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GALL POLYMORPHISM OF CORAL-INHABITING CRABS (DECAPODA, CRYPTOCHIRIDAE): A NEW PERSPECTIVE

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Key words: evolution, phylogeny, polymorphism, morphometry, scleractinia, Cryptochiridae.

ABSTRACT

Coral-inhabiting gall crabs are either obligate symbionts or parasitic associates with their host corals. They form a variety of galls/pits inside the skeleton of living corals. Nine genera of gall crabs on several scleractinian corals were used to test the hypothesis that galls vary among cryptochirid genera. Phylogenetic and morphometric observations were combined to analyze the possible evolutionary significance of gall construction. A high degree of conservation of gall shapes was observed in relation to the gall crabs' phylogeny. Gall/pit morphology and fidelity was studied in each of the different species of gall crabs. In addition, the correlation analysis results showed a significant linear relationship between crab size (carapace width) and its gall/pit size (opening diameter of gall/pit) ($p < 0.001$), demonstrating that crabs have the ability to create the gall/pit size which suits to their own size. Phylogenetically related crab species exhibit similar gall shapes; thus, the galls/pit morphology can be considered as an extention of the crabs' phenotypes.

I. INTRODUCTION

Coral-inhabiting Gall crabs belonging to the family Cryptochiridae, are obligate symbionts of stony corals (Scleractinia). Cryptochirids settle as megalopae on scleractinian corals, and

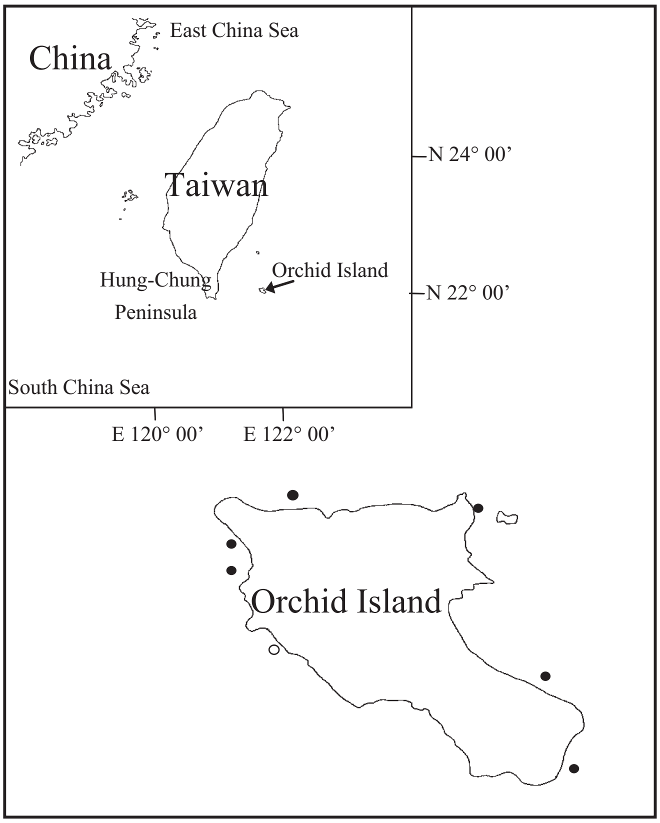

Fig. 1. Map of Taiwan showing sampling sites around Orchid Island.

somehow induce the host coral to grow together and around them [3, 11, 16], and form a variety of galls or pits inside the skeleton of living corals [10, 13]. They not only live within the coral skeleton and use corals as a habitat, but also use the mucus of the host coral as a source of nutrients [8, 15]. In addition, they also filter suspended particles that may slough off corals including their feces [1]. Gall crabs were described already about 150 years ago, but little is known about their biology, ecology, taxonomy, and zoogeographic distribution [10]. Recently, there has been a renewed interest in the distribution and behaviour of gall crabs [2, 5, 6, 14, 17, 18] and

