Systematics, Evolution and Biogeography of Viviparous

Sea snakes of the Indo-Pacific

A thesis submitted in fulfillment of the requirements for the degree of

Doctor of Philosophy

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Abstract

Viviparous sea snakes are an exceptionally diverse radiation of secondarily marine reptiles that inhabit the shallow tropical and subtropical waters of the Indian and Pacific Oceans with the peak diversity in the Indo-Australian Archipelago (IAA). Although sea snake biology, natural history and diversity are relatively well known, they have a highly unstable taxonomy, and poorly understood evolutionary and biogeographic histories. This thesis examined the systematics, species limits, historical biogeography and diversification of Indo-Pacific viviparous sea snakes using molecular phylogenetics and a combination of external and internal morphological characters.

In the second chapter of this thesis, I describe a highly distinctive new species of viviparous sea snake from shallow estuarine waters of the Gulf of Carpentaria, northern Australia. Molecular analyses placed the new species, named 'rough scaled' sea snake, *Hydrophis donaldi*, as a deeply divergent lineage within the *Hydrophis* subgroup.

A multi-locus analysis and a morphological examination of the dangerously venomous and widely distributed 'beaked' sea snakes, *Hydrophis schistosus*, in the third chapter showed that they actually consist of two separate species in Asia and Australia that are not each other's closest relatives. This finding suggested that the beaked sea snakes represent an extreme case of convergent phenotypic evolution in response to similar dietary specialisations, providing important implications for snakebite management.

In the third chapter of this thesis I investigated how past and present barriers to dispersal caused by historical geoclimatic events in the IWP have influenced fine-scale population genetic structure and speciation in the widely distributed 'spine-bellied' sea snake, *Hydrophis curtus*. Analyses of mitochondrial and nuclear sequences and microsatellite variation sampled across the IWP strongly indicated population subdivision in *H. curtus* with a deep species level genetic break across the Indian Ocean and West Pacific. These findings further demonstrated that the Indo-Pacific biogeographic barrier in the Plio-Pleistocene may have a significant role in generation of biodiversity in the IAA.

Phylogenetic analyses and biogeographic reconstructions of Indo-West Pacific (IWP)

viviparous sea snakes in chapter four indicate that despite their origins in Australasia, sea snakes underwent an explosive *in-situ* radiation during the last 2.5 to 0.3 million years after colonizing Southeast Asia with subsequent dispersals to Australasia and the Indian Ocean. The high speciation rates in the core *Hydrophis* group and allopatric population divergence between the Indian and Pacific Oceans indicate an association with the Pleistocene sea level changes. Together these findings provide important insights to the origins and maintenance of high biodiversity in this marine biodiversity hotspot.

Findings on species boundaries, endemism and population structure in this thesis will directly benefit sea snake conservation and marine reserve management in the IWP. However, a need for more basic systematic studies on sea snakes is strongly implied by the discovery of cryptic lineages and the new species. The inability of temporal diversification patterns to explain the rapid speciation of *Hydrophis* suggests that non-geographic speciation might be a major driving force in sea snake speciation. Hence other avenues of research (e.g niche relationships, adaptation genomics) may provide possible explanations to the high species diversity.

Thesis Declaration

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Kanishka D. B. Ukuwela

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