THE SYSTEMATICS OF PORTUNOIDEA RAFINESQUE, 1815, AND THE EVOLUTION OF SYMBIOTIC SWIMMING CRABS

By

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To my wife, Alice Catches

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Here I investigate the systematics, molecular phylogenetics and morphological evolution of symbiotic lineages in the brachyuran superfamily Portunoidea.

In Chapter 2 molecular phylogenetic analyses of 168 portunoid taxa reveal that the eight valid Portunoidea families fall into four lineages, recognized here as Brusinidae, Carcinidae, Geryonidae and Portunidae. However, while the latter three constitute a Portunoidea *sensu stricto* clade, the placement of Brunsinidae in the superfamily remains uncertain. Within the Portunidae the subfamily Caphyrinae is shown to be polyphyletic and the Thalamitinae paraphyletic. The symbiotic caphyrine genera *Caphyra* and *Lissocarcinus* form a clade within the Thalamitinae genus *Thalamita*, while the non-symbiotic caphyrine *Coelocarcinus* falls within the family Carcinidae. I redefine Thalamitinae to also include the genera *Caphyra, Lissocarcinus*, and *Cronius*. I erect two new genera to accommodate *Thalamita sensu lato* species that are derived within the former Caphyrinae.

Chapter 3 provides a systematic review of the symbiotic genus *Lissocarcinus*. Molecular phylogenetic analyses and morphological work demonstrate that the genus is

more diverse than previously thought, with at least 10 valid taxa, including three new genetically and morphologically distinct species.

In Chapter 4 a geometric morphometric (GMM) approach is used to investigate evolutionary patterns of carapace shape change associated with the emergence of symbiosis within Thalamitinae. Carapace shape is a functionally significant trait associated with swimming efficiency. Non-symbiotic portunoids, including most thalamitine crabs, are efficient swimmers while symbiotic forms are not. I demonstrate that carapace shape change within Thalamitinae tracks phylogeny and that the greatest disparity accumulated during the emergence of the symbiotic portunid tribe Caphyrini.

CHAPTER 1
INTRODUCTION

Background

The superfamily Portunoidea Rafinesque, 1815, (455 spp.) is a large group of marine crabs that includes commercially important species, significant invasives, and a number of ecologically divergent lineages that radiated across tropical, temperate, and deep-ocean habitats. Collectively referred to as “swimming crabs”, members of this clade are known for being aggressive, opportunistic omnivores that are fast, agile and well adapted to swimming (Hartnoll, 1971; Hazlett, 1971; Spiridonov et al., 2014; Williams, 1981). Portunoids play important, even dominant, ecological roles in their respective environments (Cannicci et al., 1996; Hazlett, 1971; Lavitra, 2009; Stasolla et al., 2016; Townsend et al., 2015). However, some portunids exhibit a divergent ecology and morphology that suggest they have abandoned the typical “swimming crab” lifestyle. Most striking among these, members of the tropical Indo-Pacific subfamily Caphyrinae Paulson, 1875, have evolved symbiotic relationships with algae, anemones, echinoderms, and soft corals (Caulier, 2013; Hay et al.,1989; Spiridonov, 1999; Stephenson & Rees, 1968). Despite the significance and novelty of this group, the nature and evolution of symbioses have received little attention (e.g. Castro, 2015; Baeza, 2015). In this dissertation I investigate the systematics, molecular phylogenetics and morphological evolution of these symbiotic swimming crabs in three research chapters.

Phylogenetics and Systematics

In Chapter 2 I conduct a molecular phylogenetic analysis of higher-level relationships within Portunoidea. Datasets are composed of previously published data

and newly generated sequences from a variety of portunoids, especially Thalamitinae and Caphyrinae taxa. Phylogenetic results are then used to evaluate the evolutionary history of swimming crabs, including the origin of symbiosis within the clade, and to update the familial and subfamilial classification. A new diagnosis of Thalamitinae and two new genera are provided.

In Chapter 3 I review the taxonomy and systematics of *Lissocarcinus* Adams & White, 1849. *Lissocarcinus* is a small (9 species), charismatic genus of symbiotic crabs in Caphyrinae. Motivated by recent collections of rarely collected species, this chapter combines molecular and morphological data to explore species diversity and evolution in the genus.

Morphological Disparity and Symbiosis in Portunidae

Morphological disparity is an important measure of biodiversity and understanding its evolutionary dynamics is a major aim of macroevolutionary research (Jablonski, 2000). Though debate persists about the relative importance of adaptive and non-adaptive modes of evolution (e.g., Rundell & Price, 2009; Weins, 2011), it is clear that considerable morphological disparity can accumulate during an evolutionary radiation and that ecology is an important force in this process (Erwin 2007; Glor, 2010; Losos, 2011; Monteiro & Nogueira, 2011; Price et al., 2011).

In Chapter 4 I use a geometric morphometric approach to investigate the evolution of carapace shape and size across Thalamitinae. I examine whether morphological change occurred before, during or after changes in body-size and whether this corresponded to the emergence of the symbiotic clade Caphyrini. I also provide an expanded molecular phylogeny of Thalamitinae, providing the framework for evaluating the phylogenetic significance of carapace shape disparity.

Finally, Chapter 5 summarizes the results of this PhD research and outlines possible directions of future research.

CHAPTER 2
MOLECULAR PHYLOGENETICS OF SWIMMING CRABS (PORTUNOIDEA) SUPPORTS A REVISED CLASSIFICATION AND REVEALS A COMPLEX, DERIVED ORIGIN OF SYMBIOSIS.

Introduction

The superfamily Portunoidea Rafinesque, 1815, (455 spp.) is a large, globally significant group of marine crabs that includes commercially important species (e.g*., Callinecets sapidus*, *Portunus pelagicus*, and *Scylla serrata*), several major invasives (e.g. *Carcinus maenus*, *Charybdis hellerii*, and *Ch. japonica*), and a number of ecologically divergent lineages that radiated across tropical, temperate, and deep-ocean habitats (Figure 2-1 to 2-3). Collectively referred to as “swimming crabs”, members of this clade are known for being aggressive, opportunistic omnivores that are fast, agile and well adapted to swimming (Hartnoll, 1971; Hazlett, 1971; Spiridonov et al., 2014; Williams, 1981). These crabs are also exceptionally good at hiding by rapidly burying in soft sediment (Bellwood, 2002). Consequently members of this clade play important, even dominant, ecological roles in their respective environments (Cannicci et al., 1996; Hazlett, 1971; Lavitra, 2009; Stasolla et al., 2016; Townsend et al., 2015). It has even been demonstrated that the activities of some portunoids can influence the primary productivity of an ecosystem (Silliman & Bertness, 2002). Both swimming and burying efficiency in these crabs is made possible by a number of features considered diagnostic of the group. These include having a broad, compressed, laterally streamlined carapace and highly modified, paddle-shaped posterior “natatory” legs (Bellwood, 2002; Cochran, 1935; Hartnoll, 1971; Spiridonov et al., 2014; Stephenson & Campbell, 1960).

However, some portunids exhibit a divergent ecology and morphology that suggest they have abandoned the typical “swimming crab” lifestyle. Most striking, members of the tropical Indo-Pacific subfamily Caphyrinae Paulson, 1875 (28 spp.) have evolved putative commensal relationships with algae, anemones, echinoderms, and soft corals (Caulier, 2013; Hay et al.,1989; Spiridonov, 1999; Stephenson & Rees, 1968). Relative to most portunids, these crabs are smaller, less streamlined and many have lost the paddle shape of their natatory legs (Figure 2-3A to 2-3D, and Figure 2-3I). Such modifications enable these species to live with and better grab onto their host. Many species also exhibit cryptic coloration consistent with their host taxa (e.g., *Caphyra rotundifrons* on *Chlorodesmis* algae and *C. loevis* on xeniid soft corals); yet others have conspicuous, contrasting colors (e.g., *Lissocarcinus laevis* on anemones). Limited but compelling work for the above three species also suggests that their diet may involve some specialization on host tissue (Caulier et al., 2014; Hay et al.,1989; Steudler et al, 1977). Finally, population work on the sea cucumber symbiont *Lissocarcinus orbicularis* (Caulier et al., 2010) and field observations of other symbiotic species (personal observations, N. Evans) suggest that mating systems in this clade may include some level of social monogamy; something not seen in “free-living” portunoids but present and well studied in other symbiotic crustaceans (Baeza & Thiel, 2007). Nevertheless, despite the significance and novelty of this group, the nature of its symbioses remains underappreciated and poorly studied (e.g. Castro, 2015; Baeza, 2015).

In contrast to these portunids, most well studied symbiotic crustaceans fall within clades that are species-rich and dominated by, or exclusively composed of, symbiotic

taxa (Baeza, 2015). This has led some to hypothesize that the emergence of symbiotic crustaceans may promote large evolutionary radiations. However, more phylogenetic analyses of clades with both symbiotic and free-living members are needed to test such hypotheses (e.g., Baeza, 2015). Recently, Evans & McKeon (2016) provided new evidence that symbiotic relationships may also be present among some species of the portunid genus *Thalamita*. However, it has long been suggested that Caphyrinae shares a close, even derived relationship with *Thalamita* and other genera of the diverse subfamily Thalamitinae Paulson, 1875 (160 spp.) (e.g., Stephenson & Campbell, 1960). The greatest diversity of thalamitine crabs exists across the same range of Indo-Pacific habitats where Caphyrinae and their reef-associated host taxa are found. Consequently, Caphyrinae and Thalamitinae together represent an interesting group for investigating the evolution of symbiosis in crustaceans. However, very little is currently known about the phylogenetic systemtics of this diverse group of crabs.

To date only three studies have conducted higher-level molecular phylogenetic analyses of Portunoidea, and used 16S rRNA or combinations of CO1, H3, 16S and 28S rRNA for up to 43 portunoid taxa (Mantelatto et al. 2009; Schubart & Reuschel, 2009; Spiridonov et al., 2014). Of these, the latter two are the only to included a caphyrine species (*Lissocarcinus orbicularis*) which was recovered falling sister to, or derived within Thalamitinae (comprised of one or six thalamitine taxa, respectively). Though these studies have significantly improved our understanding of portunoid systematics, synthesis of this work is complicated by a lack of overlap in both taxa and the molecular data sampled. The objective of this study is to compile and augment existing molecular data to conduct a more comprehensive molecular phylogenetic

analysis of higher-level relationships within Portunoidea while also focusing on an investigation of relationships within and between Thalamitinae and Caphyrinae. Results of this work will be used to generate an updated family and subfamily classification of the superfamily, and reevaluate the systematic diagnoses of Thalamitinae and Caphyrinae.

A Brief Review of Portunoid Classification

Considerable systematic work was carried out on Portunoidea during the 19th and 20th centuries, often in conjunction with work on the morphologically similar Cancroidea (see review in Karasawa et al., 2008; Schubart & Reuschel, 2009). Towards the end of this period Stephenson revised and largely stabilized portunoid classification (best summarized in Stephenson, 1972). However, morpho-taxonomic work has continued for the group, sometimes revealing surprisingly unique new lineages (e.g. *Atoportunus* Ng & Takeda, 2003). In recent years genetic data has increasingly been combined with morphological work to resolve species complexes (e.g. Keenan et al. 1998; Lai et al., 2010; Robles et al., 2007), but neither molecular or morphological phylogenetic analyses have been widely applied to the group. In addition to the above mentioned molecular studies, only the morphological cladistic analyses of Karasawa et al. (2008) has significantly contributed to our understanding of higher-level relationships within the clade. None of this work has considered more than approximately 40 of the 455 extant portunoid species. Nevertheless, beginning with Ng et al. (2008), four different schemes have been proposed for the familial and subfamilial classification of Portunoidea (Figure 2-4). Here I revise this work by proposing a new classification scheme for the group in light of a more comprehensive molecular phylogenetic analysis of the superfamily.

Materials and Methods

Vouchered Material and Taxonomic Identifications

Sequence data generated for this study was derived from 137 vouchered specimens listed in Table 2-1 and deposited in the following collections: the Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (UF); the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC). Morphological examinations were made using these and other specimens in UF and USNM.

Species identifications were made using primary and secondary taxonomic literature (e.g., Edmondson, 1954; Stephenson, 1972a; Stephenson & Hudson, 1956; Wee & Ng, 1995) and through comparison with type material or vouchers previously identified by M.J. Rathbun, W. Stephenson, or V. Spiridonov. Identification and taxon sampling were also aided through analyses of a large, unpublished collection of CO1 DNA barcode data generated from approximately 1000 USNM and UF portunoid specimens. In most cases this enabled comparison of multiple “barcoded” specimens per species. Inclusion of all DNA barcode data is beyond the scope of this study but is forthcoming in several investigations led by C.P. Meyer, G. Paulay or N. Evans.

The classification scheme of Ng et al. (2008) generally followed here. Additionally, for the sake of clarity, the *Portunus* subgeneric classification scheme of Ng et al. (2008) was also adopted, but modifications were made to be consistent with Spiridonov et al. (2014). Specifically, *Cycloachelous* was treated here as a valid subgenus and *Lupocycloporus* a valid genus. Lineage specific species diversities were

generally drawn from Davie et al. (2015b), De Grave et al. (2009) and Spiridonov et al. (2014) and not updated beyond these publications.

DNA Extractions, Amplification and Sequencing

Molecular work was conducted at the Florida Museum of Natural History and the Smithsonian Institution's Laboratories of Analytical Biology. DNA was primarily extracted using a standard phenol-chloroform protocol by hand or on an Autogen Prep 956 Extractor (AutoGen Inc., Holliston, MA, USA). A total of 345 sequences from four molecular markers (16S rRNA, CO1, 28S rRNA, and H3) were generated from 114 portunoid species. For 76 of these species this represents the first published sequence data. Amplifications were carried out following protocols outlined in Evans & Paulay (2012), Lasley et al. (2014), and Leray & Knowlton (2015). Typically this included the use of a "step-down" PCR profile (see Evans & Paulay, 2012). This approach involves using a higher annealing temperature for the first 5 PCR cycles followed by 30 cycles at a lower annealing temperature. Table 2-2 lists primer pairs, annealing temperatures and resulting fragment sizes for each marker. Amplification of 16S rRNA resulted in at least 500 bps of sequence, but one primer set yielded a 1.2 kb fragment that includes tRNA-Leu and part of NADH1. Both 16S fragments were combined into a single dataset that, unless otherwise stated, is referred to here as 16S data (fragment distinctions are shown in Table 2-1). Clean up, cycle sequencing, and purification were carried out on all successful PCR products using Exosap-It (Affymetrix Inc., USA), ABI BigDye terminator V3.1 reactions, and a Sephadex G-50 protocol. Resulting products were bidirectionally sequenced on an ABI 3130xl genetic analyzer (Applied Biosystems). Consensus sequences were generated using Geneious v. 7.1.8 (Kearse et al., 2012) and submitted to GenBank. GenBank accession numbers are listed in Table 2-1.

