



Allopatric speciation of *Meteterakis* (Heterakoidea: Heterakidae), a highly dispersible parasitic nematode, in the East Asian islands

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ABSTRACT

To clarify how the species diversity of highly dispersible parasites has developed, molecular phylogenetic analyses of *Meteterakis* spp., multi-host endoparasitic nematodes of reptiles and amphibians from the East Asian islands, were conducted. The results demonstrated the existence of two major clades, the J- and A-groups, with exclusive geographic ranges that are discordant with the host faunal province. However, diversification within the J-group was concordant with the host biogeography and suggested co-divergence of this group with vicariance of the host fauna. In contrast, the phylogenetic pattern within the A-group was discordant with host biogeography and implied diversification by repeated colonization. In addition, the mosaic distribution pattern of a J-group and an A-group species in the Japanese Archipelago, along with comparison of population genetic parameters and the genetic distance from their closest relatives, suggested the initial occurrence of a J-group lineage followed by exclusion in the western part of this region caused by invasion of an A-group lineage. Thus, the present study suggested that the species diversity of highly dispersible parasites including *Meteterakis* is formed not only by co-divergence with host faunal vicariance but also by peripatric speciation and exclusive interactions between species.

1. Introduction

Parasites exhibit high species diversity, and elucidation of their diversification factors is a fundamental question in evolutionary biology. Some researchers expected that several ecological factors, such as host specificity, mobility of hosts and parasites, and life cycle, influenced the patterns of parasite species diversity [1,2], because these may affect the dispersal ability of parasites; this can influence the intra-specific genetic diversity and the rate of allopatric speciation.

Dispersal ability is one of the most important factors influencing intra- and inter-specific diversity [3]. Low dispersal ability leads to a low rate in gene flow and promotes inter-population genetic divergence, and high dispersal leads to a high rate in gene flow and suppresses inter-population genetic divergence. Several studies have compared the degree of intra-specific genetic divergences between parasite species which exhibit different host use and range [4–8]. These studies revealed that parasites having mobile hosts or wide host ranges tended to have reduced intra-specific genetic divergence, and concluded that the mobility of hosts and host richness (the number of possible host taxa) are major determinants of the dispersal ability of parasites [4–8]. Nonetheless, highly dispersible parasite taxa have a certain species diversity [e.g., [9]], and their diversification process remains to be studied.

Given that parasite dispersal ability is mostly regulated by host movements [e.g., [6]], and high dispersal ability should increase the chance of geographic range expansion [10], two modes of allopatric speciation of highly dispersible parasites are possible: (1) isolation of entire host fauna leads to vicariant allopatric speciation of parasites; and (2) extreme geographic range expansion ability increases the chances of peripatric speciation, caused by dispersal to an unoccupied area followed by speciation. To clarify the extent of contributions of these modes of allopatric speciation, one of the best strategies is an inference of historical biogeography of a group of parasites which encompasses allopatric closely related species and uses multiple hosts and/or a mobile host with a well-established biogeographic background.

Meteterakis Karve, 1930 (Heterakoidea; Heterakidae) is a multi-host parasitic nematode which mainly parasitizes the rectum of several species of lizards and frogs [11]; it has neither intermediate hosts nor a free-living phase [12]. Four named species of *Meteterakis* with exclusive distributions are currently known from the East Asian islands: *Meteterakis japonica* (Wilkie, 1930) in the eastern Japanese Archipelago (Fig. 1B), *Meteterakis amamiensis* Hasegawa, 1990 in the western Japanese Archipelago and Amamioshima Island (Amami Group of the Central Ryukyus, Fig. 1B, C), *Meteterakis ishikawanai* Hasegawa, 1987 in the Okinawa Group of the Central Ryukyus (Fig. 1C), and *Meteterakis*

