



Phylogeny and biogeography of the *Enhydris* clade (Serpentes: Homalopsidae)

DARYL R. KARNS^{1,2}, VIMOKSALEHI LUKOSCHEK^{2,3}, JENNIFER OSTERHAGE^{1,2},
JOHN C. MURPHY² & HAROLD K. VORIS^{2,4}

¹Department of Biology, Rivers Institute, Hanover College, Hanover, IN 47243. E-mail: karns@hanover.edu

²Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605. E-mail: hvoris@fieldmuseum.org

³Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, 92697. E-mail: vimoksalehi.lukoschek@uci.edu.au

⁴Corresponding author. E-mail hvoris@fieldmuseum.org

Abstract

Previous molecular phylogenetic hypotheses for the Homalopsidae, the Oriental-Australian Rear-fanged Water Snakes indicate that *Enhydris*, the most speciose genus in the Homalopsidae (22 of 37 species), is polyphyletic and may consist of five separate lineages. We expand on earlier phylogenetic hypotheses using three mitochondrial fragments and one nuclear gene, previously shown to be rapidly evolving in snakes, to determine relationships among six closely related species: *Enhydris enhydris*, *E. subtaeniata*, *E. chinensis*, *E. innominata*, *E. jagorii*, and *E. longicauda*. Four of these species (*E. subtaeniata*, *E. innominata*, *E. jagorii*, and *E. longicauda*) are restricted to river basins in Indochina, while *E. chinensis* is found in southern China and *E. enhydris* is widely distributed from India across Southeast Asia. Our phylogenetic analyses indicate that these species are monophyletic and we recognize this clade as the *Enhydris* clade *sensu stricto* for nomenclatural reasons. Our analysis shows that *E. chinensis* is sister-species to a well-supported clade comprising the remaining species of the *Enhydris* clade (mean p distance between *E. chinensis* and other in-group taxa was 13.1%, range: 12.7–13.4%). *Enhydris innominata*, *E. longicauda* and *E. jagorii* also formed a strongly supported clade with very low interspecific p distances (mean 0.28%, range: 0–0.46%). We were unable to resolve relationships between *E. enhydris* and *E. subtaeniata* (mean divergence of 9.4%, range: 9.2–9.7%), and between these two species and *E. innominata*, *E. longicauda* and *E. jagorii*. We summarize classical morphological (scalation and coloration) characteristics of these species in the context of the molecular phylogeny. The *Enhydris* clade comprises a substantial portion of the vertebrate biomass of Southeast Asia and we discuss aspects of its biogeography, morphology and systematics.

Key words: Southeast Asia, Thailand, water snakes, mud snakes, mitochondrial DNA

Introduction

The semi-aquatic snake communities of Southeast Asia are dominated by the Homalopsidae, the Oriental-Australian Rear-fanged Water Snakes (Murphy 2007; Karns *et al.* 2005; Karns *et al.* 2010). The Homalopsidae are distributed from Pakistan and the Indian subcontinent across Southeast Asia to northern Australia. All homalopsids are semi-aquatic, primarily nocturnal, and usually associated with mud substrates. Eight of the 37 species (22%) are coastal marine species living in mangrove forests, tidal mudflats, near-shore coastal waters, and estuarial habitats. The freshwater species are found in ponds, streams, rivers, wetlands, agricultural wetlands (e.g., rice paddies), and lakes (Murphy 2007). Most homalopsids eat fish, frogs, or tadpoles, but feeding on crustaceans is well documented in three of the coastal marine species (Voris & Murphy 2002). They are opisthoglyphous and have large venom glands with deeply grooved rear fangs for delivering hemotoxic and proteolytic venom (Fry *et al.* 2008). Homalopsids are relatively small in size (most species < 1 m adult snout-vent length).