Taxon Sampling and Composition of Molecular Datasets

A molecular dataset comprised of 174 operational taxonomic units (OTUs) was constructed for this study. This dataset combined 344 newly generated sequences with 176 previously published fragments of 16S rRNA, CO1, 28S rRNA, and H3 data. Published sequences were mostly drawn from recent phylogenetic studies on Portunoidea, including Mantelatto et al. (2009), Schubart & Reuschel (2009), and Spiridonov et al. (2014). With some exceptions, taxon sampling was designed to include portunoid lineages at or above the species-level, avoiding genetically and morphologically highly conserved species complexes, especially those previously investigated (e.g., *Callinectes* by Robles et al., 2007; *Portunus pelagicus* by Lai et al., 2010). The complete dataset includes 168 ingroup portunoid taxa and 6 outgroup taxa. The relative position of Portunoidea within Brachyura remains poorly resolved (Tsang et al., 2014) so outgroup taxa were selected with reference to previous studies, but efforts were made to minimize the inclusion of particularly divergent non-portunoid taxa (preliminary analyses not shown). Details of each OTU are listed in Table 2-1, including taxonomy, GenBank accession numbers, voucher information, and source publications. One hundred and eight of these OTUs consist of sequences generated from a single vouchered specimen. For most of the remaining multi-specimen OTUs, species-level matches were confirmed with additional newly generated or previously published CO1 or 16S rRNA data (not shown). This approach permitted the inclusion of longer, more complete sequence data. Nevertheless OTUs with missing data were unavoidable.

In an effort to mitigate the impact of missing data, two reduced concatenated datasets were also constructed from the original. The first included 163 taxa, representing all OTUs with at least 16S rRNA data. The second included 138 taxa,

representing all OTUs with at least 16S rRNA and CO1 data. Additionally, each molecular marker was analyzed separately before concatenation, thus constituting four additional datasets. However, for the 28S rRNA only dataset, just 66 of the total 85 sequences were included; an approach that avoided all 28S sequences with less than 500 bps of data, most of which span the uninformative D1 region. Finally, preliminary analyses of 16S rRNA recovered the putative portunoid taxon *Brusinia profunda* falling far outside Portunoidea. This important taxon and its newly generated 16S rRNA data (voucher USNM277519; GenBank KX425018; Fig. 2-1A) was not included in the above datasets. Instead, this 517 bps sequence was added to an additional "Brusinia-16S" dataset that combined all 163 sequences from the 16S rRNA only dataset and 145, mostly brachyuran, 16S rRNA sequences analyzed by Tsang et al. (2014). Taxon identity, GenBank numbers, and voucher IDs for all data used from Tsang et al. (2014) appear as tip labels in the resulting phylogeny. In summary, eight molecular datasets were constructed for phylogenetic analyses. Each dataset is summarized in Table 2-3, including marker composition, alignment length and the number of parsimony informative sites.

Modified Identifications of Published Sequences

Several published portunoid sequences appear to have been misidentified and were corrected as follows. The CO1 sequence data for *Charybdis natator* presented in Spiridonov et al. (2014) matched that of *Ch. granulata* (GenBank KT365713; Voucher ZRC-2000.0771; Phuket, Thailand; specimen examined, identity confirmed) but not the *Ch. natator* used in this study (Table 2-1). Consequently, CO1, H3 and 28S sequence data for *Ch. natator* from Spiridonov et al. (2014) was included in this study but identified as *Ch. granulata*. Likewise, phylogenetic analyses of H3 sequence data for

Thalamita sima from Spiridonov et al. (2014) (GenBank JX398122) strongly suggests that it represents contamination from a separate *Ch. bimaculata* specimen. That is, this sequence matches that of *Ch. bimaculata* generated for this study and that from Spiridonov et al. (2014) (analyses not shown). This sequence was not included in this study. However, 28S data and CO1 data from this specimen (GenBank JX398086 and JX398105, respectively) are not similarly suspect. Phylogenetic analyses of CO1 data (not shown) with additional new sequences for *Th. sima* (GenBank KT588224 and KT365786) confirm that Spiridonov et al. (2014) collected and sequenced a correctly identified *Th. sima* specimen.

Sequence Alignment and Phylogenetic Analyses

Sequence alignments were constructed using MAFFT v 7.123b (Katoh & Standley, 2013) under the E-INS-i setting. Unreliably aligned columns for 16S and 28S rRNA datasets were identified and removed using Guidance2 (Sela et al. 2015), similarly employing MAFFT's E-INS-i settings (--genafpair --maxiterate 1000). Each Guidance2 run evaluated 400 alternative alignments generated from 100 alternative guide trees. Columns with a confidence score below 0.9 were trimmed from the final alignment. The *Brusinia*-16S dataset was similarly aligned, but its total length was trimmed to just 447 bps, covering only those sites available in the 16S dataset of Tsang et al. (2014). Substitution models and partition schemes were evaluated for each dataset using the BIC criterion and a greedy search algorithm in Partitionfinder v.1.1.1 (Lanfear et al., 2012). For each dataset all models were evaluated as well as just the reduced set available in MrBayes (Ronquist et al., 2012). A single partition and a GTR+I+G model was chosen for the Brusinia-16S dataset. The best scoring schemes

for the remaining seven datasets are outlined in Tables 2-4 and 2-5 and were used in subsequent partitioned phylogenetic analyses.

Maximum likelihood (ML) phylogenetic analyses were carried out on all datasets using GARLI 2.0 (Zwickl 2006). For each concatenated dataset and the Brusinia-16S dataset, ML analyses consisted of at least 100 independent searches and included both random and fast ML stepwise starting trees (attachmentspertaxon = 50, 100, or 2N+1). For single marker datasets at least 20 independent ML searches were performed with stepwise starting trees (attachmentspertaxon = 100). Nodal support for each of the best scoring ML topology was evaluated with 500 bootstrap replicates generated using the same parameters. Bayesian analyses (BI) were performed on each concatenated datasets using MrBayes v3.2.5 (Ronquist et al., 2012). A standard MrBayes MCMC analysis (nruns=2 nchains=4) was run on each dataset and lasted 25 million generations, sampling every 10,000 generations. An arbitrary burn-in value of 2.5 million generations was used for the 138 OTU and 163 OTU concatenated datasets. A higher burn-in value of 7 million generations was needed for the 174 OTU concatenated dataset. The standard deviation of split frequencies was confirmed to be less than 0.01 for each analysis. Convergence was further evaluated using Tracer v.1.6 (Rambaut et al., 2014) and included confirmation that each run attained ESS values greater than 200. All phylogenetic analyses were carried out on the CIPRES Science Gateway (Miller et al., 2010). FigTree v1.4.0 was used to visualize trees and generate resulting figures.

Results and Discussion

Phylogenetic analyses of up to 4 molecular markers were carried out on 168 portunoid taxa; 76 for the first time. Resulting topologies and support values are

summarized in Figures 2-5 to 2-10. With few exceptions (discussed below), phylogenetic analyses of the three concatenated datasets recovered consistent topologies that displayed significant support for most of the same clades (Figures 2-7 and 2-8). However, analyses of the 174 OTU dataset, which had the greatest proportion of missing data, often recovered lower support values for each clade. Clades typically exhibited the greatest support in analyses of the 138 OTU dataset, which contained the least amount of missing data. However, some topological incongruence was recovered was between ML and BI analyses of the 138 OTU dataset (compare Figure 2-9B with asterisks in Figure 2-8B). This conflict was associated with deeper nodes in Portunidae and involved the relative placement of a well-supported "*Achelous*" clade (discussed below). This conflict may be an artifact of the low taxon sampling available for non-thalamitine portunids, a general shortcoming in all analyses. Single marker ML analyses also displayed no significant conflicted with concatenated analyses, but generally recovered poorly resolved topologies (Figures 2-5 and 2-6). The following sections present a clade-by-clade discussion of the results for the ML and BI analyses of the 163 and 138 OTU concatenated datasets. The ML topologies for these two datasets are presented together in Figure 2-8. In text, support values are reported together with those for the 163 OTU topology appearing first, and those for the 138 OTU topology appearing second (e.g., bs 70%, 100%, pp 0.95, 1.0). Results the other analyses, including that for the 16S-*Brusinia* dataset, are also presented when relevant.

Portunoidea

Analyses recovered a strongly supported monophyletic Portunoidea (bs 91%, 99%, pp 1.0, 1.0) comprised of three major, well-supported lineages (but see discussion regarding *Ovalipes*). These three lineages include taxa from seven of the eight currently

valid portunoid families, and their relative composition is consistent with, but displays greater resolution than recovered in Schubart & Reuschel (2009) and Spiridonov et al. (2014). Summarizing these previous works, Davie et al. (2015a) suggested that the composition and status of each portunoid family may need to be reappraised, but only after all genera have been considered. However, given a shared morphology (see detailed discussions of Davie et al., 2015b; Guinot et al., 2013; Karasawa et al., 2008; Spiridonov et al., 2014), and in light of the results presented below, the current number of valid portunoid families appears overstated. Here I propose a number of changes to the classification for Portunoidea including the recognition of three instead of eight families (summarized in Figure 2-4; reflected in Figure 2-8). Where appropriate, additional lower-level results are also discussed.

Geryonidae Colosi, 1923. The first major portunoid clade recovered in the present study was the family Geryonidae *sensu* Schubart & Reuschel (2009; but not Geryonidae *sensu* Spiridonov et al., 2014). This well-supported lineage is comprised of *Benthochascon*, *Chaceon*, *Geryon*, *Ovalipes*, and *Raymanninus* (bs 69%, 92%, pp 1.0, 0.99). Spiridonov et al. (2014) (Figure 2-4) established Ovalipidae to accommodate *Ovalipes*, but otherwise left Geryonidae intact. Being conservative, I move *Ovalipes* back to Geryonidae, and lower Ovalipidae to a subfamily, Ovalipinae, status nov. However, this taxonomic decision warrants some further study given that the placement of the hybrid OTU-017 (*O. stephensoni* + *O. floridanus*) renders *Ovalipes* paraphyletic. Yet this placement exhibits no support, is clearly unstable, and was based on just 16S and 28S rRNA data (461 bps and 618 bps, respectively). This OTU's relative placement is also poorly resolved in each single gene analysis, but was recovered with

Raymanninus (with virtually no support) as sister to all other *Ovalipes* in the *Brusinia*-16S ML analyses (Figure 2-10; discussed below). Nevertheless, the relative placement of this OTU is taxonomically important. Morphologically *O. stephensoni* and *O. floridanus* are sister species that are most closely related with the unsampled generic type *O. ocellatus* (Herbst, 1799) (see Parker et al., 1998). If additional work finds further support for the polyphyly of *Ovalipes*, then Ovalipidae would be valid but species derived within Geryonidae would constitute a distinct genus, likely *Aeneacancer* Ward, 1933 (type species *Ovalipes* [*Aeneacancer*] *molleri* Ward, 1933; see cladistic analyses of Parker et al., 1998).

Carcinidae MacLay, 1838. The second major well-supported portunoid clade consists of members from the portunoid families Carcinidae, Pirimelidae, Polybiidae, and Thiidae as well as the surprising inclusion of the *Coelocarcinus*, previously classified as a caphyrine portunid (bs 64%, 93%, pp 1.0, 1.0). Here I propose that each of these lineages be recognized as a subfamily in the family Carcinidae (see Figure 2-4). The composition and diagnoses of these subfamilies should mostly follow that outlined by Spiridonov et al. (2014), but given that a polyphyletic Polybiinae was also recovered, the matter needs further study.

Coelocarcininae Števčić, 2005. *Coelocarcinus* (Figure 2-2B) are morphologically peculiar, infrequently collected crabs that were historically placed within the portunid subfamily Caphyrinae. Unlike most caphyrine crabs, this genus appears not to be commensal, but is found in *Halimeda*-sand apparently mimicking dead segments of calcified alga (Ng, 2002; personal observation). On morphological grounds Karasawa et al. (2008) argued that this genus was not a portunoid but possibly belonged to the

family Hepatidae (now Aethridae). Here I recover two *Coelocarcinus* taxa as a single, long-branched clade within a well-supported Carcinidae (Figure 2-8). Phylogenetically long-branched taxa can be more vulnerable to artifactual, well-supported placements (e.g., see Evans 2010), however there is evidence to suggest that this is not the case for *Coelocarcinus*. Phylogenetic ML analyses of the *Brusinia*-16S dataset (Figure 2-7) included *Coelocarcinus* and hundreds of other brachyuran taxa and the same Carcinidae placement of this genus was recovered. Here I recognize the tribe Coelocarcinini, as a valid carcinid subfamily, Coelocarcininae Števčić, 2005, status nov.

***Polybius* Leach, 1820, and *Liocarcinus* Stimpson, 1871.** Concatenated analyses presented here are the first to combine 16S rRNA, CO1 and H3 data for the genera *Polybius* and *Liocarcinus*. Consistent with Schubart & Reuschel (2009) and Spiridonov et al. (2014), these recover *Polybius henslowii* as derived within a strongly supported *Liocarcinus* clade, as sister to *L. holsatus* (Figure 2-8). Both *L. holsatus* and *P. henslowii* are generic types, with *Polybius* Leach, 1820 taking precedence. Consequently, these genera should be synonymized, moving all 12 *Liocarcinus* species to *Polybius*. However the data analyzed here was all previously published, with several OTUs comprised of sequences generated by different researchers from different specimens, some without voucher material (Table 2-1). Before these genera are synonymized additional analyses should be carried out that consider morphology and sequence data from additional vouchered specimens.

Portunidae Rafinesque, 1815. The third well-supported major portunoid clade consists only of the Portunidae *sensu* Spiridonov et al. (2014), excepting *Coelocarcinus* (bs 97%, 98%, pp 1.0, 1.0). These results confirm those of Schubart & Reuschel (2009)

by recovering Portunidae as a distinct lineage that does not include carcinid crabs (but see Figure 2-1 for other portunid classifications).

Brusiniidae Števčić, 1991. *Brusinia* is a morphologically peculiar genus of small, deep-sea crabs exhibiting many morphological features consistent with membership in Portunoidea (Figure 2-1A). Originally assigned to the geryonid genus *Benthochascon*, this distinct lineage was raised to generic status by Števčić (1991) who also erected the tribe Brusiniini Števčić, 1991. This clade was subsequently moved from Geryonidae to Carcininae (Crosnier and Moosa, 2002; Števčić, 2005), then to Polybiinae (Ng et al., 2008; Karasawa et al., 2008), and finally raised to family level status by Spiridonov et al. (2014). Here I generated the first molecular data for this genus consisting of 16S rRNA from *Brusinia profunda*. However, preliminary ML analyses failed to recover a placement of this species near or within Portunoidea and thus this sequence was left out of subsequent concatenated analyses. Consideration of lab procedures and extensive analyses of available Brachyura sequence data indicate that this sequence is not likely a contaminant so further analyses were also conducted. Maximum likelihood analyses were conducted on *Brusinia profunda* in a dataset comprised of 309 taxa using all 16S data from this study and all 16S data analyzed in Tsang et al. (2014). Results also recovered *Brusinia* well outside Portunoidea (Figure 2-10), albeit with low support. Yet, with notable exceptions, the overall topology of Brachyura was surprisingly consistent with that recovered by Tsang et al. (2014) from a concatenated dataset of eight genes. Moreover, the Portunoidea was also recovered as monophyletic, and exhibited a topology broadly consistent with that recovered in the concatenate analyses presented here. These results suggest that Brusiniidae is a

distinct lineage within the brachyuran subsection Heterotremata. However, further molecular and morphological work is needed to resolve the placement of this clade.

