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Title: Evolutionary diversification of coral-dwelling gall crabs (Cryptochiridae)

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Summary

Gall crabs (Brachyura: Thoracotremata: Cryptochiridae) are small, coral-dwelling crabs that live in obligate association with their host corals, on which they rely for food and shelter. They commonly occur on coral reefs, but are often overlooked because of their diminutive size and hidden lifestyle. To date most research on gall crabs has focused on their systematics and taxonomy. This PhD thesis deals with various aspects of Cryptochiridae evolution and diversification. It is divided into five sections, each containing one or more chapters.

In the section **Phylogeny and taxonomy** the classification of the Cryptochiridae within the Thoracotremata is discussed first, based on 16S mtDNA sequences of 68 thoracotreme crab species, and sequence data obtained from 10 gall crab species belonging to nine genera. The monophyly of the Cryptochiridae is confirmed, which was debated by Wetzer *et al.* (2009). Data from additional molecular markers are needed to define the position of the Cryptochiridae within the Thoracotremata more precisely (**chapter 1**). In the following chapters several gall crab species are described as new to science. *Opecarcinus cathyae* is described from Indonesia and Malaysia, where it inhabits the coral species *Pavona bipartita* and *P. clavus*, both belonging to the Agariciidae (**chapter 2**). An endemic new species from the Red Sea and Oman is described as *Fizesereneia panda*; it inhabits the corals *Lobophyllia corymbosa*, *L. hemprichii* and *Symphyllia recta*, all belonging to the Lobophylliidae (**chapter 3**). *Lithoscaptus semperi* is described from Indonesia and Malaysia, where it lives in association with the free-living coral species *Trachyphyllia geoffroyi*, belonging to the Merulinidae (**chapter 4**). *Fungicola syzygia* is a cryptic new species closely related to *F. fagei*. This species was discovered by its host specificity in combination with molecular and morphological data. Both *Fungicola* species live in association with mushroom corals (Fungiidae). Based on morphology alone they are difficult to separate (**chapter 5**). In the last chapter of this section, a molecular clock approach is used to estimate the origin of the Cryptochiridae based on nucleotide substitution rates. The age of the most recent common ancestor is estimated at 50-23 Mya (early Eocene – early Miocene). Accelerated diversification is observed during the last 10-2 Mya (**chapter 6**).

The section **Host specificity and coevolution** starts with a study on the host associations of Atlantic gall crabs, resulting in eight newly recorded host corals. These new records include common Atlantic coral species like *Colpohyllia natans*, *Diploria labyrinthiformis*, and *Meandrina meandrites*. In addition, the gall crab *Kroppcarcinus siderastreicola* is newly recorded from the Caribbean Sea. An observation of the ‘visiting’ mating system is documented for the gall crab *Troglocarcinus corallicola*. In this mating system males of symbiotic crab species move from host to host in search of potential female mates (**chapter 7**). In **chapter 8** the host preferences and colour pattern of the Indo-Pacific species *Pseudocryptochirus viridis* are described, and new distribution records for Australia, Indonesia and Malaysia are presented. The evolution of the association between mushroom corals and their associated gall crabs is discussed in **chapter 9**. Based on museum collections, many new Indo-Pacific distribution records are documented. A phylogeny reconstruction of the Fungiidae is used to infer the evolution of crab-coral associations. These associations were tested for coevolutionary events in the programme Jane 4.0. This analysis reveals that cospeciation (in wide sense) is a likely scenario for the observed host specificity between mushroom corals and gall crabs. In **chapter 10** the coevolution scenario is tested on extended coral and gall crab phylogenies. Phylogeny reconstructions of the corals are based on studies already published in the literature, whereas the gall crab phylogeny is reconstructed by

using 16S, COI and histone H3 molecular markers. Coevolutionary analyses on the observed associations shows a wide range of cospeciation, host switching and duplication events between gall crabs and corals.

In the section **Biogeography**, the species *Neotroglocarcinus dawydoffi* is discussed, which shows (based on molecular data) an unforeseen biogeographic clustering between specimens from the Red Sea, eastern Indonesia, eastern Malaysia and New Caledonia. These groupings could not be explained by host specificity or cryptic speciation, and are not observed in closely related species. The observed patterns are therefore attributed to geographic isolation (**chapter 11**). The next chapter deals with the gall crab diversity in the Red Sea – a well-recognized biogeographic region of endemism – and uses gall crabs and their distribution in the Indo-Malayan region as a model. Marine biodiversity is highest in the latter area, however. The Red Sea is a secondary diversity centre with around 30% endemic species (**chapter 12**).

The section **Distributions over reefs and continental shelves** discusses the cross-shelf distribution of mushroom coral-associated gall crabs across the Spermonde shelf in Indonesia. Their occurrence rate is highest on mid- and offshore shelf zones. In addition, their host preference switches with varying depths, mostly when their common host is not present (**chapter 13**). The next chapter discusses the distribution of gall crabs in mushroom corals on reefs in Semporna, Malaysia. The results show that gall crabs commonly occur on non-disturbed reefs, without a clear preference for sheltered or exposed sites. Near-shore reefs that are impacted by natural or anthropogenic stress were not, or only sparsely, inhabited by gall crabs (**chapter 14**).

The last section of this PhD thesis is on **Reproductive morphology**. The female reproductive morphology is described for three gall crab species, using histological methods. The species have different dwelling morphologies, that range from shallow depressions to semi-closed pits. The results suggest that different gall crab species may have different reproductive strategies, which is possibly linked to the type of dwelling they inhabit. The results also confirm that, based on the female reproductive system, gall crabs should be classified within the Thoracotremata (**chapter 15**).