**Author**: Meij, Sancia Esmeralda Theonilla van der
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# Chapter 12

## The Red Sea and Arabia are a diversity and endemism hotspot for coral-dwelling gall crabs (Cryptochiridae)

Sancia E.T. van der Meij, Michael L. Berumen & Gustav Paulay

### Abstract

The Red Sea and Arabia are renowned for marine endemism and diversity, mostly based on studies of the coral and fish fauna. To place the Red Sea in a broader biogeographic context we aim to study: 1) the proportional diversity of coral-dwelling gall crabs by comparing their composition and diversity in the Indo-Malayan area and the Red Sea; and 2) to determine if endemic species are present in the Red Sea (or just outside the basin) and what their approximate age is. Gall crabs were collected from a wide range of scleractinian corals in the Red Sea and Arabian peninsula and compared with collections from the Indo-Malayan area. Arabian occurrence records from the literature were also assembled. Sequence data (COI), morphology, and distribution were used to delineate Evolutionary Significant Units (ESUs). Pairwise genetic divergence between Red Sea and Indo-Malayan populations of wide ranging species, and between endemic species and their sister species was calculated as patristic distance. We recorded 36 species of Cryptochiridae from the Red Sea and Arabia, of which 11 appear to be endemic. Most of the wide-ranging species occupied the same host(s) in the Red Sea and Indo-Malaya, although with some exceptions. Genetic divergence between endemics and their closest relatives ranged between 2.3-11.4% p-distance. Wide-ranging species tend to show little differentiation: nine share haplotypes, and 17 have <1% sequence divergence between Red Sea and Indo-Malaya. The Red Sea has the second highest diversity of gall crabs after Indo-Malaya. Deep divergence of endemics pre-date the Last Glacial, when Red Sea habitats were impacted by highly saline waters in the restricted basin. The wider range of several endemics in Arabia suggests that the Gulf of Aden was a key area in the origin and survival of endemics.

Manuscript under review

## Introduction

The Indo-West Pacific (IWP), the largest and most diverse marine biogeographic region, extends across well over half the tropics from the Red Sea and South Africa to Hawaii and Easter Island. Despite this vast geographic extent, it has a relatively homogeneous fauna, with many species ranging from Africa to Polynesia, not infrequently with considerable genetic homogeneity (e.g. Lessios *et al.,* 1999; 2003). Nevertheless most species have narrower ranges, limited by environmental conditions or dispersal barriers, giving rise to prominent patterns in diversity and endemism that derive from dynamics of origination, extinction, and distributional change. The most striking patterns relate to the distribution of diversity and endemism.

The ranges of many tropical marine species overlap in a centre of maximum marine biodiversity in the Indo-Malayan area (IM) – also referred to as the Coral Triangle – which supports the greatest diversity in the marine biosphere (Ekman, 1935, 1953; Hoeksema, 2007; Briggs and Bowen, 2013). Diversity falls eastward across the Pacific and more unevenly westward, with secondary peaks in the SW Indian Ocean and Red Sea. Endemism within the IWP is high in peripheral areas, such as the Red Sea, Hawaii, and other remote islands in Oceania. Endemics in these areas are typically sister species of more wide-ranging species, and are thought to have a role in diversification (Ladd, 1960; Kay, 1980; Malay and Paulay, 2010).

The Red Sea and neighbouring waters around the Arabian Peninsula are a diversity and endemism hotspot (DiBattista *et al*., review 1, 2). The area harbours diverse coral reefs across a broad range of environmental conditions, ranging from oligotrophic, coral-dominated systems in the northern Red Sea to mixed kelp-coral communities in southern Oman (Sheppard *et al*., 1992; Ngugi *et al*., 2012; Raitsos *et al*., 2013). It is separated from other Indian Ocean reefs to the south by coasts under the influence of intense monsoonal upwelling that largely lack reefs and reef corals from Somalia to India. This barrier, together with unusual reef systems in many areas of Arabia, provides isolation and selection that facilitate the evolution of endemics.

The Red Sea is an especially well-known area of endemism (e.g. Guinot, 1966; Briggs and Bowen, 2012), yet paradoxically most its biota is expected to be very young, of Holocene age. During glacial periods the basin may have become so hypersaline that many or most species could not survive (Braithwaite, 1987; Siddall *et al*., 2003). Three hypotheses may resolve this paradox: endemics are young, not strictly restricted to the basin, or survived within the basin in refugia.