Portunidae Subfamilies

The validity and composition of portunid subfamilies has long been debated (see discussions and reviews in Davie et al., 2015a; Karasawa et al. 2008; Mantelatto et al., 2009; Nguyen, 2013; Schubart & Reuschel, 2009; Spiridonov et al. 2014). Current consensus is that most portunid subfamilies may not represent reciprocally monophyletic clades but are taxonomically useful groupings that should be retained until more thorough analyses are conducted (e.g., Davie et al., 2015a). Chief among these, Portuninae and its largest genus *Portunus* are widely understood to be paraphyletic. However, Karasawa et al. (2008)–and to some extent Spiridonov et al. (2014)–departed from Portuninae *sensu* Ng et al. (2008) by recognizing the portunid subfamilies Atoportuninae, Lupocyclinae, Necronectinae, and Portuninae; in addition to Caphyrinae, Carupinae, Podophthalminae, and Thalamitinae (Figure 2-4). To the extent possible, the status of each of these seven portunid subfamilies is revaluated here in light of new phylogenetic results (Figure 2-8). However, while Thalamitinae and Caphyrinae are well-sampled, it should be understood that most other portunid subfamilies are not. Higher resolution and support values recovered for Thalamitinae demonstrate that increased taxon sampling for other subfamilies should significantly improve the phylogenetic resolution of these clades. Yet, results of this and other work also suggest that the molecular markers used here cannot fully resolve deeper nodes in the family (cf. Lasley et. al. 2014; Thoma et. al. 2014).

Carupinae Paulson, 1875, *sensu lato*. Carupinae (Figure 2-1C and 2-1D) is a fascinating group of morphologically peculiar, highly modified portunid crabs. Relative to

other portunids members of this group are often smaller, smoother, and have more reduced eyes and much narrower paddle-shaped “natatory” legs). Most attribute these modifications to their ecology as rubble-dwelling, cavernicolous, or even anchialine crabs (e.g., Fujita & Naruse, 2011; Ng, 2011; Ng & Takeda, 2003). This subfamily includes the genera *Carupa*, *Catoptrus*, *Kume*, *Libystes*, *Richerellus* and *Pele*. *Atoportunus* is also sometimes considered (Ng, 2011; Ng & Takeda, 2003). However, Karasawa et al. (2008) found morphological cladistic support for the subfamily Atoportuninae Števčić, 2005 being comprised of *Atoportunus* and *Laleonectes*. Molecular phylogenetic work has subsequently supported an affinity of *Laleonectes* with Carupinae (Schubart & Reuschel, 2009; Spiridonov et al. 2014). Together these findings led Spiridonov et al. (2014) to suggest that a Carupinae *sensu lato* clade likely included Atoportuninae *sensu* Karasawa et al. (2008), but that data for *Atoportunus* was needed. The present study includes the first molecular data generated for *Atoportunus*. Phylogenetic analyses of the 163 OTU concatenated dataset recover a weakly supported Carupinae + Atoportuninae clade (bs <50%, pp 1.0, Figure 2-8A), but analyses of the138 OTU dataset does not (although it also does not provide strong support against it, Figure 2-8B). Consistent with Schubart & Reuschel (2009) these analyses also recover *Carupa* and *Lybistes* as poly- and paraphyletic. These findings include a placement of *Catoptrus nitidus* derived within or sister to *Lybistes* (bs 99%, 100%, pp 1.0, 1.0). However, a second *Catoptrus* OTU (*Catoptrus* aff. *nitidus*) shared no affinity with *Lybistes*, instead grouping with *Atoportunus* (bs 59%, 70%, pp <0.95, 0.98). Carupinae clearly needs further study. However, there is now some (though very

weak) molecular support for the suggestion that Carupinae *sensu* lato includes *Atoportunus* and *Laleonectes*.

Lupocyclinae Alcock, 1899. Lupocyclinae *sensu* Karasawa et al. (2008) includes *Lupocyclus* and *Carupella*, while Lupocyclinae *sensu* Spiridonov et al. (2014) includes *Lupocyclus* and *Lupocycloporus* (=*Portunus* [*Lupocycloporus*] *sensu* Ng et al., 2008) but does not explicitly place *Carupella* in any subfamily. Here only weak support was recovered for a poorly sampled monophyletic Lupocyclinae (bs <50%, <50%, pp <0.95, 0.99) and the placement of *Lupocyloporus* renders *Lupocyclus* paraphyletic (Figure 2-8A). Data from *Carupella* was not available for analysis.

Necronectinae Glaessner, 1928. Necronectinae is comprised of the Indo-Pacific *Scylla* and monotypic West African *Sanquerus* Manning, 1989. The carapace of *Sanquerus* is similar to that of *Scylla*, but its chelipeds are distinct and (at least superficially) exhibit similarities to those of *Euphylax* (personal observation from illustrations and description in Manning, 1989). The present study includes no data for *Sanquerus* but does include all four *Scylla* species. Results recover strong support for the monophyly of *Scylla* (bs 99%, 97%, pp 1.0, 1.0) with species relationships consistent to those recovered by Keenan et al. (1998, based on CO1, 16S rRNA and allozyme data). *Scylla* demonstrates some phylogenetic affinity to *Podophthalmus* and Carupinae but this relationship exhibits no strong support. Additional analyses need to include *Sanquerus*.

Podophthalminae Stimpson, 1860. This subfamily is comprised of the genera *Euphylax* and *Podophthalmus* (including *Vojmirophthalmus* Števčić, 2011 [=*Podophthalmus minabensis* Sakai, 1961]). These crabs exhibit unusually long

eyestalks that render the orbital regions enormous and the frontal margin greatly reduced (Figure 2-1F). The affinity of these genera has never been significantly challenged, but Garth & Stephenson (1966) noted general difference between the morphology of the eyestalks, anterolateral carapace margin and male first gonopods. Spiridonov et al. (2014) noted that morphologically and genetically these genera are distinct among portunids. However, results presented here are the first to analyze the placement of these two genera together. Though data was limited for *Euphylax* (16S rRNA only), single marker and concatenated analyses failed to recover a monophyletic Podophthalminae (Figure 2-5A and 2-8A). *Podophthalmus* demonstrated some topological affinity to Neconectinae and Carupinae, but always with little or no support. *Euphylax* showed no relative affinity to any portunid clade, instead always diverging alone from deeper nodes in Portunidae, but bearing no support (Figure 2-5A and 2-8A). These results do not significantly challenge nor resolve the validity or composition of Podophthalminae.

Portuninae Rafinesque, 1815. As previously discussed, the monophyly of Portuninae and its largest genus, *Portunus* (98 extant species), has long been challenged. Some of this controversy can be attributed to an expansion of the genus by Stephenson & Campbell (1959) and Stephenson (1972a), which included the incorporation of several morphologically similar but previously separate genera. Ng et al. (2008) mostly followed this classification, but also retained many of these synonymized genera as subgenera. A number of recent studies have provided evidence that these clades are morphologically and phylogenetically distinct, with some clearly worthy of generic status (Karasawa et al. 2008; Mantelatto et al., 2009; Nguyen, 2013;

Schubart & Reuschel, 2009; Spiridonov et al. 2014). Consistent with these studies, phylogenetic analyses here recover a Portuninae comprised of three clades and a *Cronius* lineage (*sensu* Mantelatto et al. 2009) falling sister to Thalamitinae (Figure 2-8; discussed below). The first of these clades, Portuninae *sensu stricto*, is strongly supported and comprised of *Arenaeus, Callinectes* and some *Portunus* species, including the generic type *P. pelagicus* (Linnaeus, 1758) (bs 96%, 97%, pp 1.0, 1.0). The second Portuninae sensu lato clade also exhibits significant support (bs 86%, 88%, pp 1.0, 1.0) and is comprised mostly of *Portunus* (*Achelous)*, some *Portunus (Portunus)* and the monotypic *Lupella forceps*. Following Mantelatto et al. (2009) many have treated *Achelous* as a distinct but not fully revised genus (e.g., Spiridonov et. al., 2014; Nguyen, 2013). The placement of *Lupella* remains to be addressed taxonomically. The third Portuninae *sensu* lato clade was weakly supported and comprised of the *Portunus* subgenera *Cycloachelous* (Figure 2-1G), *Monomia* and a paraphyletic *Xiphonectes* (bs 64%, 66%, pp <0.95, <0.95). Only the 174 OTU dataset included multiple members of *Cycloachelous* and *Monomia*. Analyses of this data recovered strong support for the monophyly of *Monomia* (bs 75%, pp 1.0; Figure 2-9A) but less support for the monophyly of *Cycloachelous* (bs <50%, pp 0.99; Figure 2-9A). Finally, the 174 OTU analyses also recovered an unusual but poorly supported placement of *Portunus (Xiphonectes) tenuipes* within the portunid subfamily Thalamitinae (bs <50%, posterior probability [pp] <0.95; Figure 2-7). Using the same data for this species (CO1 and 313 bps of 28S rRNA) Spiridonov et al. (2014) raised some concern when the same unusual placement was recovered. However, this result is likely artifactual and finds no other support from morphology or the molecular results presented here. Further work is

clearly needed to resolve *Portunus s.s.* as well as Portuninae *s.l.*, neither of which were recovered as monophyletic.

Thalamitinae Paulson, 1875. Following Stephenson (1972a), Thalamitinae was placed in Portuninae where it stayed until Apel & Spiridonov (1998) reestablished its subfamily status and provided a new morphological diagnosis of the group. Today, with 160 extant species, Thalamitinae (*sensu* Spiridonov et al., 2014) is the most diverse portunid subfamily (Figure 2-2). Nevertheless many continue to question the validity of this subfamily (e.g., Davie et al. 2015a). This can be partly attributed to the portunine genus *Cronius* (*sensu* Mantelatto et al., 2009) which presents a morphology intermediate to that of *Portunus* and the thalamitine genus *Charybdis* (see discussion below and Garth & Stephenson, 1966; Spiridonov et al., 2014). Regarding this topic, some have pointed to molecular work of Mantelatto et al. (2009) which recovered and discussed a clade comprised of *Cronius* + *Laleonectes* and a monophyletic Thalamitinae. However, Mantelatto et al. (2009) actually recovered no support for this relationship (NJ and parsimony bs <50%, BI pp=0.59). Conversely, while some have argued that *Cronius* may actual share a greater affinity with *Charybdis* than *Portunus* (Garth & Stephenson, 1966, p.14), only recently has it been suggested, based on morphological grounds, that *Cronius* may have a closer affinity with Thalamitinae than Portuninae (Spiridonov et al., 2014). Here, molecular results recover *Cronius* falling sister to Thalamitinae with little to moderate support (bs <50%, 66%, pp <0.95, 1.0). Considered within the context of morphology (discussed below), these results provide compelling evidence that *Cronius* is more appropriately classified as a thalamitine crab. Below a new diagnosis of Thlamatinae is provided that accommodates *Cronius*.

Putting *Cronius* aside, my analyses recover strong support for a Thalamitinae *sensu* Apel & Spiridonov (1998) that includes the Caphyrinae genera *Caphyra* and *Lissocarcinus* (bs 68%, 92%, pp 0.97, 1.0). These two symbiotic genera also appear highly derived within an otherwise moderately supported *Thalamita* clade (bs 62%, 66%, pp 1.0, 1.0). This derived placement renders both *Thalamita* and *Caphyra* paraphyletic (discussed below). This result is not surprising given that the morphological affinity of Caphyrinae and Thalamitinae has long been recognized and the suggestion of a derived position of Caphyrinae (by Stephenson & Campbell, 1960) has received some, but limited molecular support (Spiridonov et al., 2014). However, the present study represents the first comprehensive phylogenetic analyses of these subfamilies, including 70 of 160 Thalamitinae and 12 of 26 Caphyrinae taxa (excluding *Coelocarcinus*). Given the results of this work, Thalamitinae is redefined below to also include *Caphyra* and *Lissocarcinus*. Additionally, I describe two new genera in order to accommodate those *Thalamita* that render *Caphyra* paraphyletic. Phylogenetic results for each major Thalamitinae clade are discussed below.

Thalamitinae Paulson, 1875, Subclades and Genera.

***Cronius* Stimpson, 1860.** Using 16S rRNA, Mantelatto et al. (2009) resurrected the species *Cronius edwardsii*, demonstrating that it was a genetically distinct, geminate species of the generic type *C. ruber*. However, the same analyses also revealed that the remaining *Cronius* species, C*. timidulus*, is actually a member of *Achelous* (=*Portunus [Achelous]*; see above). These results are confirmed here using 16S and CO1 data from new specimens for all three species.

***Thalamitoides* A. Milne-Edwards, 1869.** *Thalamitoides* is a morphologically peculiar thalamitine genus with a short, but laterally expanded carapace, with

exceptionally wide set eyes and a correspondingly wide front (Figure 2-2B). Though sometimes thought to have a greater affinity to *Thalamita*, phylogenetic results place the genus sister to the remaining Thalamitinae, with moderate to strong support (bs 68%, 92%, pp 0.97, 1.0; Figure 2-8).

***Gonioinfradens* Leene, 1938.** Once classified as a subgenus of *Charybdis*, the monotypic *Gonioinfradens* (Figure 2-2C) is easily distinguished from *Charybdis* by having four instead of six well-developed anterolateral teeth. These crabs also have a subsidiary tooth following their first anterolateral tooth, a trait present in only a few other *Charybdis* species. Recognizing these species as distinct, Leene (1938) described the Charybdis subgenera *Gonioinfradens* and *Goniosupradens*. Apel and Spiridonov (1998) subsequently raised *Gonioinfradens* but not *Goniosupradens* to a generic rank. Phylogenetic analyses presented here are the first to include either subgenus. Concatenated analyses recover *Gonioinfradens* as sister to a well-supported *Charybdis sensu lato* clade (including *Goniosupradens*). However, support for this placement is moderate or weak (bs 59%, 56%, pp 1.0, <0.95).

***Goniosupradens* Leene, 1938, status nov.** Concatenated analyses recovered strong support for a reciprocally monophyletic clade including all three *Goniosupradens* species and *Charybdis hawaiensis* (bs 99%, 100%, pp 1.0, 1.0). Moreover, this clade fell sister to a monophyletic *Charybdis sensu stricto* (bs 97%, 99%, pp 1.0, 1.0). *Charybdis hawaiensis* (=*Goniosupradens hawaiensis*, comb. nov.) was thought to have affinity with *Ch. orientalis* (e.g., Edmondson, 1954) but a reevaluation of its morphology (below) suggests that these similarities are superficial. Here *Goniosupradens* (Figure 2-

2D) is raised to generic rank and a new diagnosis is provided that incorporates *G. hawaiensis*.

***Charybdis* De Haan, 1833.** Concatenated analyses recovered a monophyletic *Charybdis* lineage (excluding *Goniosupradens*) with strong support (bs 93%, 97%, pp 1.0, 1.0). There was no support for other proposed *Charybdis* subgenera (e.g., *Goniohellenus* and *Gonioneptunus*), although, analyses included only 18 of 65 *Charybdis* species.

***Thalamonyx* A. Milne-Edwards, 1873, status nov.** The status of *Thalamonyx* has long been questioned as these crabs exhibit a peculiar morphology with similarities to *Thalamita*, *Charybdis* and *Caphyra* (Leene, 1938). Eventually this genus was synonymized with *Thalamita* (Stephenson & Hudson, 1957). However, more recently Spiridonov et al. (2014) implied that *Thalamonyx* was valid but did not formally reestablish it. Results presented here are the first to include molecular data for the genus and they recover strong support for *Thalamonyx gracilipes* falling sister to the *Thalamita sensu stricto* clade (bs 90%, 96%, pp 0.99, 1.0; Figure 2-8). Given this species' distinct morphology and that several *Thalamita sensu lato* clades will constitute additional genera (discussed below), the generic status of *Thalamonyx* is reinstated here and a new diagnosis is provided.

