Evolutionary diversification of coral-dwelling gall crabs (Cryptochiridae)

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Aan mijn ouders

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> *"There is no task more fascinating to the naturalist than breaking up a block of some branching coral, such as* Pocillopora *or* Madrepora*, and dislodging from among its boughs the various animals that shelter there; nor of all these latter is there any more interesting than the crab* Hapalocarcinus*, which gives rise to the well-known galls that Semper [1881] described in his Animal Life."* (Borradaile, 1921)

Gall crabs (family Cryptochiridae) have fascinated scientists since the discovery of the first species described by William Stimpson in 1859. These crabs settle on stony corals (Scleractinia) as megalopa larvae and force the corals to form galls or pits as protective shelters around them. Their obligate association with scleractinian corals, hidden lifestyle, diminutive size and modified body shape (to fit their host) makes them stand out from all other crab species.

Cryptochiridae are amongst the smallest of crabs, ranging in carapace size from a few millimetres to about a centimetre at the most. There is conspicuous sexual dimorphism, with males being much smaller than females. Males mostly inhabit a dwelling on the same coral as a female, but may also be free-living on corals. Females of most species are permanently confined to their host, relying on it for food and shelter (Kropp, 1986). Their huge brood pouches, when ovigerous, prevent the females from being mobile. The males are mobile and visit the females for mating; hence their mating system is dubbed the 'visiting' mating system (Baeza and Thiel, 2007; Asakura, 2009).

For many years scientists have wondered where to place the family among the other crabs. Gall crabs have been linked to a wide range of families, and many researchers considered them to be closely related to pea crabs (Pinnotheridae) because of their similar size and host dependency. Although their placement within the overall crab phylogeny remained somewhat equivocal, they are placed in their own family and superfamily (Kropp and Manning, 1985). Over the years, many gall crab species have been described by Fize and Serène (1957), Takeda and Tamura (e.g. 1980, 1981, 1983) and Kropp (e.g. 1989, 1990a). The family Cryptochiridae currently consists of 21 genera and 51 species (Davie, 2014). Ongoing studies based on morphological, molecular and host specificity data revealed many cryptic species new to science (van der Meij, 2015, unpublished).

Gall crabs are recorded from shallow and deeper waters (over 500 m), but the majority of the species live in reef corals in the photic zone (Kropp and Manning, 1987; Kropp, 1990a; see also Van der Meij *et al*., 2015). Although gall crabs occur in almost all of the world's tropical oceans, they have their highest level of species and generic diversification in the Indo-West Pacific, where the coral diversity is highest (Fize and Serène, 1957; Kropp, 1990a; Hoeksema, 2007).

Many crabs have been recorded to live in some kind of association with stony corals (Stella *et al*., 2011), especially in branching corals belonging to the Acroporidae and Pocilloporidae. Cryptochiridae inhabit a wide range of branching and non-branching coral families, with Acroporidae, Euphylliidae and Poritidae as the most notable exceptions (Kropp, 1990a; van der Meij, unpublished). Gall crabs are very speciose as associates of Merulinidae and Agariciidae, in which many (closely related) coral species are inhabited by a host-specific gall crab species.

The interspecific interactions between gall crabs and their host corals trigger many research questions. Their unusual mode of life gives rise to questions about their phylogenetic position, which can be studied from molecular and morphological perspectives. Their close association with

their host corals allows for studies on (cryptic) speciation and possible coevolution - or more specifically i) coadaption or cospeciation, or ii) sequential evolution. Proven cospeciation or sequential evolution could make it possible to use gall crabs as phylogenetic indicators in scleractinian evolution. Studies on coevolutionary events in the marine realm are scarce – especially those focusing on invertebrates – and could hence provide novel insights in underlying mechanisms triggering diversification when compared to studies on terrestrial organisms. In a biogeographical context species diversity patterns of gall crabs can be compared with those of their scleractinian hosts, which are one of the most extensively investigated taxa in Indo-West Pacific biogeography. The symbiotic nature of the association allows for other comparisons, e.g. their distribution patterns at more local scale with regard to their abundance along environmental gradients, which is still a vastly unexplored field of study. Because gall crab dwellings can be observed and counted on reefs by experienced observers they can be used in studies on the distribution gall crabs over reefs and host species.

Thesis outline

After Fize (1956), Kropp (1988a) and Zayasu (2014), this is the fourth PhD thesis dealing with Cryptochiridae. It succeeds the work of a number of dedicated gall crab workers, in particular Potts, Utinomi [= Hiro], Fize and Serène, Takeda and Tamura, and Kropp. This thesis is divided into five sections, each containing one or more chapters, dealing with different aspects of cryptochirid evolution.

The section **Phylogeny and taxonomy** deals with the monophyly of the Cryptochiridae and their classification within the Thoracotremata (**chapter 1**). In the following chapters four new species are described: a new species from Indonesia and Malaysia, which is associated with the closely related coral species *Pavona bipartita* and *P. clavus* (Agariciidae) (**chapter 2**), a new species endemic to the Red Sea and Oman where it inhabits Lobophylliidae (**chapter 3**), a new species from Indonesia and Malaysia associated with the free-living coral *Trachyphyllia geoffroyi* (**chapter 4**) and a new and cryptic Fungiidae-associated species with a widespread distribution in the Indo-Pacific discovered by its host specificity in combination with molecular and morphological data (**chapter 5**). In the final chapter of this section, a molecular clock approach was used to estimate the time of origin of the Cryptochiridae and the diversification within the family based on nucleotide substitution rates (**chapter 6**).

The section **Host specificity and coevolution** is introduced by a study on the host specificity of Atlantic gall crabs, including new host coral records, extensions of known distribution ranges and an observation of their mating system (**chapter 7**). Host preferences and colour patterns for the Indo-Pacific species *Pseudocryptochirus viridis* are described in **chapter 8**, including new distribution records. In **chapter 9** the evolution of the association between gall crabs and mushroom corals is studied, which includes a test for possible coevolution between the Fungiidae and four Cryptochiridae species. Finally, coral and gall crab phylogeny reconstructions are compared, looking for congruence, by a test for coevolutionary events (**chapter 10**).

The section **Biogeography** starts with a study on the biogeographic patterns of *Neotroglocarcinus dawydoffi*, which occurs in the Red Sea, Indonesia and New Caledonia (**chapter 11**). Diversity patterns in the Red Sea – as a well-recognized biogeographic region of endemism – are studied by using gall crabs and their distribution in the Indo-Malayan region as a model (**chapter 12**).

The section **Distributions over reefs and shelves** deals with the cross-shelf distribution of mushroom coral-associated gall crabs across the Spermonde shelf in Indonesia (**chapter 13**). It also deals with the distribution of gall crabs in Fungiidae on reefs in the Semporna area, eastern Sabah, Malaysia (**chapter 14**).

The last section is on **Reproductive morphology**. The female reproductive morphology of three gall crab species is described using histological methods, and compared with that of other thoracotreme crabs (**chapter 15**).