Research into the processes responsible for the pattern of diversity in the IWP have taken two approaches – top down, where predictions from general drivers are tested against patterns of distribution (e.g. Rosen, 1978; Bellwood and Hughes, 2001; Bellwood *et al*., 2005) or bottom up, where phylogenetic reconstruction dissects how species arose and distributions developed in a particular clade (e.g. Westneat and Alfaro, 2005; Hodge *et al*., 2014). Both the power and limitation of the first approach comes from its breadth - the pattern is most evident and robust at the biotic level, but it is challenging to dissect multiple drivers from a single data set (but see Bellwood and Hughes, 2001; Bellwood *et al*., 2005) and the evolutionary origin of diversity is not directly investigated. Indeed, reviews of alternative hypotheses about IWP diversity and diversification have found that multiple processes are responsible, rather than single drivers as proposed by several hypotheses (Paulay, 1997; DiBattista *et al*., 2013). The second approach allows a more direct investigation of diversification, but its narrower scope limits generalization. The accumulation of bottom up studies across taxa is bridging the gap between these approaches, allowing an evaluation of the generality vs. variability of patterns and processes. Comparisons of taxa with different traits allow exploration of how these impact the dynamics of diversification.

**Fig. 1.** Gall crab dwellings in **A**, *Stylophora* **B**, *Pavona explanulata* **C**, *Oulophyllia crispa* **D**, *Dipsastraea* **E**, *Astrea curta* **F**, *Platygyra*; dwellings indicated by arrows. All pictures are from the Red Sea.

Thorough sampling and phylogenetic analysis of diverse clades is an effective method for investigating diversification. We focus on the gall crab family Cryptochiridae. They are an especially interesting group because they 1) live obligately in corals, providing a comparative evolutionary context against their hosts, one of the most investigated taxa in IWP biogeography, 2) are symbiotic, thus allowing discrimination of the role played by geographical setting (dispersal) and ecology (host) in diversification, and 3) can be efficiently sampled because they are visible on the reef surface (Fig. 1), like corals and fish, two taxa that have been the mainstay of reef ecological and biogeographical analyses partly for this reason.

The Cryptochiridae is a monophyletic family of obligate symbionts, residing in galls, tunnels, or pits in the skeleton of scleractinian corals (van der Meij and Schubart, 2014). The family consists of 21 genera, 49 described species (Ng *et al*., 2008; Davie, 2014), and numerous undescribed taxa under study (van der Meij, unpubl.). They are recorded from shallow to deeper waters (to 512 m), but the majority of known species live in the photic zone (Kropp and Manning, 1987; Kropp, 1990a). Although gall crabs occur in almost all of the world's tropical oceans, they are most diverse in the IWP, like their coral hosts (Fize and Serène, 1957; Kropp, 1990a; Hoeksema, 2007). Much of their ecology, life history, and biogeography are virtually unstudied (Kropp, 1990a; van der Meij and Schubart, 2014).

Focused collecting, taxonomic, and phylogenetic study by SETvdM in Indo-Malaya has created a new basis for analysing cryptochirid diversity and evolution. With the fauna of the IWP diversity centre now well documented, we collected gall crabs in Arabia for comparison. Cryptochirids, like most non-coral invertebrates, are very much understudied in the Red Sea (Berumen *et al.,* 2013). The first gall crab species was described from Hawaii by Stimpson (1859), but the second, *Cryptochirus coralliodytes* Heller, 1861, was described from the Red Sea. Since then only one gall crab has been described from the Red Sea and three additional species recorded (see van der Meij and Reijnen, 2014; van der Meij *et al*., 2015)). This is surprising considering the proximity to Europe and substantial attention the Red Sea fauna has received from early taxonomists like Klunzinger and Ehrenberg. Five species have been recorded from Oman by Hogarth (1989): *Cryptochirus coralliodytes*, *Lithoscaptus paradoxus*, *Hapalocarcinus marsupialis* [species complex], *Hiroia sheni* [= *Xynomaia sheni*], and *Neotroglocarcinus monodi* [= *Neotroglocarcinus hongkongensis*], identified by Roy Kropp, without host records and no mention of coral vouchers. Gall crabs have not been previously recorded from the Gulf of Aden.