***Thalamita* Latreille, 1829.** With 89 species, *Thalamita* is the largest portunid genus. Unlike *Portunus*, its monophyly has never been significantly challenged. However *Thalamita* is morphologically diverse, sometimes confusingly so, and it has always been thought to have a close affinity to *Charybdis*. Stephenson & Hudson (1957) even suggested that the two genera may "constitute an unbroken series", blending one

into the other, however this is not supported by the present phylogenetic analysis. Nevertheless, the derived placement of Caphyrinae within *Thalamita* renders this genus paraphyletic. With the exception of those *Thalamita* species falling within the resulting monophyletic "*Caphyrini*" clade, three clades and one "grade" of *Thalamita* taxa were recovered. Each of these four clades are labeled in Figure 2-8B and discussed below.

Thalamita admete (Herbst, 1803) is the generic type. With few exceptions members traditionally grouped with this species (e.g., see Stephenson & Hudson, 1957) are recovered here falling within a moderately supported *Thalamita sensu stricto* clade (bs 57%, 64%, pp 0.99, 0.99, Figure 2-8). This clade includes only small to moderate sized *Thalamita* species that are morphologically similar and often hard to distinguish. They all exhibit two wide frontal lobes with equally wide, mostly parallel, inner orbital margins. Male first gonopods are long, less stout and never significantly flared relative to similarly sized *Thalamita sensu lato* taxa. Fourteen species were recovered in this clade, but the group likely includes many additional species not considered here. Nevertheless, some species traditionally assigned to this group were not recovered in the clade. Specifically, *Th. oculea* and *Th. sima* exhibit a similar size and carapace morphology to *Th. admete* but their gonopod morphology is different (discussed below) and phylogenetically they group with members of *Thalamita s.l.* Clade III (Figure 2-8; discussed below). Unfortunately, a new diagnosis of *Thalamita s.s.* at this time would be premature. While the present study does include over half of all *Thalamita s.l.* taxa, several morphologically important species have not been included (e.g., *Th.* annulipes, *Th. margaritimana,* and *Th. platypenis*) and poor phylogenetic resolution at several important nodes complicates the delineation of clades within the group. Additional work

on *Thalamita s.l.* is underway by V. Spiridonov and N. Evans both separately and in collaboration.

The remaining *Thalamita* (*Thalamita s.l.* Clade II, III and IV) and “Caphyrini” form a moderately-well supported clade (bs 62%, 66%, pp 1.0, 1.0). The earliest diverging *Thalamita s.l.* taxa form a grade (“Clade” II, Figure 2-8), paraphyletic to the remaining *Thalamita s.l.* clades (Clades III and IV). While carapace morphology (e.g., frontal lobes and anterolateral teeth) varies substantially across this grade of small sized *Thalamita*, the male first gonopods possess a diagnostically stout and often flared morphology. However this gonopod morphology is also shared with members of the *Thalamita s.l.* Clade III. Clade III forms a distinct, strongly supported lineage (bs 100%, 99%, pp 1.0, 1.0) of small to medium sized species. Complicating the diagnosis of this clade, some species have a two-lobed frontal margin striking similarity to that of *Thalamita s.s.* (Clade I), while others exhibit six frontal lobes similar to that seen in some members of *Thalmita s.l.* “Clade” II. Finally, *Thalamita s.l.* Clade IV is strongly supported (bs 79%, 98%, pp 1.0, 1.0) and comprised only of large, morphologically similar *Thalamita* species. Sometimes referred to as the “Prymna” group (after *Th. prymna*; Stephenson & Hudson, 1957), all members if this clade have a similarly shaped six-lobed frontal margin, four to five similar anterolateral teeth, and a relatively long, gradually tapering male first gonopod.

Caphyrini Paul'son, 1875. A moderately well-supported clade (bs 50%, 71%, pp 1.0, 1.0) comprised of *Caphyra*, *Lissocarcinus,* and six former *Thalamita* species is recognized here as a redefined Caphyrini (Figure 2-3). Monophyly of *Lissocarcinus* was strongly supported (bs 98%, 100%, pp 1.0, 1.0), and fell sister to a well-supported clade

comprised of the remaining Caphyrini taxa (bs 59%, 100%, pp 1.0, 1.0). This latter clade is morphologically diverse and includes a *Caphyra sensu stricto* clade as well as two lineages with species formerly assigned to *Thalamita*, but also including *C. rotundifrons*. The first of these lineages is comprised of the morphologically distinct, geminate species *Th. longifrons* and *Th. murinae*. Long considered worthy of generic status both species are facultative commensals of nephtheid soft coral (see below; Evans & McKeon, 2016; Spiridonov & Neumann, 2008). To accommodate these species I erect the new genus *Zygita*. The second lineage was recovered with poor support but includes *Th. woodmasoni* and *Th. cooperi*; species likewise considered part of a morphologically distinct *Thalamita* clade (the "Woodmasoni" group; Vannini, 1983). Here I establish the new genus *Trierarchus* comprised of these species (and all other "Woodmasoni" species) as well as *Th. squamosa* (=*Trierachus squamosus* comb. nov.) and *C. rotundifrons* (=*Trierarchus rotundifrons* comb. nov.). Compelling evidence suggests that members of *Trierarchus* are symbiotic, forming facultative or obligate associations with algae (see below). Furthermore, the removal of the divergent, algal-commensal *C. rotundifrons* leaves a strongly supported *Caphyra s.s.* clade (bs 100%, 100%, pp 1.0, 1.0), comprised now only of species known to be commensal on soft corals. Finally, though analyses considered no more than 7 of the 16 *Caphyra s.s.* species, results suggest that the genus may consist of two morphologically and ecologically distinct subclades (Figure 2-8), with members of one clade (*C. bedoti, C. tridens, and C. yookadai*) primarily being obligate commensals of alcyoniid soft corals, and members of the other (including *C. loevis* and *C.* cf. *fulva*) obligate commensals of xeniid soft corals (Crosnier, 1975b; Stephenson & Reed, 1968; data from UF holdings).

Systematic Account

Family Portunidae Rafinesque, 1815

Subfamily Thalamitinae Paul'son, 1875

Figures 2-2, 2-3, and 2-11 A-C,

- – Thalamitinae Paul'son, 1875: 69. Type genus: *Thalamita* Latreille, 1829.
- = Caphyrinae Paul'son, 1875: 69. Type genus: *Caphyra* Guérin, 1832.

Diagnosis. Cephalothorax subcircular, subhexagonal or subtrapezoidal; slightly (e.g., some *Caphyra*) to substantially (e.g., *Thalamitoides*) broader than long. Anterolateral margin (including outer orbital angle) with two to nine, but typically four to six, teeth; rarely nearly entire (e.g., some [especially abnormal] *Lissocarcinus* and *Caphyra*). If anterolateral teeth number greater than six, just five (rarely six) are large and well developed; the remaining are small, subsidiary teeth that appear between larger teeth (e.g., see *Cronius* and *Goniosupradens*). Rarely the first anterolateral tooth appears truncate and notched resembling an additional tooth (e.g., *Charybdis feriatus*). Basal antennal segment transversely broadened or lying obliquely, and entering or filling orbital hiatus. Antennal peduncle and flagellum completely or nearly completely excluded from orbit. Chelipeds the same length or longer than ambulatory legs, typically bearing spines on the merus, carpus and manus; manus with up to seven (positionally homologous) costae that form smooth, sharp, granular, or spiniform ridges. Ambulatory legs compressed; last pair typically with paddle-shaped propodi and dactyli, but sometimes otherwise modified. Male first gonopod with subterminal spinules, spines, or bristles. Diagnosis modified from Thalamitinae and Caphyrinae sensu Apel and

Spiridonov (1998), *Cronius* sensu Rathbun (1930) and Garth and Stephenson (1966), and *Caphyra* sensu Apel and Steudel (2001).

Genera included:

- *Caphyra* Guérin, 1832
- *Charybdis* De Haan, 1833
- *Cronius* Stimpson, 1860
- *Gonioinfradens* Leene, 1938
- *Goniosupradens* Leene, 1938, status nov.
- *Lissocarcinus* Adams & White, 1849
- *Thalamita* Latreille, 1829
- *Thalamitoides* A. Milne-Edwards, 1869
- *Thalamonyx* A. Milne-Edwards, 1873, status nov.
- *Trierarchus* Evans, gen. nov.
- *Zygita* Evans, gen. nov.

Remarks. With the addition of *Caphyra, Cronius* and *Lissocarcinus*, Thalamitinae now includes 188 species (Spiridonov et al. 2014) and is the largest portunoid subfamily. *Cronius* notably expands the diagnosis of the subfamily to include members that possess nine anterolateral teeth. Though molecular support is modest (see above), an overall morphological similarity between *Cronius* and *Charybdis* has been noted (Garth & Stephenson, 1966). Furthermore, *Cronius* exhibits a number of traits considered diagnostic of Thalamitinae. These include exclusion of the antennal flagellum from the orbit by the basal antennal joint, no more than six large anterolateral teeth, and a male first gonopod with subterminal bristles or “hairs” (see discussions in Garth & Stephenson, 1966; Spiridonov et al., 2014).

The seven positionally homologous costae present on the cheliped manus of thalamitine crabs are depicted and numbered in Figure 2-11 A-C. This numbering scheme is used in generic diagnoses below. These costae are likely shared across Portunidae, possibly Portunoidea, but further work is needed to assess their homology.

Likewise, anterolateral teeth share homology across Portunidae and possibly Portunoidea. Important transitional forms (e.g., *Cronius*) may help identify the homology of these teeth. For example, the anterolateral carapace margin of *Cronius* displays teeth of alternating size, with five large teeth each followed by one of four reduced (or subequal) teeth (Figure 2-2A). This morphology suggests that the five anterolateral teeth typically present in *Thalamita* sensu lato taxa likely correspond (in order) to teeth numbers one, three, five, seven, and nine in *Portunus s.l*. Underlying musculature further supports this; some teeth maintained in derived thalamitine taxa are known to be muscle attachment points in Portuninae taxa, while those that are reduced or "lost" are not (e.g., see Cochran, 1935). Delineating the homology of anterolateral teeth among all portunoids would be taxonomically useful.

Genus *Goniosupradens* Leene, 1938, status nov.

Figure 2-2 D.

- Type species: *Portunus erythrodactylus* Lamark, 1818, subsequent designation by Davie (2002); gender masculine.

Diagnosis. Cephalothorax subhexagonal, slightly broader than long. Frontal margin with six well-developed teeth or lobes, excluding inner supraorbital lobes. Anterolateral border (including outer orbital angle) with five large, well-developed, forward-sweeping teeth and one, two, or sometimes three small, subsidiary teeth. Subsidiary teeth not significantly swept forward but terminating approximately perpendicular to the anterolateral border, and appearing on the posterior margin of, or just following, each well-developed tooth such that they occupy tooth positions two, four, or six. Last (epibranchial) anterolateral tooth subequal to and never significantly extending laterally beyond the preceding (fourth) well-developed tooth. Posterior margin

of carapace forming a curve with the posterolateral margin. Basal antennal segment transversely broadened and filling orbital hiatus. Antennal peduncle and flagellum completely excluded from orbit. Cheliped merus typically bearing three spines along the anterior border and distally with a broad, sometime spiniform tooth or lobe. Inner angle of carpus with a strong, well-developed spine; outer angle with three spinules. Cheliped manus typically bearing five spines on the upper surface; two spines along Costa 1, two spines along Costa 2, and one spine on the outer proximal edge at the articulation with the carpus just above the beginning of Costa 3; Costae 3 to 5 always well developed; Costae 6 and 7 granular, or smooth and poorly developed. Natatory legs with paddle-shaped propodi and dactyli; posterior border of propodi with spines or spinules. Diagnosis modified from Leene (1938) to include *Goniosupradens hawaiensis*, comb. nov., after Edmondson (1954).

Species included:

- *Goniosupradens acutifrons* (De Man, 1879)
- *Goniosupradens erythrodactylus* (Lamarck, 1818)
    - =*Thalamita pulchra* Randall, 1840
    - =*Thalamita teschoiraei* A. Milne-Edwards, 1859
- *Goniosupradens hawaiensis* (Edmondson, 1954), comb. nov.
- *Goniosupradens obtusifrons* (Leene, 1937)

Remarks. Historically, *G. hawaiensis* (=*Charybdis hawaiensis*) was considered closely related to *Ch. orientalis* (e.g., Edmondson, 1954), but the similarities are superficial. Once thought diagnostic of these species, the first “subsidiary” anterolateral tooth is more reduced in *G. hawaiensis* in a manner consistent with other *Goniosupradens*. In *Ch. orientalis* this tooth is reduced, but exhibits a different shape. More importantly *G. hawaiensis*, like all *Goniosupradens*, bears an epibranchial, anterolateral tooth subequal to and never significantly extending laterally beyond the

preceding tooth. The opposite condition is present in Ch. *orientalis* and most other *Charybdis* (compare Figures 2-2D and 2-2E). Finally, the related *Gonioinfradens* has four, rather than five well-developed anterolateral teeth (compare Figures 2-2C and 2-2D), but these genera share a similar, likely homologous, subsidiary anterolateral teeth.

Genus *Thalamonyx* A. Milne-Edwards, 1873, status nov.

Figure 2-2 F and 2-11 D

- Type species: *Goniosoma danae* A. Milne-Edwards, 1869, subsequent designation by Rathbun, 1922; gender masculine.

Diagnosis. Cephalothorax subhexagonal, approaching subcircular; moderately convex dorsally; mature specimens always slightly broader than long. Frontal margin of carapace not much wider than posterior margin and comprised of two lobes (excluding inner supraorbital margin) separated by a small, distinct notch and extending forward well beyond the inner supraorbital margin; lobes frequently slightly sinuous or concave near the inner margin such that each appears subtly bilobed. Inner supraorbital margin arched and less than one third as wide as frontal lobes. Five, sharp anterolateral teeth; first largest and directed forward; remaining subequal and swept forward forming an oblique, inclined boarder similar to that in *Charybdis*. Basal antennal segment filling orbital hiatus and with a very low crest bearing no spines or conspicuous granules. Antennal peduncle and flagellum completely excluded from orbit. Chelipeds equal or subequal, not robust, Cheliped merus bearing three spines on a granular anterior border; posterior boarder subtly squamous. Cheliped carpus with a strong, well-developed spine on inner angle and three spinules on outer angle. Cheliped manus lightly granular all over; one spine on Costa 1, one spine on Costa 2; one spine on the outer proximal edge at the articulation with the carpus just above the beginning of Costa

3; Costa 3 to 5 granular but increasingly well developed; Costa 6 granular or smooth and poorly developed; Costa 7 sometimes granular and well developed. Cheliped dactylus minutely granular near upper proximal margin. Natatory legs with paddle shaped propodi and dactyli; posterior boarder of propodi without spinules. Male first gonopod short, broad, curved, broadening slightly towards a wide, obliquely ending tip; subterminal outer border viewed in profile bearing stout, mostly paired bristles numbering approximately nine, followed by additional thinner bristles; a sparse row of spinules also present; subterminal inner border with five long, hook-shaped bristles followed by approximately four mostly straight, variously angled bristles. Female genital opening relatively large, located near anterior margin of sternite.

