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Ubiquity of *Sicyopterus lagocephalus* (Teleostei: Gobioidei) and phylogeography of the genus *Sicyopterus* in the Indo-Pacific area inferred from mitochondrial cytochrome *b* gene

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Abstract

Sicyopterus lagocephalus is a Gobiidae Sicydiinae (Teleostei) thought to inhabit Indo-Pacific island rivers from Comoros Islands in the Indian Ocean to Australs Islands (French Polynesia) in the Pacific Ocean. Its biological cycle comprises a marine planctonic larval phase of several months allowing it to migrate from island to island, but the other species of the genus, with such a larval stage, have generally a more restricted range and are often endemic. To understand the organisation of a species with such a wide distribution, mtDNA cytochrome *b* sequences were amplified for 55 specimens of this genus covering most of its distribution range together with six close endemic species and other gobiids used as outgroups. The main result is the confirmation of the ubiquity of *S. lagocephalus* that occurs over a range of 18,000 km in the Indian and Pacific Oceans. Two clades were identified within this species, one clustering most of French Polynesian haplotypes and the other clustering most of Mascarene (including Comoros) haplotypes. The overall pattern of distribution and phylogenetic relationship suggests that the lineages leading to endemic species originated earlier than *S. lagocephalus*. This latter seems to be a secondary migrant species, having colonised both Indian and Pacific Oceans with a few exceptions, situated at the border of the range (Madagascar, Marquesas, Rapa). According to the results, the phylogeny of the *Sicyopterus* group, the age of the different lineages and the past history of the colonisation of the Indo-Pacific islands are discussed.

Keywords: *Sicyopterus lagocephalus*; Gobiidae; Molecular phylogeny; Mitochondrial DNA; Dispersion; Pelagic larvae

1. Introduction

In the Indo-Pacific and Caribbean regions, insular river systems are colonised by Gobiidae with a life cycle adapted to the ecological conditions which prevail in these distinctive habitats, which are young oligotrophic rivers subject to extreme climatic and hydrological seasonal variation. These species spawn in freshwaters, the free embryos drift downstream to the sea where they undergo a planctonic phase, before returning to the rivers to grow and reproduce (Manacop, 1953; Keith, 2003), hence they are termed amphidromous

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(McDowall, 1997). The practical details of their biological cycle and the factors leading to such extreme evolution in amphidromous gobies are poorly known (McDowall, 1993), despite the fact that these gobies contribute most to the diversity of fish communities in the Indo-Pacific and the Caribbean insular systems, and have the highest levels of endemism (Watson, 1991; Radtke and Kinzie, 1996; Keith, 2002, 2003; Keith et al., 2002; Lim et al., 2002; Marquet et al., 2003).

Amphidromous gobies belong mainly to 11 genera and they comprise nearly 170 species (Keith, 2003). At certain times of the year, the biomass of larvae migrating upstream is so great that they are an important source of food for local human populations in certain island archipelagos (Bell, 1999).

Among amphidromous gobies, in the subfamily Sicydiinae, the genus *Sicyopterus* is the most diversified with 25–30 species (Watson et al., 2000) distributed in Indo-Pacific area from Madagascar and Comoros to French Polynesia, covering more than 18,000 km west-east. Only one species, *Sicyopterus lagocephalus* (Pallas, 1770), seems to be distributed throughout this entire range (Keith et al., 1999, 2002; Watson et al., 2000; Marquet et al., 2003); the others species generally have a more restricted distribution area and they are endemic to a small group of islands. *S. lagocephalus* therefore often lives in sympatry with endemic species of *Sicyopterus*: *S. pugnans* in the rivers of Society Archipelago (French Polynesia) in Tahiti, Moorea and Raiatea (Keith et al., 2002), *S. sarazini* in New Caledonia (Marquet et al., 2003), *S. aiensis* in Vanuatu (Keith et al., 2004), etc. Sometimes, the sympatry appears with endemic species of another genus such as *Cotylopus* in the Mascarene (Keith et al., 1999) or Comoros archipelagos (Keith, 2002; Keith et al., 2005). In some cases, the endemic species is the only *Sicyopterus* species present in the archipelago like in the Marquesas islands with *S. marquesensis* or Rapa island with *S. rapa* (Keith et al., 2002).

As amphidromous gobies have a specific biological cycle, the only possibility for the dispersion of the species and the colonisation of remote islands is the larval planctonic marine phase. The duration of this planctonic stage in this group of gobies varies from 91 to 169 days for several species of the Pacific and Caribbean region (Keith, 2003) although a mean of 201 ± 40 days has been measured for the *Sicyopterus lagocephalus* species (Hoareau et al., 2004). As a first hypothesis, the strength and direction of marine currents as well as the duration of the planctonic phase could influence the dispersion ability and therefore the size of the species distribution area.

Sicyopterus lagocephalus and its distribution range has astonished ichthyologists for a long time. Before the meristic work of Watson et al. (2000), concluding that there is a single species distributed in Indo-Pacific area, several authors thought that this species was restricted to Indian Ocean (Pellegrin, 1933; Koumans, 1953). Recently, Sparks and Nelson (2004) doubted the existence of a single species throughout the Indo-Pacific range and indicated that the name of *S. lagocephalus* was doubtful because of the loss of the Holotype and nomenclatural issues. The nomenclatural aspect is being investigated (M. Kottelat, pers. comm.). For the time being, we use the name *S. lagocephalus* as described and defined by Watson et al. (2000).

Because the uniqueness of *S. lagocephalus* is discussed and because its expected range is huge, it seems to be interesting to study the phylogenetic relationships among *Sicyopterus* species to understand the biogeography of these fishes in insular systems of this region.

The aim of this study is to analyse, using mtDNA cytochrome b (cyt *b*) sequences, representative taxa of the genus *Sicyopterus*, and specially the ubiquity of the species *S. lagocephalus*, in order to determine whether its huge range is really occupied by only one species, and to describe its possible genetic subdivisions. Moreover, a phylogenetic tree involving other *Sicyopterus* species will provide improved knowledge about the evolutionary history of this group of gobiids. The phylogeny of this group will improve our understanding of the contrasted distribution of these related species throughout the Indian and Pacific Oceans and will help to explain the colonisation of these oceans by the *Sicyopterus* genus.

2. Materials and methods

A total of 55 specimens of the genus *Sicyopterus* from seven species and 13 islands (Fig. 1) was collected to cover most of the diversity of the genus, plus five specimens of the genus *Cotylopus* (two species) and two of the European genus *Pomatoschistus* (Gobiidae). *Cotylopus* is used as outgroup for *Sicyopterus* because of its genetic closeness. *Pomatoschistus*, a more distant temperate gobiid, is used as outgroup for both former genera.

The *Sicyopterus* samples were captured, between 2000 and 2004, from Mascarene islands (Réunion, Mauritius), Madagascar, and Comoros (Mayotte) in the Indian Ocean, to Vanuatu, New Caledonia, and French Polynesia—in the Marquesas (Tahuata), Society (Moorea, Huahine) and Australs (Rurutu, Tubuai, Raivavae, Rapa) archipelagos- in the Pacific Ocean (Fig. 1). Species were morphologically determined as *lagocephalus* (almost everywhere, except in Tahuata, Madagascar, and Rapa), *aiensis* (Vanuatu), *marquesensis* (Tahuata), *pugnans* (Moorea, Society Islands), *franouxi* (Madagascar), *sp1* (Madagascar), and *rapa* (Rapa, Australs Islands). Collected specimens were compared to the Types specimens of the collection of the National Museum of Natural History from Paris, except for