The obligate nature of the symbioses between gall crabs and corals suggests that differences in diversity and endemism may in part be related to changes in the host coral fauna. Red Sea corals have been reviewed by Scheer and Pillai (1983), Sheppard and Sheppard (1991), and Veron (2000), with 307 species recorded, including 20 endemics (DiBattista *et al*., review 1). The range of some 'endemics' extends to the Gulf of Aden or further around the Arabian peninsula. About 600 reef coral species are known from Indo-Malaya (Huang *et al*., 2014a), with up to 581, including 31 Indo-Malayan endemics, recorded from a single locality (Veron, 2000). The Arabian Gulf hosts 66 corals, while 126 species are recorded in the Gulf of Oman (Sheppard and Sheppard, 1991; DiBattista *et al.,* review 1).

We identify and genetically compare gall crab from the Red Sea and neighbouring Arabian seas to address the following questions. How diverse are cryptochirids in the region? Does the region appear to be a diversity hotspot? Does the proportional diversity of different gall crab genera differ between Indo-Malaya and the Red Sea? How many species are endemic, and how are these distributed among regional basins and seas? Are there likely Red Sea endemics and what is their age? Is there a relationship between coral and crab endemism – do endemic corals tend to have endemic cryptochirids? Answers to these questions will help place the Red Sea in a broader biogeographic context (Bowen *et al.,* 2013).

## Material and Methods

Gall crabs were collected in the southern Red Sea from Al-Lith to Jizan during a biodiversity cruise in March 2013, and from reefs offshore from Thuwal, in the central Red Sea, in March 2013 and November 2014. Gall crabs were collected in Oman on a series of expeditions between 1999-2008, in the Gulf of Oman and Masirah Island. Collections were made in Djibouti during a biodiversity cruise in Feb.-March 2012. Indo-Malayan collections for comparison came from extensive studies by SETvdM in Indonesia (Raja Ampat, Bunaken, Ternate, Lembeh) and Malaysia (Semporna, Kudat) between 2007 and 2012.

Corals were searched for galls and pits, photographed, and split with hammer and chisel. Crabs were photographed and then preserved in 80% ethanol. The material is deposited in the Naturalis Biodiversity Center (RMNH), Leiden, the Netherlands, and Florida Museum of Natural History, University of Florida (UF), Gainesville, USA. Gall crabs were identified based on Fize and Serène (1957) and Kropp (1990a). Recognized species from ongoing taxonomic revisions (e.g. van der Meij, 2015a), are referred to as sp. A, B, C, etc. Host corals in the Red Sea were identified following Scheer and Pillai (1983) and Sheppard and Sheppard (1991), and with the help of Francesca Benzoni who was present on some expeditions; in the IM following Veron and Pichon (1976), Veron *et al*., (1977), Veron and Pichon (1980), Hoeksema (1989), and Veron (2000). Nomenclature for crabs and corals follows Cairns (2014) and Davie (2014).

We follow DiBattista *et al*. (review 1)'s terminology for endemism, with slight modifications: 1) Red Sea endemic: species found only in the Red Sea (including Gulf of Aqaba), 2) Red Sea to Gulf of Aden endemic: species found only in the Red Sea and Gulf of Aden (including Djibouti), 3) Arabian endemic: species found in the Red Sea and beyond the Gulf of Aden in the waters surrounding the Arabian peninsula. Literature records from the Arabian area were evaluated