Species included:

- *Thalamonyx danae* (A. Milne-Edwards, 1869)
    - = *Thalamita anomala* Stephenson and Hudson, 1957
- *Thalamonyx gracilipes* A. Milne-Edwards, 1869

Remarks. The G1 of this genus is very distinct (Figure 2-11 D, but see also Stephenson & Rees, 1967a, p.20, Figure 2D; Nguyen, 2013, Figure 15), as is the female genital opening (personal communication, V. Spiridonov). Ng et al. (2008, note 25, p. 158; but not p. 154) created some confusion by misidentifying the type species of this genus, which is *Goniosoma danae* Milne-Edwards, 1869, not *Thalamita danae* Stimpson, 1858. When Stephenson and Hudson (1957) designated *Thalamonyx* a junior synonym of *Thalamita*, the species *Th. danae* (Milne-Edwards, 1869) became a jr. secondary homonym of *Th. danae* Stimpson, 1858. As a result the authors renamed *Th. danae* (Milne-Edwards, 1869) to *Thalamita anomala* (Stephenson and Hudson, 1957). In accordance with Article 59.4 of ICZN (1999), *Thalamonyx danae* (Milne-

Edwards, 1869) is reinstated here as a valid species and *Thalamita anomala* (Stephenson and Hudson, 1957) its junior synonym. Though no *Th. danae* (Milne-Edwards, 1869) specimens were examined for this study, it sister status with *Th. gracilipes* (sampled here) is without question. Several authors have even suggested that these species be synonymized, though this has never been fully investigated or adopted (see discussion Stephenson and Rees, 1967a, p.20).

As others have noted, the *Thalamonyx* specimen illustrated by Crosnier (1962, Figure 153) is that of an immature male; both its carapace and male first gonopod are not fully developed and should not be used to diagnose adult specimens. Finally, *Thalamita parvidens* (Rathbun, 1907), originally described in *Thalmonyx*, bears close morphological affinity with *Th. chaptalii*. Molecular results presented confirm this affinity and the species does not belong in *Thalamonyx.*

Genus *Zygita* gen. nov.

Figure 2-3E and 2-11 F-I, ZooBank address TBD.

- Type species: Goniosoma longifrons A. Milne-Edwards, 1869, by present designation.

Diagnosis. Cephalothorax subhexagonal; approximately 1.5 times broader than long. Frontal margin with six well-developed, bluntly rounded or pointed teeth, of approximately even width, separated by deep notches. Inner supraorbital margin oblique and spiniform. Infraorbital lobe well developed terminating in a spiniform or bluntly rounded point. Basal antennal segment filling orbital hiatus with a granular crest bearing at least one spine. Anterolateral border (including outer orbital angle) with five large, well-developed sharp teeth forming an oblique, inclined boarder reminiscent of *Thalamonyx* and *Charybdis*. Carapace, chelipeds and ambulatory legs subtly to

substantially granular and sparsely or densely covered with plumose setae (easily worn away in preserved specimens). Chelipeds ischia sometimes with distal spine near anterior articulation with merus. Cheliped meri with three spines on anterior margin, plus a distal spinule near articulation with carpus; a similar ventral distal spine with an associated lobule is also present. Cheliped carpus granular to subtly spiniform with two nearly perpendicular granular costae running dorsally towards and merging along a well-developed spine at the inner angle; upper surface bearing an additional spine in addition to three typical of the outer angle. Cheliped manus bearing at least two spines along Costa 1 and two along Costa 2; one spine on the outer proximal edge at the articulation with the carpus just above the beginning of a sparsely granular Costa 3; Costa 4 distinct and granular ending distally in a sharp or dull spinule; Costa 5 granular and distinct; squamiform sculpture extending ventrally from Costa 5 to a poorly defined Costa 6; Costa 7 granular and often well-developed; dactylus noticeably granular or serrate at upper proximal end but smoothing out distally. Meri of ambulatory legs bearing a ventral posterodistal spine; carpi with a dorsal anteriodistal spine; propodi with a ventral posterodistal spine (sometimes absent on first leg). Natatory legs with coxae bearing a stout, well-developed spinule dorsad; ischia with granular to spiniform distal border; meri with two well-developed spines along dorsal posterodistal border, and one well-developed spine on ventral posterodistal border; carpi with well-developed spine on ventral posterodistal boarder; propodi longer than broad, paddle-shaped with spines or spinules along posterior border; dactyli lancelet-shaped dactyli (especially in juveniles), but approaching paddle-shaped in larger individuals. G1 curved and tapering with a row

of one to twelve subterminal bristles on inner border; bristles continue more sparsely on lower surface and extend to outer upper surface.

Species included:

- *Zygita longifrons* (A. Milne-Edwards, 1869), comb. nov.
  - = *Thalamita spinimera* Stephenson and Rees, 1967
  - = *Thalamita yoronensis* Sakai, 1969
- *Zygita murinae* (Zarenkov, 1971), comb. nov.

Taxonomic Remarks. The distinct morphology of this rarely collected genus is well known and deserving of generic rank (see discussions Stephenson & Rees, 1967b; Spiridonov & Neumann, 2008). *Zygita* cannot be easily confused with any other portunoid taxa. The most diagnostic traits of this genus includes the presence of a sharp or dull spinule at the distal end of manus Costa 4 (indicated in Figure 2-11 F); meri of the ambulatory legs bearing a ventral posterodistal spine (indicated in Figure 2-11 G); natatory legs with coxae bearing a stout, well-developed dorsal spinule (indicated in Figure 2-11 H) and carpi bearing a well-developed spine on the ventral posterodistal boarder (indicated in Figure 2-11 I).

Ecological Remarks. In their original description of *Thalamita spinimera,* Stephenson & Rees (1967b) suggested these crabs were “ectocommensal” on Alcyonaria (=Octocorallia). This was based on one specimen collected from soft coral exhibiting a morphology with “special additions to the basic [*Thalamita*] body plan” (Stephens & Rees, 1967b, p. 97). In their revision of this group, Spiridonov & Neumann (2008) were unable to confirm this association, but they only considered seven specimens. Evans & McKeon (2016) compiled compelling in situ photographs and collections records for 24 specimens and found that 46% (11 specimens) were found in association with soft corals, seven of which belonged to the family Nephtheidae, in what

is likely a facultative association. Phylogenetic results strongly support a relationship between these crabs and *Lissocarcinus* and *Caphyra*; the former includes species symbiotic with anemones, while the latter is symbiotic with soft corals .

Etymology. *Thalamita* originally bore the name *Thalamites* (Low et al., 2013), named after the oarsmen occupying the lowest tier of a Trireme, a popular three-tiered ancient Greek warship. In keeping with this tradition, *Zygita* originates from the word Zygite, the name given to oarsmen occupying the middle tier of a Trireme. Gender feminine. As *Thalamita* sensu lato is further revised this etymology could be extended.

Genus *Trierarchus* gen. nov.

Figures 2-3 F-J and 2-11 E, ZooBank address TBD.

- Type species*: Thalamita woodmasoni* Alcock, 1899, by present designation.

Diagnosis. Cephalothorax subhexagonal or subcircular; mature specimens always broader than long. Frontal margin (excluding inner supraorbital margin) flat or rounded and comprised of one to six, but typically four weakly distinguished lobes. Four lobed species typically with median lobes approximately three times as wide as lateral lobes. Inner supraorbital margin sometimes nearly absent (e.g. *Tr. rotundifrons)* but typically subtly rounded and oblique with a breadth never greater than one-third the total breadth of the frontal lobes. Basal antennal segment filling orbital hiatus with a smooth or minutely granular crest, never with spines. Anterolateral border (including outer orbital margin) with four well-developed teeth swept forward; a rudimentary tooth sometimes present between the third and fourth anterolateral teeth. Carapace, chelipeds and (sometimes) ambulatory legs subtly to substantially granular with squamiform markings and sparsely or densely covered with plumose setae (easily worn away in preserved specimens). Cheliped meri with at least three spines on anterior

border in mature specimens; posterior ventral surface typically with substantial granular squamiform markings. Cheliped carpi granular to subtly spiniform with two nearly perpendicular granular costae running dorsally towards and merging along a well-developed spine at the inner angle; three spines or spinules on the outer angle. Cheliped manus typically with two spines along Costa 1 and one or two along Costa 2; one spine or tubercle on the outer proximal edge at the articulation with the carpus just above the beginning of a sparsely granular or nearly absent Costa 3; Costa 4 typically distinct and granular extending into the pollex; Costa 5 granular and distinct; weakly squamiform sculpture extending ventrally from costa five to a poorly defined Costa 6; Costa 7 sometimes granular and well-developed. Natatory legs with propodi longer than broad, paddle-shaped with spines or spinules along posterior border; dactyli lancelet-shaped dactyli (especially in juveniles), but approaching paddle-shaped in larger individuals. G1 curved and swelling slightly towards a club-shaped end distally pointed towards the outer border with a bluntly rounded tip; subterminal bristles always present on inner upper surface and typically dense being comprised of several rows continuing sparsely or densely to lower surface where they extend nearly to the terminal tip as well as continue to an outer upper surface that is likewise typically covered with subterminal bristles; larger subterminal bristle sockets distinct and visible when bristles are damaged or missing.

Species included:

- *Trierarchus acanthophallus* (Chen and Yang 2008), comb. nov.
- *Trierarchus cooperi* (Borradaile, 1902), comb. nov.
- *Trierarchus corrugatus* (Stephenson & Rees, 1961), comb. nov.
- *Trierarchus crosnieri* Vannini, 1983, comb. nov.
- *Trierarchus demani* (Nobili, 1905), comb. nov.
    - *=?Thalamita trilineata* Stephenson & Hudson, 1957

    - =*?Thalamita invicta* Thallwitz, 1891
- *Trierarchus procorrugatus* (Dai, Yang, Song & Chen, 1986), comb. nov.
- *Trierarchus rotundifrons* (A. Milne-Edwards, 1869), comb. nov.
- *Trierarchus sankarankuttyi* (Crosnier and Thomassin, 1974)*,* comb. nov.
- *Trierarchus squamosus* (Stephenson & Hudson, 1957*),* comb. nov.
- *Trierarchus woodmasoni* (Alcock, 1899*),* comb. nov.
- *Trierarchus taprobanica* Alcock, 1899*,* comb. nov.

Taxonomic Remarks. The diagnostic characters of *Trierarchus* include the G1, anterolateral margin and presence of squamiform markings and plumose setae. The G1 of this genus is very distinct and particularly useful (Figure 2-11 E, see also Crosnier, 1975a, Figure 8; Crosnier & Thomassin, 1974, Figure 8 D; Chen & Yang, 2008, Figure 7; Dai et al., 1986, Figure 137 A). However, *Tr. squamosus* and *Tr. rotundifrons* exhibit variations on this form (e.g., see illustrations Stephenson & Hudson, 1956, Figures 2K and 3K; Stephenson & Campbell, 1960, Figures 1H and 2J). Additionally, *Tr. rotundifrons* (Figure 2-3I) is morphologically highly divergent for other members of this genus, likely because of its obligate commensal relationship. Its natatory legs are modified into clasping hooks with distinct setae that help firmly anchor it to its host. This species is also smooth, lacking squamiform markings, most plumose setae and nearly all of the costae on the chelipeds. Curiously the morphological affinity of *Tr. rotundifrons* to other *Trierarchus* is best represented by comparison with the genetically more distant *Tr. woodmasoni* (compare Figure 2-3F with 2-3I). Finally, *Thalamita bouvieri* is sometimes confused with *Tr. woodmasoni* (e.g., see discussion in Crosnier, 1975a); however, while its frontal margin and G1 bear some similarity, its four-toothed anterolateral margin has a significantly reduced third tooth, where on *Trierarchus* this tooth is always well-developed. Phylogenetic results presented here do not support *Th. bouvieri*'s placement in this genus.

Species delineation in this group remains problematic (e.g., see discussion in Crosnier, 1975a) and a revision is needed. Morphologically *Tr. sankarankuttyi* and *Tr. procorrugatus* have a strong affinity with *Tr. cooperi*, but the material they were described from was limited and interspecific differences are poorly delineated (see Crosnier & Thomassin, 1974; Dai et al. 1986). Furthermore, while two well-supported, genetically distinct *Tr.* cf. *cooperi* lineages were recovered in the present study (sp. A and sp. B), examination of multiple DNA barcoded specimens from each lineage failed to reveal clear morphological distinctions between the taxa (analyses not shown; but see discussion of color below). Moreover, many individuals from both genetic lineages fit a diagnosis of *Tr. corrugatus* (Stephenson & Rees, 1961). This inter- and intraspecific variation likely explains why Crosnier (1962) synonymized this species with *Tr. cooperi*, though they are currently treated as distinct (e.g., Ng et al. 2008; Nguyen, 2013). Comparison of sequenced specimens of *Tr. woodmasoni* from across the Indo-Pacific (analyses not shown) also suggests that *Tr. crosnieri, Tr. taprobanica,* and *Tr. woodmasoni* are intraspecific variants. Thus *Trierarchus* appears to be comprised of fewer valid species than currently recognized.

Ecological Remarks. Members of *Trierarchus* tend to inhabit high-energy, shallow marine environments, often in association with algae (Vannini, 1983; Hay et al., 1989; UF collection data; personal observations). In Guam *Tr. rotundifrons* is always found in association with *Chlorodesmis* algae in exposed reefs, *Tr.* cf. *cooperi* is recovered by sieving living *Halimeda* (note the light green live color in sp. B, Figure 2-3H), and *Tr. woodmasoni* is reliably recovered from sieving *Sargassum* and other codistributed algae. In Moorea Island (French Polynesia), *Tr.* cf. *cooperi* is typically

recovered by sieving and breaking coral rubble from fore reef environments. However, unlike *Tr.* cf. *cooperi* recovered in Guam, the species collected in Moorea (sp. A, Figure 2-3G) displays a live color mottled with red, orange and purple hues; shades common among coralline algae, sponges and other encrusting marine life in such substrate. Nevertheless, with the exception of *Tr. rotundifrons*, which is demonstrably an obligate commensal (Hay et al., 1989), other commensal associations suggested for this genus are speculative and need to be tested. Finally, in contrast to other species, the rarely collected *Tr. squamosus* appears to prefer protected lagoonal waters, but no further microhabitat data or live colors are available for it.

Etymology. This genus bears the name given to the captains of ancient Greek Trireme warships. For context see the etymology of *Zygita* (above). Gender masculine.

Table 2-1. Taxon sampling and operational taxonomic unit (OTU) composition of sequence data used for phylogenetic analyses.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Cancroidea: Cancridae:									
Cancer pagurus Linnaeus, 1758	OTU-001	FM207653	*JQ306000	**DQ079668	**DQ079781	A, B	SMF 32764 / *MB 89000194 / **BYU KC2158	France / *England / **NA	Schubart & Reuschel (2009) / *da Silva et al. (2011) / **Porter et al. (2005)
Carpilioidea: Carpiliidae:									
Carpilius convexus (Forskal, 1775)	OTU-002	FM208748	*JX398091	*JX398111	*JX398073	A	SMF 32771 / *ZMMU Ma3438	French Polynesia / *Vietnam, Nhatrang Bay	Schubart & Reuschel (2009) / *Spiridonov et al. (2014)

* & ** Distinct attributes for second and third specimens in multi-specimen OTUs, respectively. Notes A=16S rRNA data include tRNA-Leu and partial NADH1 sequences; B=28S rRNA sequences > 500 bps and were included in analyses of 28S only data; C=included only in single marker and 174 OTU concatenated analyses. BYU=Monte L. Bean Life Science Museum, Brigham Young University, Provo; CCDB=Crustacean Collection of the Department of Biology, University of São Paulo, São Paulo; CSIRO=CSIRO Marine Research collections, Hobart; MB=Museu Nacional de Historia Natural, Universidade de Lisboa, Lisbon; MNHN=Muséum National d'Histoire Naturelle, Paris; MZUCR=Zoology Museum, Universidad de Costa Rica, San José; MZUF=La Specola, Museo Zoologico Universita di Firenze, Florence; NTOU=National Taiwan Ocean University, Keelung; SMF=Senckenberg Research Institute and Natural History Museum in Frankfurt; UF=Florida Museum of Natural History, University of Florida, Gainesville; ULLZ=Zoological Collection, University of Louisiana at Lafayette, Lafayette; USNM=Smithsonian National Museum of Natural History, Washington; ZMMU=Zoological Museum of the Moscow University, Moscow; ZRC=the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, Singapore.