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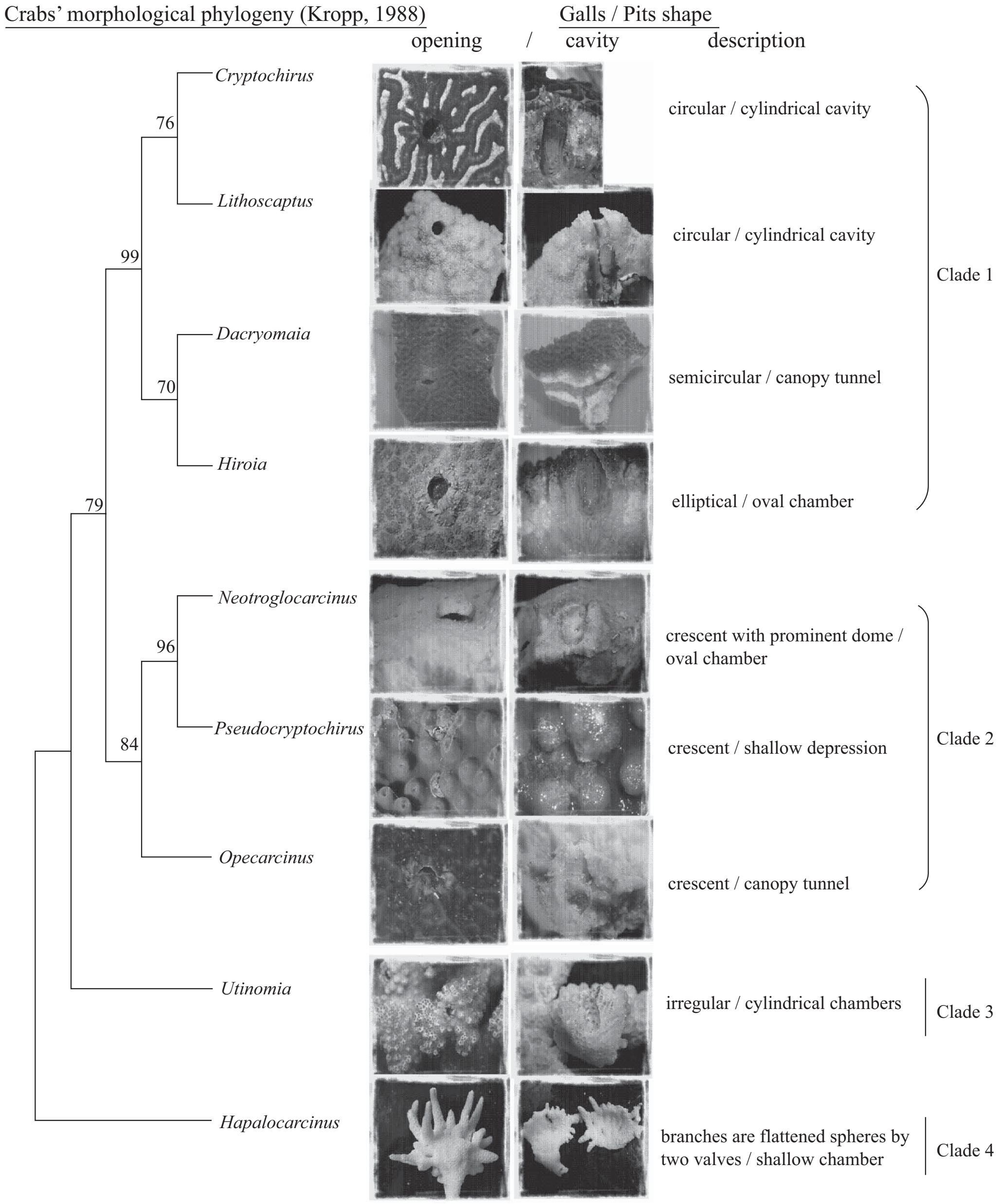

Fig. 2. Phylogenetic relationships of the Cryptochiridae, MP analysis using the full dataset with the 36 discrete crab morphology characters included [9]. Values above the branches are the bootstrap values (1000 replicates). Mapping was based on gall/pit shape description.

some studies were made on the genera *Hapalocarcinus* [7] and *Cryptochirus* [15]. Kropp [10] revealed several morphological inconsistencies and taxonomic errors by previous authors while describing the family.

Orchid Island, a small, remote island (22°1'N 121°5'E), S.E. of Taiwan, is located in the northwestern Pacific. It has a number of well developed coral reef communities. These coral reefs provide various habitats favourable for gall crabs.

In the present study, nine genera of gall crabs from several scleractinian corals were used to test the hypothesis that gall formation may be determined by the crabs. Phylogenetic and morphometric evidences were combined to evaluate the possible manipulative significance of gall construction.

II. MATERIALS AND METHODS

1. Sample Collection

From 109 fragments of coral colonies belonging to 9 coral genera were inhabited by mature gall crabs. These were inspected by SCUBA diving and then collected at a depth of 1 to 15 m from the coastal coral reefs of Orchid Island; the sampling sites are shown in Fig. 1. Fresh crabs and coral (gall or pit) were stored in 95% ethanol after collection.