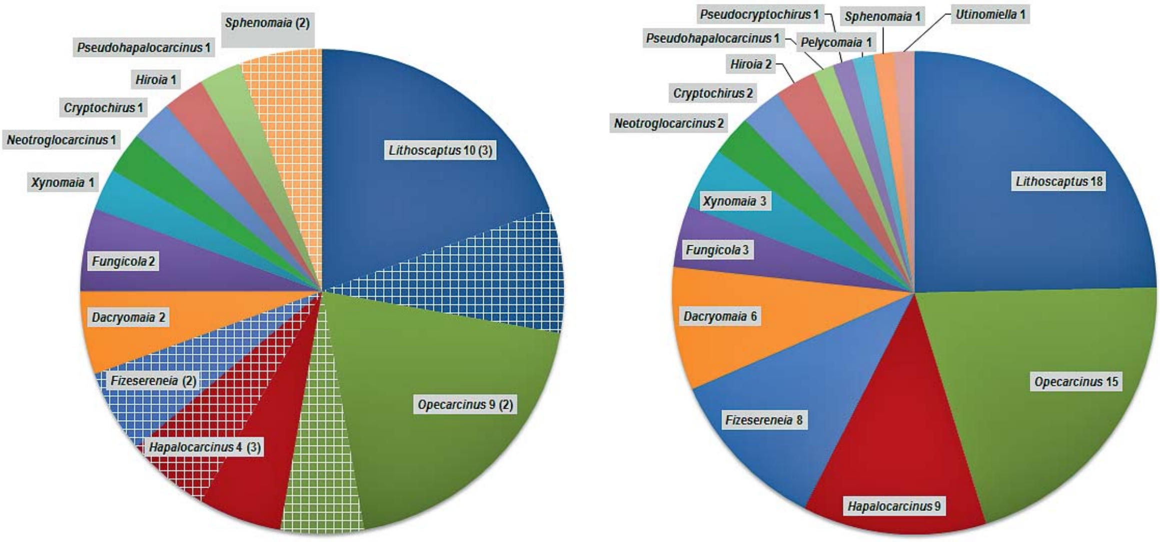

**Fig. 2.** Generic composition of Cryptochiridae in Red Sea (left) and Indo-Malaya (right). Numbers of species (endemics) provided per genus; endemic species also indicated by the chequered pattern.

based on current species concepts, synonymies (Davie, 2014), and consideration of nomenclatural concepts at the time of their publications.

Sequence data, morphology, and distribution were used to delineate Evolutionary Significant Units (ESUs). We defined ESUs as populations that are reciprocally monophyletic in two or more independent characters, thus demonstrating lack of gene flow. All Red Sea, Oman, and Djibouti material, as well as representative specimens of the same putative species (based on morphology and coral hosts) from the IM, were sequenced for the Folmer region of cytochrome c oxidase subunit I (HC02198 and LCO1490 primers (RMNH) and dgHCO2198 and dgLCO1490 (UF) (Folmer *et al*., 1994; Meyer, 2003); see van der Meij, 2015a). Pairwise genetic divergence between Red Sea and IM populations of wide ranging species, and between endemic species and their sister species, was calculated as patristic distance in MEGA 6.06 (Tamura *et al*., 2013). Gall crabs were considered to be endemic when specimens were morphologically distinct and/or were divergent and reciprocally monophyletic in COI sequences from other populations sampled.

## Results

### *Diversity and composition of fauna*

We recorded 36 species from the Red Sea, an 86% increase over what was previously known. IM harbours at least 73 species, thus about twice as many as the Red Sea (Fize and Serene, 1957; Kropp 1990; van der Meij, unpubl. data; Fig. 2). Ten and six species are now recorded from Oman and Djibouti, respectively, but these faunas are too incompletely known to allow meaningful comparisons (Table 1).

The Red Sea fauna is dominated by *Lithoscaptus* (10 species) and *Opecarcinus* (9 species), respectively associated with Merulinidae (former Faviidae) and Agariciidae. These genera comprise more than half the Red Sea diversity. Similarly, 33 of 73 species in the IM belong to these genera. Three quarters of the gall crabs in both areas are species of *Lithoscaptus*, *Opecarcinus*, *Hapalocarcinus*, *Fizesereneia* and *Dacryomaia* (Fig. 2).

Eleven species, or almost 1/3 of the fauna, appear to be endemic to the basin or Arabia. Two of these 11 were recorded from Djibouti and five from Oman, leaving six species known only

**Table 1.** Pairwise genetic divergence (as patristic distance) between Red Sea and Indo-Malayan populations of wide ranging species, and between endemic species (bold) and their sister species.

