

## MOLECULAR EVIDENCE FOR DIRECT DEVELOPMENT IN THE RHACOPHORID FROG, *PHILAUTUS ACUTUS* (RHACOPHORIDAE, ANURA) FROM BORNEO

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**ABSTRACT.** — The tree frogs of the taxon Rhacophoridae are known for their impressive diversity of reproductive strategies. Direct development on land has been described in the Old World Bush Frogs belonging to the genera *Philautus*, *Pseudophilautus*, and *Raorchestes*. However, in numerous species especially within the Bornean *Philautus*, breeding behaviours remain unknown. In this paper, we match a clutch of eggs found on Gunung Mulu National Park, Sarawak, Malaysia (Borneo), using genetic barcoding to syntopically occurring adults of *Philautus acutus*. This species is known only from its type locality in the montane forests at high elevations on Gunung Mulu. The eggs were found on leaf litter of the forest floor and are characterised by a protective, compact, outer jelly capsule. The froglets inside the eggs were at advanced stages of development and showed a bifurcating dorsal pattern similar to adults of *P. acutus*. Beside the discovery of its breeding behaviour, we add a description of the habitat of this rare species. Furthermore, this account of aerial direct development in a *Philautus* species from Borneo contributes to our understanding of the evolution of reproductive strategies within the lineage. Finally, we present a review of observations of the breeding behaviour in Bornean *Philautus* species available in the literature.

**KEY WORDS.** — Rhacophoridae, *Philautus acutus*, ecology, reproduction, direct development

### INTRODUCTION

The evolution of complex reproductive behaviour in tropical tree frogs belonging to the family Rhacophoridae has been the topic of numerous phylogenetic studies, using both morphological and molecular data (e.g., Liem, 1970; Ye et al., 1999; Delorme et al., 2005; Yu et al., 2007, 2008, 2009; Biju et al., 2008; Grosjean et al., 2008; Li et al., 2008, 2009; Hertwig et al., 2012). While a majority of rhacophorid tree frogs produce one of several different types of foam nests and have free-swimming, ectotrophic tadpoles, the numerous species of Bush Frogs from south and south-east Asia belonging to the genera *Philautus* Gistel, 1848, *Pseudophilautus* Laurent,

1943, and *Raorchestes* Biju et al., 2010, are notable exceptions for exhibiting direct development (Alcala & Brown, 1982; Brown & Alcala, 1983; Grosjean et al., 2008). In this mode of reproduction, a free-swimming larval stage is absent and the lecithotrophic larva completes its development and metamorphosis on land within the egg. Direct development is interpreted as an adaptation to habitats with few or no surface waterbodies that are typical breeding habitats for other amphibian lineages (see Alcala, 1962; Marmayou et al., 2000; Callery et al., 2001), presumably an effect of local climatic or geomorphological conditions. At higher elevations of tropical montane forests, amphibians from various lineages (including *Eleutherodactylus*, *Brachycephalus*, *Myersiella*,