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Diversity of Indo-West Pacific *Siphonaria* (Mollusca: Gastropoda: Euthyneura)

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Abstract

Species of the limpet genus *Siphonaria* (Gastropoda: Euthyneura) are commonly found in the rocky intertidal, worldwide, except in the Arctic. In total, 205 species-group names are available and not permanently invalid. However, estimating the actual species diversity of *Siphonaria* has remained challenging, mainly because past authors have interpreted differently the variation of shell characters, resulting in different taxonomic accounts. Species diversity of *Siphonaria* is evaluated for the first time here based on DNA sequence data (three mitochondrial gene fragments: COI, 12S, and 16S) and a large sampling focusing on the tropical and subtropical Indo-West Pacific (from eastern Africa to Hawaii): new sequences are provided for 153 individuals, 123 of which were collected from 93 locations throughout the Indo-West Pacific. In total, 41 species (molecular units) are recognized worldwide (31 from the Indo-West Pacific), all of which are strongly supported. Potential names are discussed for those 41 species, based on traditional taxonomy. The shells of 66 of the individuals from which DNA was extracted are illustrated: intra- and inter-specific variation is documented in detail and discussed in the light of new molecular results. It is shown that many species could hardly be identified based on the shell only, because the variation of shell characters is too high and overlaps between species. Geographically, no species is found across the entire Indo-West Pacific, where quite a few species seem to be endemic to restricted areas. The biogeography of *Siphonaria* in the Indo-West Pacific is compared to other groups.

Key words: Biogeography, limpet, phylogeography, Pulmonata, shell variation, taxonomy

Introduction

Species of the limpet genus *Siphonaria* are commonly found in the rocky intertidal. They are also called “false” limpets because they are phylogenetically unrelated to the Patellogastropoda, or “true” limpets: patellogastropods are one of the early branches of the gastropod tree while *Siphonaria* belongs to the Euthyneura, at the tip of the gastropod tree (Dayrat *et al.* 2011; White *et al.* 2011). The exact phylogenetic position of *Siphonaria* is unclear, and its sister-taxon is not known. Another false limpet genus, *Trimusculus*, for a long time thought to be closely related to *Siphonaria*, is actually quite distant phylogenetically (Dayrat *et al.* 2011; White *et al.* 2011).

Siphonaria is distributed worldwide, except in the Arctic. Our knowledge of species diversity and distribution is still largely based on Hubendick’s (1946) monograph. Out of 204 species-group names, Hubendick (1946) accepted 70 valid species, 24 of which are from the tropical and subtropical Indo-West Pacific (from eastern Africa to Hawaii, within ~35ºN and ~35ºS). Hubendick (1946) delineated species based exclusively on shell characters. He also used a few anatomical characters related to the shape of the epiphallus (in the reproductive system) to classify *Siphonaria* in two subgenera (*Siphonaria* and *Liriola*) and five sections within each subgenus. However, anatomy has been largely overlooked in *Siphonaria*. A few additional studies focused on the local diversity of *Siphonaria*, espacially in South Africa (Chambers *et al.* 1996, 1998; Teske *et al.* 2007) and Australia (Jenkins 1981, 1983, 1984). The mode of larval development was documented in some species (both direct developers and planctonic larvae are found in *Siphonaria*) but remains unknown for most species (Chambers & McQuaid 1994a, 1994b).

The use of non-morphological data in *Siphonaria* taxonomy is still in its infancy. Electrophoresis and

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compare units found here with units that could be obtained with nuclear markers. Thus, new non-mitochondrial sequences would provide invaluable information. New sequences would help improve species distribution in the Indo-West Pacific, especially from regions that have been poorly sampled so far, such as the Indian Ocean. Although the Indo-West Pacific was the main focus of the present contribution, new sequences should also be added from other biogeographic regions, especially those bordering the Indo-West Pacific (e.g., temperate Southwestern Pacific, the Tropical Eastern Pacific, and South Africa, to possibly better understand the worldwide history of diversification, invasion and extinction in *Siphonaria*.

Although the three markers targeted here helped answer our two primary questions, a few additional markers may help get stronger support for the deeper nodes, which in turn would help revise *Siphonaria* supra-specific systematics. However, it was shown that the two subgenera (*Siphonaria* and *Liriola*) proposed by Hubendick (1946) are not natural and thus need to be redefined.

Obviously, detailed taxonomic work is needed to find names for the species delineated here with sequence data, especially those that belong to the '*laciniosa*' and '*atra*' groups, for which many species names are available. All types will have to be examined, as well as historical museum collections. Internal anatomy should also be explored as well. Hubendick (1946) did describe a few anatomical characters at both specific and supra-specific levels. It is shown here that the few anatomical characters used by Hubendick to delineate subgenera are problematic, but it is possible that species delineated here differ anatomically although they do not seem to differ conchologically.

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