| | | | | | | | | COI divergence | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | RS - IM | Sister species |
| Genus | Species | Host Red Sea / Arabia | Red Sea/Arabia (endemic) | Red Sea | Oman | Djibouti | Indo-Malaya | p-distance | p-distance |
| *Cryptochirus* | *coralliodytes* | *Platygyra* | 0 | 1a | 1d | 1 | 1 | 0.0-1.7% | |
| *Dacryomaia* | sp. A | *Leptastrea* | 0 | 1 | | | 1 | 1.8-2.9% | |
| *Dacryomaia* | sp. B | *Leptastrea* | 0 | 1 | | | 1 | 0.0-1.8% | |
| *Fizesereneia* | ***panda*** | ***Lobophyllia ehrenbergi,*** *L. hemprichii* | 1 | 1 | 1 | | | | 2.3% |
| *Fizesereneia* | **aff. *panda*** | *Acanthastrea* sp. | 1 | 1 | 1 | | | | unknown |
| *Fungicola* | *syzygia* | *Pleuractis, Cycloseris* | 0 | 1b | | | 1 | 0.0-0.8% | |
| *Fungicola* | *utinomi* | *Fungia, Lithophyllon* | 0 | 1 | | | 1 | 0.0-1.1% | |
| *Hapalocarcinus* | **aff. *marsupialis 1**** | *Pocillopora damicornis* | 1 | 1c | d | 1 | | | 9.0% |
| *Hapalocarcinus* | **aff. *marsupialis 2**** | *Pocillopora* | 1 | 1 | | | | | 3.3% |
| *Hapalocarcinus* | aff. *marsupialis 3** | *Pocillopora,* ***Stylophora wellsi,*** *Stylophora* sp. | 0 | 1 | | | 1 | 0.3-1.7% | |
| *Hapalocarcinus* | aff. *marsupialis 4** | *Pocillopora* cf. *verrucosa* | 0 | 1 | | | 1 | 0.6-1.3% | |
| *Hiroia* | cf. *krempfi** | *Hydnophora exesa* | 0 | 1 | | | 1 | 1.2-2.0% | |
| *Lithoscaptus* | cf. *helleri** | *Favites* cf. *flexuosa* | 0 | 1 | | | 1 | 2.5-2.7% | |
| *Lithoscaptus* | *nami [R}* | *Hydnophora* cf. *exesa* | 0 | 1 | | | 1 | 0.5-2.3% | |
| *Lithoscaptus* | *paradoxus* | *Platygyra* | 0 | 1 | 1d | 1 | 1 | 1.1-2.0% | |
| *Lithoscaptus* | aff. *paradoxus* | *Leptoria phrygia* | 0 | 1 | | | 1 | 1.4-2.3% | |
| *Lithoscaptus* | cf. *prionotus** | *Oulophyllia crispa* | 0 | 1 | | 1 | 1 | 0.8% | |
| *Lithoscaptus* | **sp. S** | ***Echinopora fructiculosa, E. forskaliana*** | 1 | 1 | 1 | 1 | | | 6.8% |
| *Lithoscaptus* | sp. A | *Dipsastraea* spp. | 0 | 1 | | 1 | 1 | 0.0-1.2% | |
| *Lithoscaptus* | sp. B | *Plesiastrea versipora* | 0 | 1 | | | 1 | 1.5-2.1% | |
| *Lithoscaptus* | **sp. K** | ***Merulina scheeri*** *(and Goniastrea pectinata?)* | 1 | 1 | 1 | | | | 2.8%, 2.3% |
| *Lithoscaptus* | **sp. L** | *Dipsastraea* | 1 | 1 | | | | | 3.5% |
| *Neotroglocarcinus* | *hongkongensis* | *Turbinaria* | 0 | | d | | 1 | | |
| *Neotroglocarcinus* | *dawydoffi* | *Turbinaria* | 0 | 1 | | | 1 | 1.0-4.8% | |
| *Opecarcinus* | *cathyae* | *Pavona clavus* | 0 | 1 | | | 1 | 0.0-1.1% | |
| *Opecarcinus* | *lobifrons* | *Gardineroseris planulata* | 0 | 1 | | | 1 | 0.0-0.6% | |
| *Opecarcinus* | sp. A* | *Leptoseris yabei* | 0 | 1 | | | 1 | 1.7-2.4% | |
| *Opecarcinus* | sp. B | *Pavona* cf. *explanulata* | 0 | 1 | | | 1 | 0.2-1.4% | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Opecarcinus* | sp. C | *Leptoseris* cf. *incrustans* | 0 | 1 | | | 1 | 0.0-1.5% | |
| *Opecarcinus* | sp. F | *Leptoseris incrustans* | 0 | 1 | | | 1 | 0.6-2.9% | |
| *Opecarcinus* | **sp. R** | *Pavona* cf. *varians / venosa* | 1 | 1 | | | | | 11,40% |
| *Opecarcinus* | **sp. S** | *Pavona* cf. *explanulata* | 1 | 1 | | | | | 4.5%, 5.4%, 4.2% |
| *Opecarcinus* | sp. V | *Pavona* | 0 | 1 | | | 1 | 0.5-1.5% | |
| *Pseudo-hapalocarcinus* | *ransoni* | *Pavona cactus, P.* cf. *decussata* (sensu Scheer and Pilai, 1983) | 0 | 1 | | | 1 | 0.8-1.7% | |
| *Sphenomaia* | **aff. *pyriformis 1**** | *Dipsastraea* cf. *laxa* | 1 | 1 | | | | | 3.1% |
| *Sphenomaia* | **aff. *pyriformis 2**** | *Astrea curta, Paramontastraea peresi* | 1 | 1 | | | | | 3.2% |
| *Xynomaia* | cf. *boissoni*** | *Mycedium elephantotus, Echinophyllia* | 0 | 1 | 1 | | 1 | 0.0-0.1% | |
| *Xynomaia* | *sheni*** | unknown | 0 | | d | | 1 | | |
| | | | 11 | 36 | 10 | 6 | 27 | | |