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Corystoidea: Corystidae:									
Corystes cassivelaunus (Pennant, 1777)	OTU-003	FM208781	*JQ306006	FM208801	NA	A	SMF 32770 / *MB 89000203	France, Bretagne / *England	Schubart & Reuschel (2009) / *da Silva et al. (2011)
Eriphioidea: Menippidae:									
Menippe rumphii (Fabricius, 1798)	OTU-004	HM637976	HM638051	HM596626	NA		ZRC 2003.211	Singapore	Lasley et al. (2013)
Parthenopoidea: Parthenopidae:									
Daldorfia horrida (Linnaeus, 1758)	OTU-005	GQ249177	*HM638031	GQ249174	NA		ZRC 2003.0651	Guam	Lai et al. (2014)
Xanthoidea: Xanthidae:									
Etisus utilis Jacquinot, 1853	OTU-006	HM798456	HM750981	*JX398108	NA		ZRC 2002.0586 / *NA	Thailand, Phuket / *Vietnam, Nhatrang Bay	Lai et al. (2011) / *Spiridonov et al. (2014)
Portunoidea: Carcinidae: Carcininae									
Carcinus maenas (Linnaeus, 1758)	OTU-007	FM208763	*FJ581597	FM208811	**DQ079798	A, B	SMF 32757 / *NA / **BYU KACmapu	France, Le Havre / *Nova Scotia / **NA	Schubart & Reuschel (2009) / *Radulovici et al. (2009) / **Porter et al. (2005)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Portunoidea: Carcinidae: Coelocarcininae									
Coelocarcinus aff. *foliatus*	OTU-009	KT365545	NA	NA	NA	A	UF 27553	Marquesas Islands	This study
Coelocarcinus foliatus Edmondson, 1930	OTU-010	KT365601	KT365724	KT425058	NA		UF 40056	Guam	This study
Portunoidea: Carcinidae: Pirimelinae									
Pirimela denticulata (Montagu, 1808)	OTU-019	FM208783	NA	FM208808	NA	A	SMF 32767	France, Guthary	Schubart & Reuschel (2009)
Sirpus zariquieyi Gordon, 1953	OTU-020	FM208784	NA	FM208809	NA	A	SMF 32768	Greece, Parga	Schubart & Reuschel (2009)
Portunoidea: Carcinidae: Platyonichinae									
Portumnus latipes (Pennant, 1777)	OTU-008	FM208764	NA	FM208812	NA	A	SMF 32758	UK, Hastings	Schubart & Reuschel (2009)
Portunoidea: Carcinidae: Polybiinae									
Bathynectes longispina (Risso, 1816)	OTU-021	KT365526	*KT365693	NA	KT365627	A, B	UF 9383 / *UF 15140	United States, Florida	This study
Bathynectes maravigna (Prestandrea, 1839)	OTU-022	FM208770	*JQ305966	FM208814	NA	A	MNHN B31441 / *NA	Alborn Sea / *Ireland	Schubart & Reuschel (2009) / *da Silva et al. (2011)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
"Liocarcinus" corrugatus (Pennant, 1777)	OTU-023	GQ268542	GQ268536	*FM208820	NA		NA / *SMF 32760	North Sea / *Spain, Ibiza	Lindley et al. (2010) / *Schubart & Reuschel (2009)
"Liocarcinus" depurator (Linnaeus, 1758)	OTU-024	FM208767	*FJ174948	*FJ174852	*FJ036939	A	MNHN B31439 / *NA	Alborn Sea / *NA	Schubart & Reuschel (2009) / *Palero (unpublished)
"Liocarcinus" holsatus (Fabricius, 1798)	OTU-025	FM208766	*GQ268538	FM208817	NA	A	SMF 32750 / *NA	Germany, Helgoland / *North Sea	Schubart & Reuschel (2009) / *Lindley et al. (2010)
"Liocarcinus" maculatus (Risso, 1827)	OTU-026	FJ174892	FJ174949	FJ174853	FJ036940		NA	NA	*Palero (unpublished)
"Liocarcinus" marmoreus (Leach, 1814)	OTU-027	GQ268547	GQ268535	NA	NA		NA	North Sea	Lindley et al. (2010)
"Liocarcinus" navigator (Herbst, 1794)	OTU-028	GQ268541	GQ268537	*FM208821	NA		NA / *SMF 32775	North Sea / *France, Normandie	Lindley et al. (2010) / *Schubart & Reuschel (2009)
"Liocarcinus" vernalis (Risso, 1816)	OTU-029	FM208768	*JX123455	NA	NA	A	SMF 32761 / *CCDB 1739	Italy, Naples / *Italy, Port Ercole	Schubart & Reuschel (2009) / *Zupolini (2012)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Macropipus tuberculatus (Roux, 1830)	OTU-030	FM208769	*GQ268530	FM208815	NA	A	MNHN B31440 / *NA	Alborn Sea / *North Sea	Schubart & Reuschel (2009) / *Lindley et al. (2010)
Necora puber (Linnaeus, 1767)	OTU-031	FM208771	*FJ755619	FM208813	**DQ079800	A, B	SMF 32749 / *NA / **BYU KAC2161	England, Hastings / *Spain / **NA	Schubart & Reuschel (2009) / *Sotelo et al. (2009) / **Porter et al. (2005)
Parathranites orientalis (Miers, 1886)	OTU-032	KJ132616	NA	KJ133173	NA		NTOUB00090	NA	Tsang et al. (2014)
Polybius henslowii Leach, 1820	OTU-033	FM208765	*JQ306041	FM208816	NA	A	SMF 32759 / *MB 89000200	Portugal / *England	Schubart & Reuschel (2009) / *da Silva et al. (2011)
Portunoidea: Carcinidae: Thiinae									
Thia scutellata (Fabricius, 1793)	OTU-034	FM208782	NA	FM208810	NA	A	SMF 32769	France, Bretagne	Schubart & Reuschel (2009)
Portunoidea: Geryonidae: Benthochasconinae									
Benthochascon hemingi Alcock & Anderson, 1899	OTU-011	FM208772	*HM750955	FM208826	NA	A	ZRC 2000.102	New Caledonia	Schubart & Reuschel (2009) / *Lai et al. (2011)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Portunoidea: Geryonidae: Geryoninae									
Chaceon granulatus (Sakai, 1978)	OTU-012	FM208775	*AB769383	FM208827	NA	A	SMF 32762 / *NA	Japan / *NA	Schubart & Reuschel (2009) / *Yanagimoto & Kobayashi (Unpublished)
Geryon longipes A. Milne-Edwards, 1882	OTU-013	FM208776	*JQ305902	FM208828	NA	A	SMF 32747 / *MB 89000638	Spain, Ibiza / *Malta	Schubart & Reuschel (2009) / *da Silva et al. (2011)
Raymanninus schmitti (Rathbun, 1931)	OTU-014	KT365560	NA	NA	KT365656	A, B	UF 9676	United States, Florida	This study
Portunoidea: Geryonidae: Ovalipinae									
Ovalipes iridescens (Miers, 1886)	OTU-015	FM208774	NA	FM208825	NA	A	ZRC 1995.855	Taiwan	Schubart & Reuschel (2009)
Ovalipes punctatus (De Haan, 1833)	OTU-016	KJ132597	*KF906404	KJ133154	NA		NTOUB00011 / *NA	NA / *China	Tsang et al. (2014) / *Zheng et al. (2015)
Ovalipes stephensoni Williams, 1976/ **O.floridanus* Hay & Shore, 1918	OTU-017	DQ388050	NA	NA	*KT365648	B	ULLZ 5678 / *UF 28577	United States, Florida	Mantelatto et al. (2009) / *This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Ovalipes trimaculatus (De Haan, 1833)	OTU-018	FM208773	*JN315648	FM208823	NA	A	MNHN B19785 / *NA	Campaign MD50 Jasus / *Chile	Schubart & Reuschel (2009) / *Haye et al., 2012
Portunoidea: Portunidae: Carupinae									
Atoportunus gustavi Ng & Takeda, 2003	OTU-035	KT365590	KT365692	NA	NA		UF 1266	Guam	This study
Carupa ohashii Takeda, 1993	OTU-036	FM208759	NA	FM208790	NA	A	SMF 32756	Okinawa Island	Schubart & Reuschel (2009)
Carupa tenuipes (var. A) Dana, 1852	OTU-037	FM208758	*KT365703	FM208789	NA	A	MNHN B31436 / *UF 16185	New Caledonia / *French Polynesia	Schubart & Reuschel (2009) / *This study
Carupa tenuipes (var. B) Dana, 1852	OTU-038	KT365533	KT365704	NA	NA	A	UF 15565	French Polynesia	This study
Catoptrus aff. *nitidus*	OTU-040	KT365534	KT365706	NA	NA	A	UF 18451	Tuamotu Islands	This study
Catoptrus nitidus A. Milne-Edwards, 1870 / **C.* cf. *nitidus*	OTU-039	FM208755	*KT365705	NA	NA	A	MNHN B31435 / *UF 1024	New Caledonia / *Guam	Schubart & Reuschel (2009) / *This study
Laleonectes nipponensis (Sakai, 1938)	OTU-052	KT365548	KT365727	*FM208792	NA	A	UF 7342 / *MNHN B31434	Guam / *French Polynesia	This study / *Schubart & Reuschel (2009)
Libystes edwardsii Alcock, 1899	OTU-041	FM208761	NA	NA	NA	A	MNHN B31437	New Caledonia	Schubart & Reuschel (2009)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Libystes nitidus A. Milne-Edwards, 1867	OTU-042	FM208762	*KT365728	NA	NA	A	MNHN B31438 / *UF 12587	New Caledonia / *Reunion Island	Schubart & Reuschel (2009) / *This study
Richerellus moosai Crosnier, 2003	OTU-043	FM208756	NA	FM208788	NA	A	MNHN B22838 (paratype)	New Caledonia	Schubart & Reuschel (2009)
Portunoidea: Portunidae: Lupocyclinae									
Lupocycloporus gracilimanus (Stimpson, 1858)	OTU-069	AM410523	*JX398092	*JX398124	*JX398076		NA / *ZMMU Ma3381	Vietnam, Nhatrang Bay	Leignel (unpublished) / *Spiridonov et al. (2014)
Lupocyclus philippinensis Semper, 1880	OTU-054	FJ152156	NA	*JX398119	*JX398077		NA / *ZMMU Ma3443	China / *Vietnam, Nhatrang Bay	Mantelatto et al. (2009) / *Spiridonov et al. (2014)
Lupocyclus quinquedentatus Rathbun, 1906	OTU-055	KT365603	KT365734	NA	KT365647	B	UF 10568	Line Islands, Kiritimati Atoll	This study
Lupocyclus rotundatus Adams & White, 1849	OTU-056	NA	NA	JX398110	JX398075	C	ZMMU Ma3441	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Portunoidea: Portunidae: Necronectinae									
Scylla olivacea (Herbst, 1796)	OTU-087	FJ827760	FJ827760	NA	NA	A	NA	NA	Sangthong (unpublished)
Scylla paramamosain Estampador, 1949	OTU-088	FJ827761	FJ827761	NA	NA	A	NA	NA	Sangthong (unpublished)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Scylla serrata (Forskal, 1775)	OTU-089	FJ827758	FJ827758	*FM208793	NA	A	NA / *MZUF 3657	NA / *Kenya, Lamu	Sangthong (unpublished) / *Schubart & Reuschel (2009)
Scylla tranquebarica (Fabricius, 1798)	OTU-090	FJ827759	FJ827759	NA	NA	A	NA	NA	Sangthong (unpublished)
Portunoidea: Portunidae: Podophthalminae									
Euphylax robustus A. Milne-Edwards, 1874	OTU-044	FJ152153	NA	NA	NA		CCDB 1122	Costa Rica, Gulf of Nicoya	Mantelatto et al. (2009)
Podophthalmus nacreus Alcock, 1899	OTU-045	NA	JX398093	NA	JX398078	C	ZMMU Ma3440	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Podophthalmus vigil (Fabricius, 1798)	OTU-046	KT365553	KT365735	*FM208787	NA	A	UF 18116 / *ZRC Y4821	French Polynesia, Moorea Island / *Malaysia, Pontian	This study / *Schubart & Reuschel (2009)
Portunoidea: Portunidae: Portuninae									
Arenaeus cribrarius (Lamarck, 1818)	OTU-047	FM208749	*JX123439	FM208799	NA	A	SMF 32753 / *CCDB 3182	United States, North Carolina / *Brasil, São Paulo	Schubart & Reuschel (2009) / *Zupolini (2012)
Arenaeus mexicanus (Gerstaecker, 1856)	OTU-048	JX123470	JX123446	NA	NA		MZUCR2430-4	Costa Rica	Zupolini (2012)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Callinectes marginatus (A. Milne-Edwards, 1861)	OTU-049	KT365527	KT365694	NA	NA	A	UF 11403	United States, Florida	This study
Callinectes ornatus Ordway, 1863	OTU-050	KT365528	NA	NA	KT365628	A, B	UF 19804	United States, Florida	This study
Callinectes sapidus Rathbun, 1896	OTU-051	AY363392	AY363392	*FM208798	**AY739194	A, B	NA / *ULLZ 3895 / **NA	United States, Mississippi / *United States, Louisiana / **NA	Place et al. (2009) / *Schubart & Reuschel (2009) / **Babbit & Patel (2005)
Lupella forceps (Fabricius, 1793)	OTU-053	FJ152155	NA	NA	NA		USNM 284565	R / V Oregon II, 1970	Mantelatto et al. (2009)
Portunus (Achelous) asper (A. Milne-Edwards, 1861)	OTU-057	FJ152158	NA	NA	NA		CCDB 1738	Mexico, Sinaloa	Mantelatto et al. (2009)
Portunus (Achelous) depressifrons (Stimpson, 1859)	OTU-058	DQ388064	*KT365738	NA	NA		ULLZ 4442 / *UF 26120	United States, Florida	Mantelatto et al. (2009) / *This study
Portunus (Achelous) floridanus Rathbun, 1930	OTU-059	DQ388058	NA	NA	NA		ULLZ 4695	Gulf of Mexico	Mantelatto et al. (2009)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Portunus (Achelous) gibbesii (Stimpson, 1859)	OTU-060	DQ388057	*KT365739	NA	**KT365650	B	ULLZ 4565 / *UF 1134 / **UF 19561	United States, Alabama, 2001 / * & ** United States, Florida	Mantelatto et al. (2009) / * & **This study
Portunus (Achelous) ordwayi (Stimpson, 1860)	OTU-061	FM208751	*KT365689	FM208794	NA	A	SMF 31988 / *UF 6426	Jamaica / *United States, Florida	Schubart & Reuschel (2009) / *This study
Portunus (Achelous) rufiremus Holthuis, 1959	OTU-062	DQ388063	NA	NA	NA		USNM 151568	French Guiana, Sinnamaryi	Mantelatto et al. (2009)
Portunus (Achelous) sebae (H. Milne Edwards, 1834)	OTU-063	DQ388067	NA	NA	NA		ULLZ 4527	United States, Florida	Mantelatto et al. (2009)
Portunus (Achelous) spinicarpus (Stimpson, 1871)	OTU-064	DQ388061	*KT365746	NA	NA		ULLZ 4618 / *UF 3969	United States, Florida	Mantelatto et al. (2009) / *This study
Portunus (Achelous) spinimanus Latreille, 1819	OTU-065	KT365558	*KT365690	NA	KT365654	A, B	UF 28417 / *UF 6692	United States, Florida	This study
Portunus (Achelous) tumidulus Stimpson, 1871	OTU-066	KT365589	KT365691	NA	NA		UF 32157	Saint Martin Island	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Portunus (Cycloachelous) granulatus (H. Milne Edwards,1834)	OTU-067	KT365605	KT365740	NA	KT365651	B	UF 4169	Guam	This study
Portunus (Cycloachelous) orbitosinus (Rathbun, 1911)	OTU-068	NA	JX398097	JX398115	JX398082	C	ZMMU Ma3378	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Portunus (Monomia) argentatus (A. Milne- Edwards, 1861)	OTU-070	NA	JX398096	JX398107	JX398081	C	ZMMU Ma3365	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Portunus (Monomia) gladiator Fabricius, 1798	OTU-071	NA	JX398095	JX398113	JX398080	C	ZMMU Ma3366	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Portunus (Monomia) petreus (Alcock, 1899)	OTU-072	KT365606	KT365743	NA	NA		UF 188	Guam	This study
Portunus (Monomia) pseudoargentatus Stephenson, 1961	OTU-073	NA	JX398094	JX398121	JX398079	C	ZMMU Ma3368	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Portunus (Portunus) anceps (Saussure, 1858)	OTU-074	KT365604	KT365736	NA	NA		UF 32492	Saint Martin Island	This study
Portunus (Portunus) hastatus (Linnaeus, 1767)	OTU-075	FM208780	NA	FM208796	NA		SMF 31989	Turkey, Beldibi	Schubart & Reuschel (2009)
Portunus (Portunus) inaequalis (Miers, 1881)	OTU-076	FM208752	NA	FM208795	NA	A	SMF 32754	Ghana, Cape Coast	Schubart & Reuschel (2009)