2. Measurement and Morphometric Analysis

Crabs were removed from the corals and identified according to the key developed by Kropp [10]. We measured the crabs' carapace width and corresponding gall/pit opening diameters, using digital calipers accurate to the 0.01 mm. In addition were the gall/pit shapes recorded for each sample. The relationship between the crab's carapace width and their galls/pits opening diameter was analyzed using linear correlation statistics. All the data were analyzed using the statistical program SigmaStat version 10.

3. Phylogenetic Analysis

The phylogeny of gall crabs that we used for comparative analysis was modified from Kropp [9]. Data sources included 36 morphological characters from 9 genera (incl. *Cryptochirus*, *Lithoscaptus*, *Hiroia*, *Neotroglocarcinus*, *Pseudocryptochirus*, *Dacryomaia*, *Opecarcinus*, *Utinomiella* and *Hapalocarcinus*). This phylogeny was inferred using maximum parsimony in PAUP* 4.0b10. The robustness of the phylogeny was evaluated using bootstrapping (1000 replicates) [4, 12] of the full dataset.

III. RESULTS AND DISCUSSION

1. Phylogeny *vs*. Gall Morphology

Maximum parsimony analysis yielded length of tree 1552 (CI = 0.50), bootstrap values indicating a suitable support (above 70%) (Fig. 2). The topology revealed four major clades, genera of *Cryptochirus*, *Lithoscaptus*, *Dacryomaia* and *Hiroia* forming clade (1), genera *Neotroglocarcinus*, *Pseudocryptochirus* and *Opecarcinus* forming clade (2). The other genera groups, referred to as *Utinomiella* and *Hapalocarcinus* were identical in topology (excluding residual 9 genera in Cryptochiridae) to the most-parsimonious tree in Kropp [9].

Mapping of gall/pit morphology, clade (1) corresponds to circular openings (from circular, semicircular to elliptical); clade (2) corresponds to crescent-shaped openings; clade (3) genus of *Utinomiella* corresponds to irregular shaped openings; clade (4) genus of *Hapalocarcinus* corresponds to bi-spherical shaped openings. Gall/ pit morphology fidelity was observed by each of the different genera of gall crabs. A high degree of accordance of gall/pit shapes was observed with the gall crabs' phylogeny.

2. Gall Measurement and Correlation Analysis

A significant linear relationship was identified between crab size (carapace width) and its gall/pit size (opening diameter of gall/pit) respectively within all 9 genera of gall crabs [*Pseudocryptochirus* (p = 0.0322), *Cryptochirus* (p = 0.000002), *Dacryomaia* (p = 0.0057), *Hiroia* (p = 0.0226), *Lithoscaptus* (p = 0.00003), *Neotroglocarcinus* (p = 0.03154), *Opecarcinus* (p = 0.0315), *Utinomiella* (p = 0.0183) and *Hapalocarcinus* (p = 0.0003)]. The correlation analysis across species also showed that the crab size corresponds to gall/pit size (r = 0.6261, p < 0.001; Fig. 3). This result suggests that crabs have the ability to create and adjust the size of gall/pit for themselves and do not randomly occupy the empty gall/pit. It seems likely that the crabs inhabit specific dwellings throughout their adult life history.

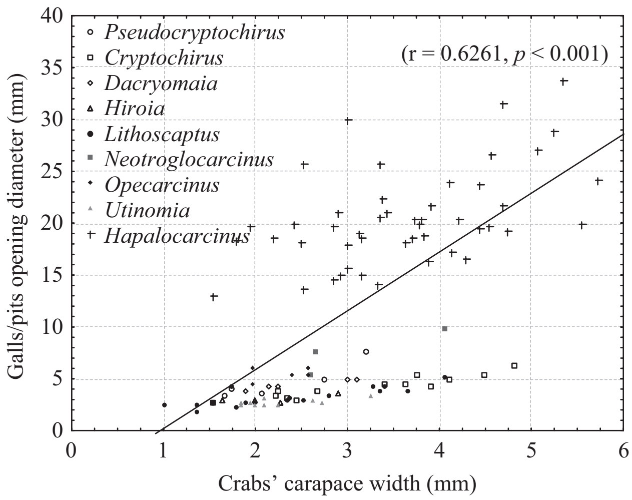

Fig. 3. Linear relationships between crabs' carapace width and their galls/pits opening diameter, established from 9 genera of gall crabs.

IV. CONCLUSION

Our most notable results show that the crabs, rather than the host corals, determine gall designs. Phylogenetically related crab species exhibit similar gall shapes. Thus, the galls can be considered as extended crab phenotypes.

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