In bold endemic for the Red Sea (and Arabia); n/a = not applicable; a = Heller, 1961; b = Kramarsky-Winter *et al.*, 1995; c = Abelson *et al.*, 1991; d = Hogarth, 1989; * cryptic species present; ** Xynomaia spp. can be difficult to identify, hence an identification error cannot be ruled out. For the literature record, however, there is no material deposit in a natural history museum.

from the Red Sea basin (Table 1). Two gall crab genera (*Fizesereneia*, *Sphenomaia*) do not share species between the Red Sea and IM, despite occupying the same hosts.

*Host relationships*

Most cryptochirid species were found only a in single species or genus of host. Four were collected in two confamilial genera each (Table 1). Five endemic corals had gall crabs: *Lobophyllia ehrenbergi*, *Echinopora forskaliana*, *E. fruticulosa*, *Merulina scheeri*, and *Stylophora wellsi* (Table 1). Four of these five hosted endemic gall crabs. The endemic crabs, however, sometimes utilized a mixture of endemic and wide-ranging hosts, e.g. *Fizesereneia panda* inhabited the endemic *Lobophyllia ehrenbergi* as well as the wide-ranging *L. hemprichii*. The wide-ranging crab *Hapalocarcinus* aff. *marsupialis 3* inhabited the endemic coral *S. wellsi*, as well as wide-ranging *Pocillopora* species.

Most crabs that occur both in the RS and IM occupy the same coral host(s) in both. Consistent with previous observations, no gall crabs were encountered in corals of the Acroporidae, Poritidae (Kropp, 1990a), or Euphylliidae (van der Meij, pers. obs). *Dacryomaia* sp. 1, occupied different hosts *Leptastrea* in the RS, but the endemic *Lithophyllon undulatum* in the IM (Hoeksema *et al.*, 2012; van der Meij and Hoeksema, 2013). Some coral genera (e.g. *Cyphastrea*, *Podabacia*) are inhabited by gall crabs in the IM but no gall crabs were found in them in the Red Sea despite search efforts. Some species, e.g. *Astrea curta*, *Dipsastraea laxa* and *Lobophyllia hemprichii*, are inhabited by different gall crabs in the RS than in IM. Some genera (*Pocillopora*, *Turbinaria*) are inhabited by multiple gall crab genera in IM, but only one species in the RS. The genera *Pelycomaia*, *Pseudocryptochirus*, and *Utinomiella* appear to be absent in the Red Sea, despite the presence of their host. The diversity in host/symbiont specificity and distributional patterns in the gall crab-coral system provides an ideal system for future work to investigate questions of co-evolution and specialist symbioses.

*Genetic distance*

Genetic divergence between the 11 endemics and their closest relatives ranged between 2.3-11.4%. Genetic distance between RS and IM specimens of wide-ranging species ranged from 0-2.9%. Nine species shared haplotypes across this ~10,000 km span.

## Discussion

*Diversity and endemism*

The 36 species recorded from the Red Sea represent the second largest diversity for gall crabs after Indo-Malaya. Although this is in part a consequence of limited sampling in other areas, the Red Sea nevertheless stands out as a centre of diversity. In comparison, Guam, extensively studied by Kropp, has 28 species (Paulay *et al*., 2003), while 23 are recorded from Japan, 18 from Vietnam (Fize and Serène, 1957), 17 from Moorea in Polynesia, (GP, unpubl.), and 5 from Hawaii (Castro, 2011).

