic plants. In contrast, the stagnant water, annual species *R. kadzusensis* is well characterised by a smaller size and is distributed in three separate populations in Kyushu, western Honshu, and the Tohoku region.

Koga et al. (2007) inferred genetic diversity and structure within and among 11 populations of *R. nipponicus* (including var. *submersus* and var. *okayamensis*) in western Honshu using inter-simple sequence repeats (ISSR) and found significant genetic differentiation among populations ( $F_{ST} = 0.84$ ). This implies that gene flow, accomplished by seed dispersal, is very low. Chloroplast DNA (cpDNA) data would help determine the geographic structure of species and populations throughout the Japanese archipelago, which extends approximately 4000 km from north to south. A cpDNA phylogeography of the Japanese archipelago would be able to refute or discover geographic structure on the islands.

We obtained genetic information on the phylogeography of the Japanese *Batrachium*. *Ranunculus nipponicus* (all three

varieties), the other two perennial species in Japan (*R. yezoensis* and *R. ashibetsuensis*), and the morphologically and ecologically differentiated species *R. kadzusensis* from Japan and Korea were included in the study. Three European species were used as outgroups in the phylogenetic analyses.

## 2. Materials and methods

### 2.1. Study sites and sampling strategy

Leaf materials from *R. nipponicus* (var. *submersus*, var. *okayamensis*, and var. *nipponicum*), *R. kadzusensis*, *R. yezoensis*, and *R. ashibetsuensis* were sampled from almost their entire geographic distribution in Japan (Table 1). Samples were collected from about five individuals in each of 46 populations. Habitats of *R. kadzusensis*, *R. yezoensis*, and *R. ashibetsuensis* were rare, and sample sizes for these species were small. We sampled a total of 212 individuals. Identification of each sample followed Kadono (1994) based on observations and measurements of ten individuals per population, but sterile samples were preserved for taxon identification (Appendix A). Collected leaves

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