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Portunus (Portunus) pelagicus (Linnaeus, 1758)	OTU-077	FM208750	*JX398106	*JX398116	*JX398074	A	CSIRO uncatalogued / *NA	Australia / *Vietnam, Nhatrang	Schubart & Reuschel (2009) / *Spiridonov et al. (2014)
Portunus (Portunus) sanguinolentus hawaiiensis Stephenson, 1968	OTU-078	KT365557	KT365744	NA	KT365653	A, B	UF 8949	United States, Hawaii	This study
Portunus (Portunus) sayi (Gibbes, 1850)	OTU-079	KT365607	KT365745	NA	NA		UF 26156	United States, Florida	This study
Portunus (Portunus) trituberculatus (Miers, 1876)	OTU-080	AB093006	AB093006	*FM208829	NA	A	NA / *NA	Japan / *China	Yamauchi et al. (2003) / *Schubart & Reuschel (Unpublished)
Portunus (Portunus) ventralis (A. Milne-Edwards, 1879)	OTU-081	KT365559	KT365747	NA	KT365655	A, B	UF 32351	France, Saint Martin	This study
Portunus (Xiphonectes) arabicus (Nobili, 1905)	OTU-082	KT365554	KT365737	NA	KT365649	A, B	UF 7735	Oman	This study
Portunus (Xiphonectes) hastatoides Fabricius, 1798	OTU-083	NA	JX398098	NA	JX398083	C	ZMMU MA3392	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Portunus (Xiphonectes) aff. *longispinosus*	OTU-084	KT365555	KT365741	NA	KT365652	A, B	UF 10477	Line Islands, Kiritimati Atoll	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Portunus (Xiphonectes) longispinosus (Dana, 1852)	OTU-085	KT365556	KT365742	NA	NA	A	UF 187	Guam	This study
Portunus (Xiphonectes) tenuipes (De Haan, 1835)	OTU-086	NA	JX398099	NA	JX398087	C	NA	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Portunoidea: Portunidae: Thalamitinae									
Caphyra bedoti (Zehntner, 1894)	OTU-091	KT365591	KT365695	KT425019	NA		ZRC NERM026	Taiwan	This study
Caphyra cf. *fulva*	OTU-093	KT365529	KT365696	KT424990	KT365629	A, B	UF 11748	Indo Pacific, Unknown	This study
Caphyra loevis (A. Milne-Edwards, 1869)	OTU-092	KT365592	KT365697	KT425009	NA		ZRC NERM025	Taiwan	This study
Caphyra sp. A	OTU-094	KT365531	KT365699	NA	NA	A	UF 5061-A	Mauritius	This study
Caphyra sp. B	OTU-095	NA	KT365700	KT425046	KT365631	B, C	UF 14454	Madagascar	This study
Caphyra tridens Richters, 1880	OTU-096	KT365532	KT365701	KT425003	KT365632	A, B	UF 15907	French Polynesia	This study
Caphyra yookadai Sakai, 1933	OTU-097	KT365593	KT365702	KT424993	NA		ZRC NERM023	Taiwan	This study
Charybdis acuta (A. Milne-Edwards, 1869)	OTU-098	KT365594	NA	KT425049	NA		UF 13466	Taiwan	This study
Charybdis anisodon (De Haan, 1850)	OTU-099	KT365536	NA	NA	NA	A	UF 11429	Philippines, Bohol Island	This study
Charybdis annulata (Fabricius, 1798)	OTU-100	KT365595	KT365708	KT425027	KT365634	B	UF 22076	Australia, Ningaloo Reef	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Charybdis bimaculata (Miers, 1886)	OTU-101	KT365596	KT365709	KT425036	*JX398089		ZRC NERM019 / ZMMU Ma3396	Vanuatu, Aurora Island / *Vietnam, Nhatrang Bay	This study / *Spiridonov et al. (2014)
Charybdis callianassa (Herbst, 1789)	OTU-102	KT365537	KT365710	KT425035	NA	A	ZRC 1993.378-384	Pakistan, Ibrahim	This study
Charybdis feriata (Linnaeus, 1758)	OTU-103	KT365538	KT365712	KT425051	KT365636	A, B	UF 3739	Taiwan	This study
Charybdis hellerii (A. Milne-Edwards, 1867)	OTU-104	KT365540	KT365715	KT424999	KT365638	A, B	UF 11430	Philippines, Bohol Island	This study
Charybdis hongkongensis Shen, 1934	OTU-105	NA	JX398100	JX398112	JX398088	C	ZMMU Ma3363	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Charybdis japonica (A. Milne-Edwards, 1861)	OTU-106	FJ460517	*KT365716	*KT425042	NA	A	NA / *ZRC 2008.0567	China	Liu & Cui (2010) / *This study
Charybdis longicollis Leene, 1938	OTU-107	KT365541	KT365717	KT425054	NA	A	UF 3179	Israel	This study
Charybdis lucifera (Fabricius, 1798)	OTU-108	KT365542	*KT365718	*KT425034	*KT365639	A, B	UF 7667 / *UF 7684	Oman	This study
Charybdis natator (Herbst, 1794)	OTU-109	KT365543	KT365719	*KT424998	NA	A	UF 3707 / *UF 21403	Taiwan / *Australia, Ningaloo Reef	This study
Charybdis granulata (De Haan, 1833)	OTU-110	NA	JX398102	JX398118	JX398090	C	NA	Vietnam, Nhatrang Bay	Spiridonov et al. (2014)
Charybdis orientalis Dana, 1852	OTU-111	KT588234	KT588225	KT781074	NA		USNM 112062	Taiwan	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Charybdis sagamiensis Parisi, 1916	OTU-112	KT365598	KT365721	NA	KT365641	B	UF 29479	Taiwan	This study
Charybdis sp.	OTU-113	KT365599	KT365722	KT425056	NA		UF 25655	Australia, Heron Island	This study
Charybdis variegata (Fabricius, 1798)	OTU-114	KT365600	KT365723	KT425043	NA		ZRC 2012.1115	India	This study
Cronius edwardsii (Lockington, 1877)	OTU-115	FJ152147	*KT588227	NA	NA	A	ULLZ 8673 / *USNM 112311	Panama, Pacific coast, 2007 / *Ecudaor, Galapagos Islands	Mantelatto et al. (2009) / *This study
Cronius ruber (Lamarck, 1818)	OTU-116	KT365546	*KT365725	KT425008	KT365642	A, B	UF 26364 / *UF 25995	United States, Florida	This study
Gonioinfradens paucidentatus (A. Milne-Edwards, 1861)	OTU-117	KT365547	KT365726	*KT588216	NA	A	UF 5109 / *UF 30184	Palau / *Marquesas Islands	This study
Goniosupradens acutifrons (De Man, 1879)	OTU-118	KT365535	*KT365707	*KT425033	*KT365633	A, B	UF 7114 / *UF 17047	Okinawa Island / *Australia, Lizard Island	This study
Goniosupradens erythrodactylus (Lamarck, 1818)	OTU-119	KT365597	KT365711	NA	KT365635	B	UF 1398	French Polynesia, Tuamotu Islands	This study
Goniosupradens hawaiensis (Edmondson, 1954) comb. nov.	OTU-120	KT365539	KT365714	KT425023	KT365637	A, B	UF 25871	Australia, Heron Island	This study
Goniosupradens obtusifrons (Leene, 1937)	OTU-121	KT365544	KT365720	KT425007	KT365640	A, B	UF 16599	Australia, Lizard Island	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Lissocarcinus arkati Kemp, 1923	OTU-122	KT365549	KT365729	KT425045	KT365643	A, B	UF 36296	Vanuatu, Espiritu Santo	This study
Lissocarcinus holothuricola (Streets, 1877)	OTU-123	KT365551	KT365731	KT425041	KT365645	A, B	UF 30203	Marquesas Islands	This study
Lissocarcinus laevis Miers, 1886	OTU-124	KT365550	KT365730	*KT425020	*KT365644	A, B	UF 204 / *UF 39136	Guam / *New Caledonia	This study
Lissocarcinus orbicularis Dana, 1852	OTU-125	KT365552	KT365732	*KT425032	NA	A	UF 15741 / *UF 15429	French Polynesia, Moorea Island	This study
Lissocarcinus polybiodes Adams & White, 1849	OTU-126	KT365602	KT365733	KT424994	KT365646	B	UF 35245	Japan, Okinawa	This study
Thalamita admete (Herbst, 1803)	OTU-127	KT365562	*KT365749	*KT425014	*KT365658	A, B	UF 7688 / *UF 16971	Oman / Australia, Lizard Island	This study
Thalamita aff. *admete*	OTU-128	KT365561	KT365748	KT424995	KT365657	A, B	UF 17745	Australia, Queensland	This study
Thalamita auauensis Rathbun, 1906	OTU-129	KT365563	KT365750	KT425022	NA	A	UF 12320	Hawaii, French Frigate Shoals	This study
Thalamita bevisi (Stebbing, 1921)	OTU-130	KT365564	KT365751	KT425048	KT365659	A, B	UF 197	Guam	This study
Thalamita bouvieri Nobili, 1906	OTU-131	KT365565	KT365752	*KT425016	KT365660	A, B	UF 24801 / *UF 17562	Australia, Heron Island / *Australia, Lizard Island	This study
Thalamita chaptalii (Audouin & Savigny, 1825)	OTU-132	KT365568	KT365758	*KT425047	*KT365663	A, B	UF 13103 / *UF 206	France, Reunion Island / *Guam	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Thalamita coeruleipes Hombron & Jacquinot, 1846	OTU-133	KT365569	KT365759	KT425057	KT365664	A, B	UF 3232	American Samoa	This study
Thalamita crenata Rüppell, 1830	OTU-134	KT365572	KT365763	*KT424991	**JX398085/ *KT365667	A, B	UF 8950 / *UF 17752 / **ZMMU Ma3343	Hawaii / *Australia, Queensland / **Vietnam	This study / **Spiridonov et al. (2014)
Thalamita danae Stimpson, 1858	OTU-135	KT365573	*KT365764	*KT425031	KT365668	A, B	UF 22114 / *UF 25992	Australia, Ningaloo Reef / *Australia, Heron Island	This study
Thalamita foresti Crosnier, 1962	OTU-136	KT365574	KT365765	KT425040	NA	A	UF 2222	Marshall Islands, Majuro Atoll	This study
Thalamita cf. *gatavakensis* sp. B	OTU-137	KT365575	*KT365766	KT424992	KT365669	A, B	UF 17469 / *UF 17486	Australia, Lizard Island	This study
Thalamita cf. *gatavakensis* sp. A	OTU-138	KT365576	KT365767	KT424997	KT365670	A, B	UF 16649	Australia, Lizard Island	This study
Thalamonyx gracilipes A. Milne-Edwards, 1873	OTU-139	KT365611	KT365768	KT425000	NA		USNM 274300	New Caledonia	This study
Thalamita granosimana Borradaile, 1902	OTU-140	KT365577	KT365769	KT425005	KT365671	A, B	UF 24790	Australia, Heron Island	This study
Thalamita integra Dana, 1852	OTU-141	KT365578	*KT365770	*KT425028	*KT365672	A, B	UF 587 / *UF 22085	Saipan / *Australia, Ningaloo Reef	This study
Thalamita kagosimensis Sakai, 1939	OTU-142	KT365612	KT365771	KT425011	KT365673	B	ZRC NERMS063	Vanuatu, Espiritu Santo	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Thalamita philippinensis Stephenson & Rees, 1967	OTU-143	KT365579	KT365772	KT425006	KT365674	A, B	UF 24920	Australia, Heron Island	This study
Thalamita aff. kukenthali	OTU-144	KT365608	KT365753	KT425052	NA		UF 33634	French Polynesia, Moorea Island	This study
Thalamita malaccensis Gordon, 1938	OTU-145	KT365614	KT365774	KT425010	NA		ZRC NERM040	Vanuatu, Aurora Island	This study
Thalamita mitsiensis Crosnier, 1962	OTU-146	KT365580	KT365775	*KT425053	KT365675	A, B	UF 21937 / *UF 190	Australia, Ningaloo Reef / *Guam	This study
Thalamita oculea Alcock, 1899	OTU-147	KT365616	KT365777	KT425044	NA		ZRC NERM056	Philippines, Panglao Island	This study
Thalamita aff. *oculea*	OTU-148	KT365609	KT365755	KT425055	NA		UF 5051	Palau	This study
Thalamita parvidens (Rathbun, 1907)	OTU-149	KT365567	KT365757	KT425037	KT365662	A, B	UF 17595	Australia, Lizard Island	This study
Thalamita picta Stimpson, 1858	OTU-150	KT365581	KT365778	KT425013	KT365677	A, B	UF 24881	Australia, Heron Island	This study
Thalamita gloriensis Crosnier, 1962	OTU-151	KT365582	KT365779	KT425038	KT365678	A, B	UF 25902	Australia, Heron Island	This study
Thalamita prymna (Herbst, 1803)	OTU-152	KT365583	KT365780	KT425025	*JX398084	A	UF 14613 / *ZMMU Ma3346	Madagascar / *Vietnam, Nhatrang Bay	This study / *Spiridonov et al. (2014)
Thalamita pseudoculea Crosnier, 1984	OTU-153	KT365610	KT365754	KT425050	NA		UF 13877	Madagascar	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Thalamita pseudopelsarti Crosnier, 2002	OTU-154	KT365584	KT365781	KT425039	KT365679	A, B	UF 16218	French Polynesia, Moorea Island	This study
Thalamita quadrilobata Miers, 1884	OTU-155	KT365585	KT365782	*KT425015	*KT365680	A, B	UF 14254 / *UF 14608	Madagascar	This study
Thalamita rubridens Apel & Spiridonov, 1998	OTU-156	KT365586	KT365783	KT425060	KT365681	A, B	UF 7700	Oman	This study
Thalamita aff. *rubridens*	OTU-157	KT365566	KT365756	KT425021	KT365661	A, B	UF 25803	Australia, Heron Island	This study
Thalamita savignyi A. Milne-Edwards, 1861	OTU-158	KT365618	KT365784	KT425061	KT365682	B	UF 7689	Oman	This study
Thalamita seurati Nobili, 1906	OTU-159	KT365587	KT365785	KT425004	KT365683	A, B	UF 12832	Reunion Island	This study
Thalamita sima H. Milne Edwards, 1834	OTU-160	KT365619	KT365786	*KT588217	**JX398086		UF 35869 / *UF 36191 / **ZMMU Ma3373	Australia, Darwin / *Singapore / **Vietnam	This study / **Spiridonov et al. (2014)
Thalamita spinicarpa Wee & Ng, 1995	OTU-161	KT365620	KT365787	KT425012	KT365684	B	UF 36225	Singapore	This study
Thalamita spinifera Borradaile, 1902	OTU-162	KT365621	KT365788	KT425001	NA		UF 33379	French Polynesia, Moorea Island	This study
Thalamita spinimana Dana, 1852	OTU-163	KT365622	KT365789	NA	KT365685	B	UF 36209	Singapore	This study
Thalamita stephensoni Crosnier, 1962	OTU-164	KT365623	KT365790	KT425059	NA		UF 17070	Australia, Lizard Island	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Thalamitoides quadridens A. Milne-Edwards, 1869	OTU-165	KT365588	*KT365792	KT425017	NA	A	UF 18495 / *UF 15637	French Polynesia, Tuamotu Islands / *Moorea Island	This study
Thalamitoides spinigera Nobili, 1905	OTU-166	KT365625	KT365793	NA	KT365687	B	UF 32881	Djibouti	This study
Thalamitoides tridens A. Milne-Edwards, 1869	OTU-167	KT365626	KT365794	NA	KT365688	B	UF 18231	Australia, Lizard Island	This study
Trierarchus cf. *cooperi* sp. A comb. nov.	OTU-168	KT365570	KT365760	KT424996	KT365665	A, B	UF 16152	French Polynesia, Moorea Island	This study
Trierarchus cf. *cooperi* sp. B comb. nov.	OTU-169	KT365571	KT365761	KT425029	KT365666	A, B	UF 16949	Australia, Lizard Island	This study
Trierarchus rotundifrons (A. Milne-Edwards, 1869) comb. nov.	OTU-170	KT365530	KT365698	*KT424989	*KT365630	A, B	UF 4079 / *UF 4057	Guam	This study
Trierarchus squamosus (Stephenson & Hudson, 1957) comb. nov.	OTU-174	KU737571	NA	NA	NA		USNM 102963	Bikini Atoll	This study
Trierarchus woodmasoni (Alcock, 1899) comb. nov.	OTU-171	KT365624	KT365791	KT425026	KT365686	B	UF 4114	Guam	This study
Zygita longifrons (A. Milne-Edwards, 1869) comb. nov.	OTU-172	KT365613	KT365773	KT425002	NA		UF 7343	Guam	This study