Over 30% of the Red Sea species are known at present only from the basin or Arabia. This is substantially higher than the typical 10-15% endemism recorded for the marine fauna of the Red Sea (DiBattista *et al*., in review 1). However studies considering the evolutionary history of several fishes using genetic data suggest that endemism in the Red Sea may be higher than currently thought (DiBattista *et al*., 2013). Similarly, an integrative study of Red Sea sea cucumbers found endemism to be much higher than suggested by morphological taxonomy alone (39% vs 21%, Paulay *et al*., in review). These results suggest that integrative taxonomic study combining morphological and molecular approaches for detecting cryptic species will substantially augment estimates of endemism.

Five of 10 species of gall crabs we collected (and thus could sequence) from Djibouti (2 of 6) and Oman (4 of 6) are ‘endemic’ to Arabia. All five were also encountered in the Red Sea. While the Gulf of Aden and Arabian Sea remain quite undersampled, the high endemism and sharing of endemics across the region suggests that most, if not all endemics, documented from the Red Sea will be found outside the basin, if their hosts occur there. The non-Arabian western Indian Ocean is yet (mostly) unstudied for gall crabs, thus it is possible that some of these putative Red Sea – Arabia endemics will be found to range into these neighbouring areas. The Red Sea – Arabia endemics appear to be absent from the IM.

The sharing of endemics between the Red Sea and Oman, suggests that gall crab endemics are broadly distributed across Arabia. This contrasts with holothuroids, where endemics in the Red Sea tend to range to the Gulf of Aden, but tend to drop out from the productive, upwelled coasts of southeastern Arabia. Corals also show a major faunal break between the Red Sea and Oman (Claereboudt, 2006; DiBattista *et al*., review 1). This potentially broader range of gall crab endemics may be related to their tolerance of high planktonic productivity.

Gall crabs were much more abundant in the southern than northern Red Sea, and were also abundant in Djibouti and Oman. A similar general pattern is apparent in coral barnacles (Pyrgomatidae) (GP, pers. obs.; Malay, unpubl.). The latter areas are characterized by high algal biomass and productivity, murkier waters, an abundance of suspension feeders, including many that live in corals (Sheppard and Salm, 1987). Consequently rates of bioerosion are high, especially in comparison with the oligotrophic northern Red Sea (Glynn, 1993; Paulay *et al*., in review). High productivity appears to favour symbiotic gall crabs and barnacles, as observed by Highsmith (1980) broadly for coral bioeroders. The southern Red Sea and Gulf of Aden may be the most diverse area in Arabia for cryptochirids, because both coral diversity and planktonic productivity are high. Low productivity in the northern Red Sea, while associated with a diverse coral fauna, may limit abundance and possibly diversity of gall crabs, while high productivity in Oman limits coral diversity, although with the addition of several endemic scleractinians (Claereboudt, 2006).

Red Sea-Arabian endemics are separated from their sister species by 2.3-11.4% p-distance in COI, indicating that they substantially predate the Holocene. Six of the endemics cluster at 2.3-3.5% p-distance separation, suggesting Pleistocene origin, and suggestive of an important vicariant event.

### *Genetic divergence*

The lack of coral habitat along the 2200-km coastline from Djibouti to southern Somalia may inhibit gene flow between the Red Sea and western Indian Ocean by limiting opportunities for steppingstone dispersal (Kemp, 1998). Similarly, lack of reef development and paucity of corals along the shores of Pakistan and eastern India (except for the Gulf of Kuch), create a dispersal barrier toward the central Indian Ocean (UNEP/IUCN, 1988).

Genetic divergence between Red Sea and IM populations of broadly distributed gall crabs is low. Nine of 25 species sampled share haplotypes, and 17 have p-distances <1%. IWP-wide connections at the haplotype-level are not uncommon among strong dispersers (e.g. Lessios *et al*., 1998; Fratini and Vannini, 2002; Holland *et al*., 2004).