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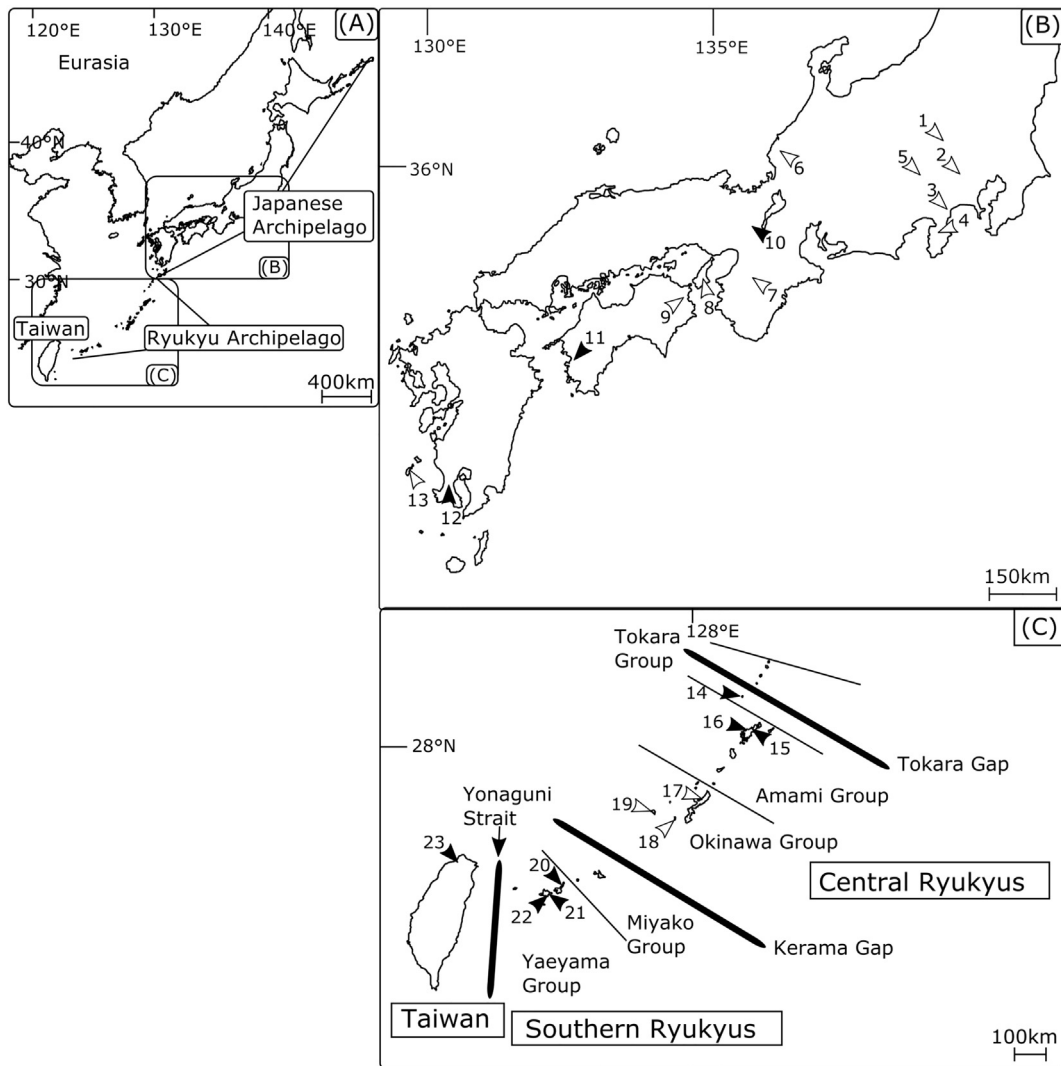


Fig. 1. Map of the East Asian islands showing: A, the entire study area in the East Asian islands; B, sampling localities in the Japanese Archipelago; C, sampling localities in the Ryukyus and Taiwan, and the boundaries of known biogeographic provinces (thick lines; see text for details). Open and solid symbols indicate J-group and A-group, respectively. See Table 1 for further details of sampling localities.

govindi Karve, 1930 in southern Taiwan (Fig. 1C). *M. govindi* is also found in India, Bangladesh, Myanmar, and China [11]. In addition, another undescribed species may occur in Miyakojima Island, the Miyako Group of the Southern Ryukyus: Hasegawa [13] reported individuals of *M. japonica* from this island, which differed from the true *M. japonica* in lacking a gubernaculum [14,15].

The known host species of *Meteterakis* in the East Asian islands consist of several frogs in the genera *Rana* Linnaeus, *Odorrana* Fei et al., *Bufo* Laurenti, and *Duttaphrynus* Frost et al.; lizards in the genera *Plestiodon* Duméril & Bibron, *Eutropis* Fitzinger, *Ateuchosaurus* Gray, *Takydromus* Daudin, and *Japalura* Gray; and a turtle in the genus *Geoemyda* Gray [13,14,16–28]. The extremely rare occurrence of *Meteterakis* in *Takydromus* and *Japalura* [20,23] strongly suggested that their infections were accidental.

The East Asian islands are composed of several island groups: the Japanese Archipelago, the Ryukyu Archipelago (northern and southern Tokara Groups, Amami Group, Okinawa Group, Miyako Group, and Yaeyama Group), and Taiwan (Fig. 1A, C). The species and subspecies distribution patterns of the native amphibians and terrestrial reptiles, including *Meteterakis* hosts, divide the East Asian islands into four biogeographical regions [29]. There are: (1) the Japanese Archipelago (including northern Tokara Group); (2) the Central Ryukyus (southern Tokara Group, Amami Group, and Okinawa Group); (3) the Southern

Ryukyus (Miyako Group and Yaeyama Group); and (4) Taiwan (Fig. 1A, C). Three sea straits, the Tokara Gap, Kerama Gap, and Yonaguni Strait (Fig. 1C), correspond to the biogeographical boundaries between the Japanese Archipelago and the Central Ryukyus, the Central and Southern Ryukyus, and the Southern Ryukyus and Taiwan, respectively. These straits have not been closed by land bridge since their establishment [29]. A recent review of biogeographic patterns of terrestrial reptiles in this region [30] suggested that: the major part of the Southern Ryukyu fauna was formed by isolation from Taiwanese fauna during the Pliocene (5.33–2.58 Ma) [31]; the major part of the Central Ryukyu fauna was formed by isolation from the other land areas during the late Miocene (23.03–5.33 Ma) [31] and; and that the Japanese Archipelago fauna was formed by isolation from the surrounding areas during the middle Miocene and by secondary interchange with the continent occurring during the Pliocene and Pleistocene (2.58–0.01 Ma) [31].

Several studies have also suggested overseas dispersal of some lizards between these major biogeographic regions [30,32–35]. Lizards, whose range expansion was also due to overseas dispersal, include *Plestiodon* and *Ateuchosaurus*, which are known hosts of *Meteterakis* spp. [30,33–35]. Thus, some of the hosts of *Meteterakis* from this area have high mobility.

Because *Meteterakis* species use highly dispersible lizard lineages,

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