



Combining morphometrics with molecular taxonomy: How different are similar foliose keratose sponges from the Australian tropics?



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ABSTRACT

Sponge taxonomy can be challenging as many groups exhibit extreme morphological plasticity induced by local environmental conditions. Foliose keratose sponges of the sub-family Phyllospongiinae (Dictyoceratida, Thorectidae: *Strepsichordaia*, *Phyllospongia* and *Carteriospongia*) are commonly found in intertidal and subtidal habitats of the Indo-Pacific. Lacking spicules, these sponges can be difficult to differentiate due to the lack of reliable morphological characters for species delineation. We use molecular phylogenies inferred from the nuclear Internal Transcribed Spacer 2 region (ITS2) and morphometrics (19 characters; 52 character states) to identify evolutionarily significant units (ESUs; sensu Moritz) within foliose Phyllospongiiniids collected from seven geographic locations across tropical eastern and Western Australia. The ITS2 topology was congruent with the tree derived from Bayesian inference of discrete morphological characters supporting expected taxonomic relationships at the genus level and the identification of five ESUs. However, phylogenies inferred from the ITS2 marker revealed multiple sequence clusters, some of which were characterised by distinct morphological features and specific geographic ranges. Our results are discussed in light of taxonomic incongruences within this study, hidden sponge diversity and the role of vicariant events in influencing present day distribution patterns.

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1. Introduction

Sponges are key residents of diverse marine habitats (Van Soest et al., 2012) and perform critical ecosystem functions (Bell, 2008). Despite their ecological and evolutionary significance (Srivastava et al., 2010), sponges are rarely represented in management and conservation programs compared to other marine invertebrates, and this is partly due to problematic field identification of sponge species (Berman et al., 2013; Wulff, 2001). Difficulties in sponge identification are attributed to the lack of morphological characters for species delineation and extreme morphological plasticity induced by local environmental conditions, often leading to considerable taxonomic confusion (Loh et al., 2012; Xavier et al., 2010). Multiple phenotypes within a single morphospecies can exist even in sympatry, with morphological groups representing either independent genealogical lineages within species ranges or

extreme morphological variants within morphospecies (Andreakis et al., 2012; Freckelton et al., 2012). In addition, universally suitable molecular markers for sponge barcoding and to support morphological observations for delineation of robust taxonomic units and discovery of new taxa, have only recently been established (Erpenbeck and Wörheide, 2007; Rua et al., 2011).

Sponge systematics and phylogenetics have traditionally relied on gross morphology and skeletal structures including spicules and spongin fibres (Hooper and Van Soest, 2002; Rua et al., 2011). In recent years, molecular phylogenetics and systematics have been informative in defining spatial and temporal relationships amongst sponge evolutionarily significant units (ESUs) (Andreakis et al., 2012; Freckelton et al., 2012; Rua et al., 2011) and for establishing taxonomy in cryptic species complexes (Blanquer and Uriz, 2007; Erpenbeck et al., 2012; Escobar et al., 2012; Xavier et al., 2010). Most importantly, when coupled with morphometrics, molecular phylogenetics can provide greater resolution when ambiguous taxonomic characters are encountered, and help reconcile conflicting hypotheses associated with the evolutionary trajectory of morphological traits, species and natural populations, shaped over genealogical periods (Schmidt-Roach et al., 2012). For example, while some studies have questioned the reliability of traditional

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taxonomic characters (i.e. spicule morphology and fibre characteristics) in delineating genetically distinct lineages of sponges (McCormack et al., 2002; Paula et al., 2011), others have identified specific morphological traits that are taxonomically informative (Borchiellini et al., 2004; Erwin and Thacker, 2007; Miller et al., 2001).

Sponges of the family Thorectidae (Demospongiae; Dictyoceratida) comprise two subfamilies, Thorectinae and Phyllospongiinae (Cook and Bergquist, 2002). The latter exhibit foliose, lamellate or folio-digitate morphologies and consist of five established genera, namely *Candidaspongia*, *Lendenfeldia*, *Phyllospongia*, *Carteriospongia* and *Strepsichordaia* (Cook and Bergquist, 2002). Species of *Phyllospongia*, *Carteriospongia* and *Strepsichordaia* are widespread across the Indo-Pacific region (Fig. 1) and contribute up to 80% of

sponge numbers and biomass in parts of the GBR (Wilkinson, 1988). Sponge abundance, coupled with their role as significant contributors to primary productivity (through symbiotic association with cyanobacteria), highlight the potential importance of this group of sponges to coral reefs (Wilkinson, 1983).