Benthic marine organisms move little as juveniles and adults, so connectivity is largely through pelagic (oceanic) stages such as larvae, and in some cases larval dispersal can be extensive (Scheltema, 1986). Larval development for Cryptochiridae is practically unknown, described only for the Atlantic *Troglocarcinus corallicola*, which has typical brachyuran development with at least 5 zoeal stages and a megalopa (Scotto and Gore, 1981). Larvae of four cryptochirid species were also identified in plankton samples from Moorea, Polynesia, using DNA-sequence data (Moorea Biocode project, unpublished data). Xanthid crabs, typically with 4 zoeal stages, show substantial homogeneity across the IWP in contrast with majoid crabs, typically with 2 zoeal stages, which tend to have restricted distributions (Moore and Paulay, in press). The extended larval development and limited genetic differentiation suggests that cryptochirids are capable of substantial dispersal, concordant with the hypothesis that species that require specialised or scarce habitats (such as specific hosts) should have competent larval stages of long duration (Miller and Hadfield, 1990). Gall crabs also appear to be able to store sperm for later use (Vehof *et al*., in press).

### *Number of corals predicts number of cryptochirids*

Gall crabs are host specific to species, genera, or families of corals. The change in diversity between the Red Sea and IM of crabs and hosts is comparable; the Red Sea has ~49% and ~51% as many gall crabs and reef corals as the IM. Whether the proportional diversity of gall crabs and corals are relatively stable across the IWP is an interesting question for further research.

### *Conclusion - Origin of Red Sea fauna*

data from numerous bottom-up studies in IWP biogeography allow comparisons of patterns and tests generalities of patterns and processes. The wealth of specific studies focused on the Red Sea-Arabian region in this volume provide interesting comparisons. Gall crabs are particularly interesting, as the first obligately-symbiotic group studied in detail.

The Red Sea and Arabia are renowned for marine endemism and diversity, and gall crabs exemplify both. Regional endemism in reef-associated organisms is likely caused by isolation of Arabia from the rest of the Indian Ocean by unsuitable habitats; notably soft bottoms and productive shores, with upwelling limiting reef development. Within Arabia the diverse physiographic and oceanographic setting further structures marine habitats, from the oligotrophic northern Red Sea to the macroalgal-dominated communities of central southern Arabia. The location of the major distributional and diversity breaks in these complex environments vary among taxa. Corals are most diverse in the north and central Red Sea, and also have high endemism there (DiBattista *et al*., review 1). Sea cucumbers are also most diverse in the Red Sea, but most endemics range across to the Gulf of Aden, with a major break in diversity and distribution lying between the Gulf of Aden and the Omani Arabian Sea coast. Data for gall crabs is more limited, but evidence suggests that their endemics are broad ranging from the Red Sea to Oman at least. These contrasts highlight the interplay between environment and phylogeny – oligotrophic areas favour photosymbiotic diversity and endemism, while productive waters that still support corals and some reef development favour coral inquilines. The contrast between coral and cryptochirid patterns is striking, surprising, and warrants further investigation.

The Red Sea has undergone drastic environmental changes during glacial times when low sea levels led to hypersaline conditions that may have killed much of the marine biota (Klausewitz, 1989; but see DiBattista *et al*., 2013). Cryptochirids and holothuroids (Paulay *et al*., in review), two groups investigated genetically in their entirety, both suggest that strict Red Sea endemics are rare. In both groups, all regional endemics pre-date the last glacial (and several previous glacial) periods, and most species extend to at least the Gulf of Aden.

There is also no evidence, for old, relictual endemism dating from the Tethys in gall crabs. The age of cryptochirids is unclear; current estimates put the origin of the clade (but not necessarily the symbiotic life style) between 83 [+/-11] Ma (Tsang *et al.,* 2014), and 36 [+/-13] Ma (van der Meij and Klaus, chapter 6). Diversification of the living gall crabs may have started as recently as < 13 [+/-6] Ma (van der Meij and Klaus, chapter 6) substantially lagging behind the Cenozoic diversification of the reef fauna. A similar late origin and diversification is evident in the coral-symbiotic fish genus *Gobiodon* (Duchene *et al*., 2013). Arabia holds no endemic cryptochirid genera, and most species are relatively young, at 2-11% COI p-distance.

Taken together, these findings suggest that the Gulf of Aden was a key area in the evolution of the Arabian marine biota, and may have served as a refuge during late Cenozoic glacial periods. The occurrence of numerous regional endemics outside the Red Sea basin in both gall crabs and sea cucumbers suggest that survival inside the Red Sea during low sea level periods is not necessary to explain their distribution. As individual case studies emerge, it is apparent that the evolutionary history of Arabian and Red Sea fauna is complex, with no 'one size fits all' explanation.

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