Species delineation within *Phyllospongia*, *Carteriospongia* and *Strepsichordaia* is difficult as they lack spicules and have a paucity of informative skeletal characters. Furthermore, species boundaries within these genera are often confused due to the co-occurrence of multiple sympatrically distributed species with overlapping gross morphologies (Bergquist et al., 1988). In this study, we use Bayesian inference of discrete morphological features (19 characters; 52 character states) and molecular phylogenies inferred from the nuclear Internal Transcribed Spacer 2 region (ITS2) to identify ESUs

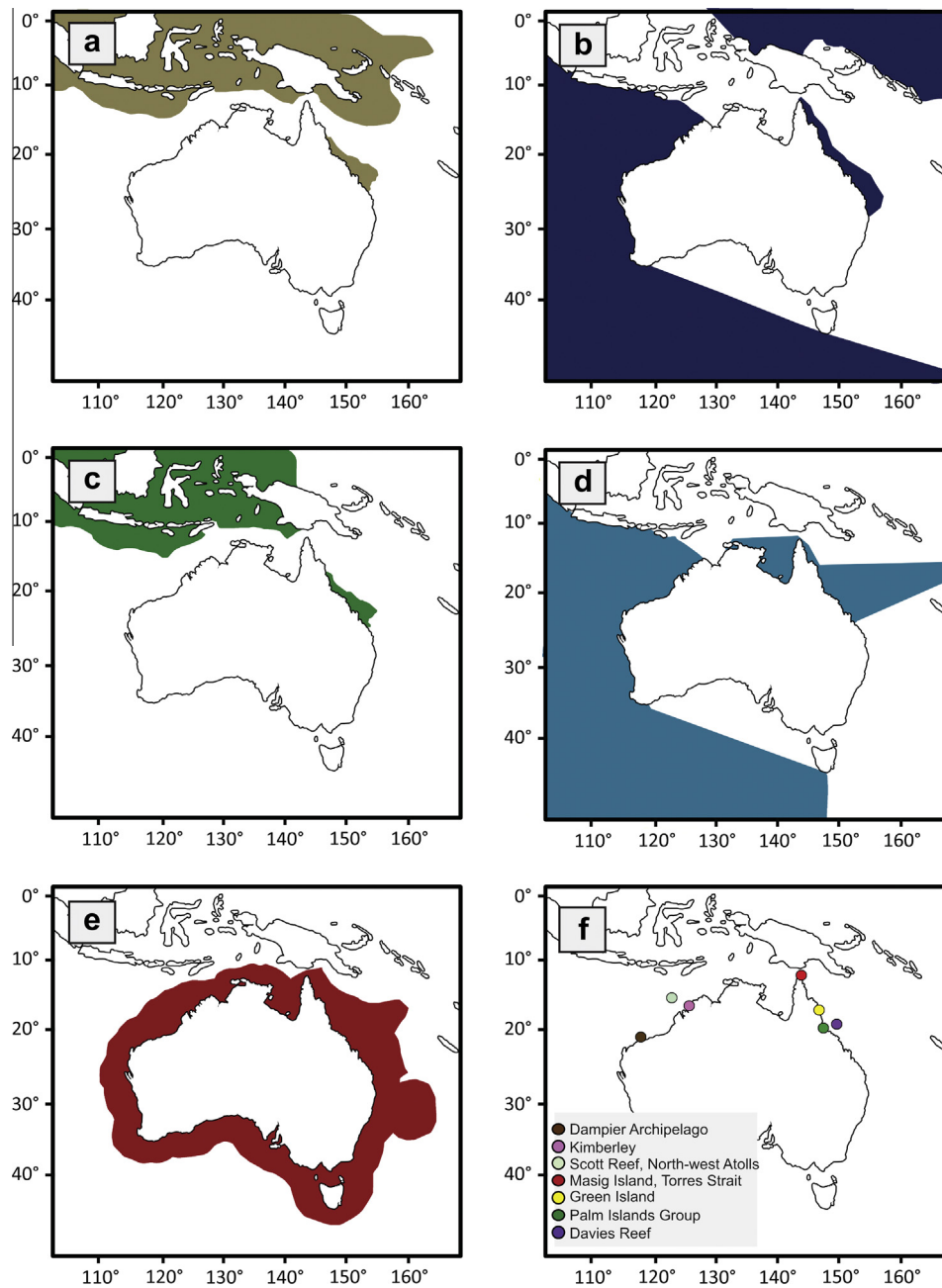


Fig. 1. Geographic distribution of (a) *Carteriospongia flabellifera*, (b) *C. foliascens*, (c) *Phyllospongia papyracea*, (d) *P. lamellosa* and (e) *Strepsichordaia lendenfeldi* across the Indo-Pacific as described on the World Porifera Database (<http://www.marinespecies.org/porifera/>; 14th February 2013). Additional geographic distributions for *C. foliascens* and *P. lamellosa* were consolidated from Queensland Museum species mudmaps. (f) Coloured dots represent sponge collection sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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