Table 2-1. Continued.

Taxon	OTU ID	16S rRNA GenBank number	CO1 GenBank number	H3 GenBank number	28S rRNA GenBank number	Notes	Voucher ID	Locality (or campaign)	Source reference or researcher
Zygita murinae (Zarenkov, 1971) comb. nov.	OTU-173	KT365615	KT365776	KT425018	KT365676	B	UF 36525	Saudi Arabia, Farasan Banks	This study

Table 2-2. Primer pairs, annealing temperatures and resulting fragment sizes for PCR reactions.

Primer Pairs - Forward / Reverse	5' - 3' Forward primer sequence	5' - 3' Reverse primer sequence	T_a	Approximate Amplicon Size	References
CO1					
dgLCO1490 / dgHCO2198	GGTCAACAAATCATAAAGAYATYGG	TAAACTTCAGGGTGACCAAARAAYCA	50ºC & 45ºC	650 bps	Geller et al. (2013)
jgLCO1490 / jgHCO2198	TITCIACIAAYCAYAARGAYATTGG	TAIACYTCIGGRTGICCRAARAAYCA	50ºC & 45ºC	650 bps	Meyer (2003)
16S rRNA + tRNA-Leu + NADH1					
NDH5 / 16L2	GCYAAYCTWACTTCATAWGAAAT	TGCCTGTTTATCAAAAACAT	48ºC & 44ºC	1.2 kb	Schubart et al. (2002)
16S rRNA					
16H11 / 16L2	AGATAGAAACCRACCTGG	see above	48ºC & 44ºC	580 bps	Schubart (2009)
crust16sF1 / crust16sR2	CCGGTYTGAACTCAAATCATGTAAA	TTGCCTGTTTATCAAAAACATGTYTRTT	50ºC & 45ºC	515 bps	Lai et al. (2009)
28S (D1-D2 region)					
LSUfw1brach / LSUrev1brach	AGCGGAGGAAAAGAAACYA	TACTAGATGGTTCGATTAGTC	50ºC & 45ºC	1.3 kbs	This study*
LSUfw2brach / LSUrev2brach	ACAAGTACCGTGAGGGAAAGTTG	ACAATCGATTTGCACGTCAG	55ºC & 50ºC	890 bps	This study*
F635 / LSUrev2brach	CCGTCTTGAAACACGGACC	see above	55ºC & 50ºC	600 bps	Medina et al. (2001)
H3					
H3af / H3ar	TGGCTCGTACCAAGCAGACVGC	TATCCTTRGGCATRATRGTGAC	50ºC & 47ºC	327 bps	Colgan et al. (1998)

*modified from Sonnenberg et al. (2007). T_a=Annealing temperatures used here in a "step-down" PCR approach.

Table 2-3. Composition of eight molecular datasets constructed for phylogenetic analyses.

Dataset name	Taxon sampling	Dataset Composition	Alignment length (bps)	Parsimony Informative Sites (bps)
16S-only	163 taxa	16S rRNA	1105	521
CO1-only	148 taxa	CO1	657	260
28S-only	66 taxa	28S rRNA D1-D2 region (>500 bps)	1224	184
H3-only	123 taxa	H3	327	106
174 taxa concatenated	174 taxa	16S rRNA - 163 taxa / CO1 - 148 taxa / 28S rRNA - 85 taxa / H3 - 123 taxa	3313	1080
163 taxa concatenated	163 taxa	16S rRNA - 163 taxa / CO1 - 138 taxa / 28S rRNA - 74 taxa / H3 - 115 taxa	3313	1074
138 taxa concatenated	138 taxa	16S rRNA - 138 taxa / CO1 - 138 taxa / 28S rRNA - 70 taxa / H3 - 103 taxa	3313	1039
Brusinia-16S	309 taxa	16S rRNA - 163 taxa (as above) + *Brusinia profunda* + 145 taxa (Tsang et al., 2014)	447	237

Table 2-4. Best scoring partition schemes for three concatenated molecular datasets.

Marker	Marker Subset	Alignment positions	174 taxa concatenated dataset				163 taxa concatenated dataset				138 taxa concatenated dataset			
			Model for ML Runs	ML Partition ID	Model for BI Runs	BI Partition ID	Model for ML Runs	ML Partition ID	Model for BI Runs	BI Partition ID	Model for ML Runs	ML Partition ID	Model for BI Runs	BI Partition ID
16S rRNA	16S rRNA	1-583	TVM+I+G	1	GTR+I+G	1	TVM+I+G	1	GTR+I+G	1	TVM+I+G	1	GTR+I+G	1
	tRNA-LEU	584-653	TVM+I+G	1	GTR+I+G	1	TVM+I+G	1	GTR+I+G	1	TVM+I+G	1	GTR+I+G	1
	ND1	654-1105	GTR+I+G	2	GTR+I+G	2	GTR+I+G	2	GTR+I+G	2	TrN+I+G	2	GTR+I+G	2
CO1	Codon Pos. 1	1106-1762\3	SYM+I+G	3	SYM+I+G	3	SYM+I+G	3	SYM+I+G	3	SYM+I+G	3	SYM+I+G	3
	Codon Pos. 2	1107-1762\3	F81+I+G	4	F81+I+G	4	F81+I+G	4	F81+I+G	4	F81+I+G	4	F81+I+G	4
	Codon Pos. 3	1108-1762\3	GTR+I+G	5	GTR+I+G	5	GTR+I+G	5	GTR+I+G	5	GTR+I+G	5	GTR+I+G	5
28S rRNA,	D1 & D2 region	1763 - 2986	GTR+I+G	6	GTR+I+G	6	GTR+I+G	6	GTR+I+G	6	GTR+I+G	6	GTR+I+G	6
H3	Codon Pos. 1	2988 - 3313\3	SYM+I+G	3	SYM+I+G	3	TrNef+I	8	SYM+I+G	3	TrNef+I	8	SYM+I+G	3
	Codon Pos. 2	2989 - 3313\3	F81+I+G	4	F81+I+G	4	TrNef+I	8	JC+I	8	TrNef+I	8	JC+I	8
	Codon Pos. 3	2987 - 3313\3	GTR+I+G	7	GTR+I+G	7	GTR+G	7	GTR+G	7	GTR+G	7	GTR+G	7

Table 2-5. Best scoring partition schemes for four single marker molecular datasets.

Marker	Taxa Count	Marker Subset	Alignment positions	Model for ML Runs	ML Partition ID
16S rRNA	163	16S rRNA	1-583	TVM+I+G	1
		tRNA-LEU	584-653	TVM+I+G	1
		ND1	654-1105	TrN+I+G	2
CO1	148	Codon Pos. 1	1-657\3	SYM+I+G	1
		Codon Pos. 2	2-657\3	F81+I+G	2
		Codon Pos. 3	3-657\3	GTR+G	3
28S rRNA	66	D1 & D2 region	1-1224	GTR+I+G	1
H3	123	Codon Pos. 1	2-327\3	TrN+I	2
		Codon Pos. 2	3-327\3	JC+I	3
		Codon Pos. 3	1-327\3	GTR+G	1

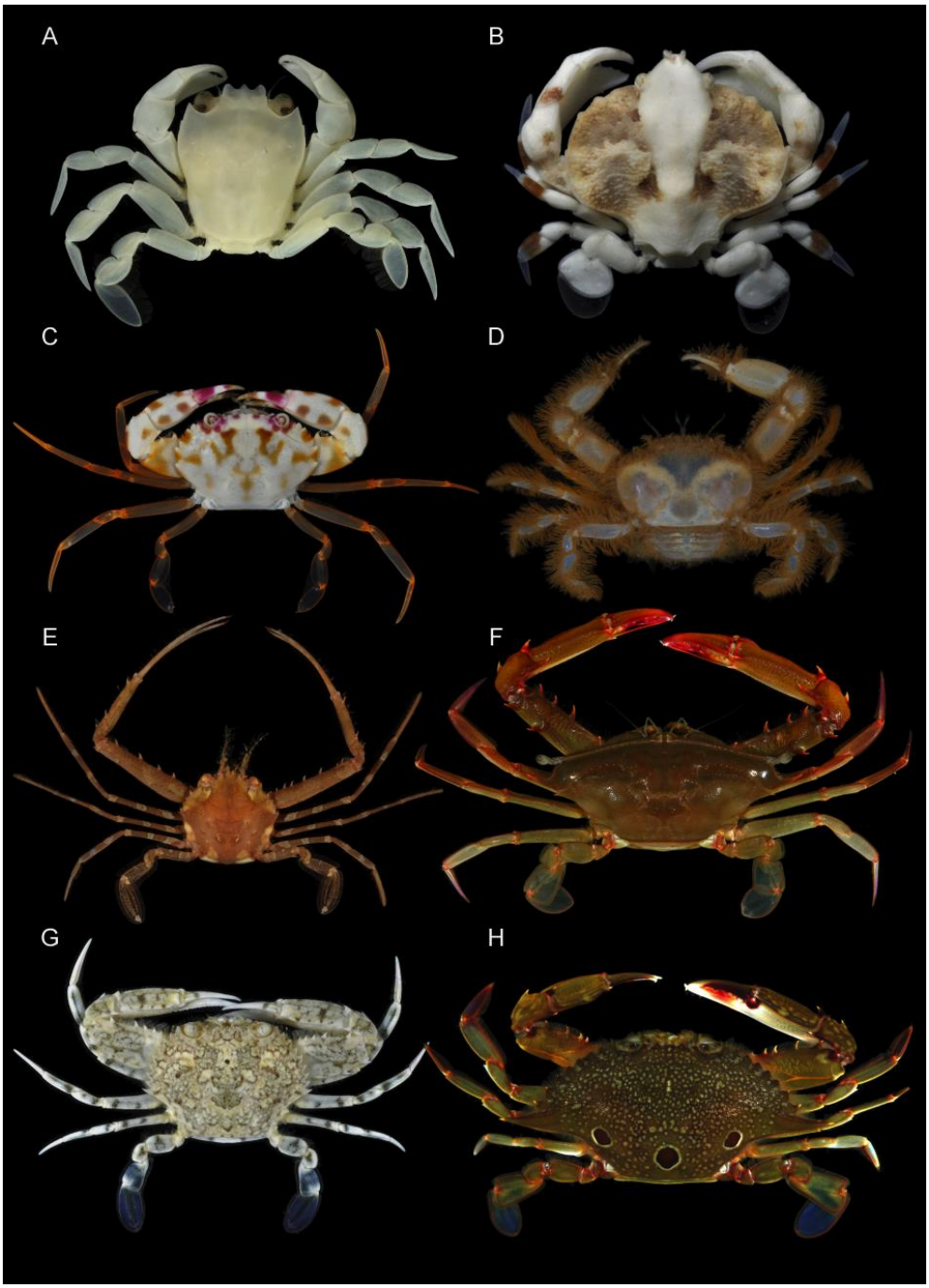

Figure 2-1. Representatives of various Portunoidea clades included in this study. A) *Brusinia profunda* (USNM 277519, preserved color), B) *Coelocarcinus foliatus* (UF 40176), C) *Carupa tenuipes* (UF 39918), D) *Libystes* (UF 23926), E) *Lupocyclus* cf. *philippinensis* (UF dPHIL_03759a), F) *Podophthalmus vigil* (UF 24543), G) *Portunus (Cycloachelous) granulatus* (UF 40021), H) *Portunus (Portunus) sanguinolentus* (UF 24538).

Figure 2-2. Representative non-symbiotic species from Thalamitinae. A) *Cronius ruber* (UF 35672), B) *Thalamitoides spinigera* (UF 36697), C) *Gonioinfradens paucidentatus* (UF 37141), D) *Goniosupradens acutifrons* (UF 7114), E) *Charybdis orientalis* (UF dPHIL_04136a), F) *Thalamonyx gracilipes* (UF dPHIL_05213a), G) *Thalamita admete* (UF 40031), H) *Thalamita chaptalii* (UF 39917), I) *Thalamita coeruleipes* (UF), J) *Thalamita philippinensis* (UF 40078).

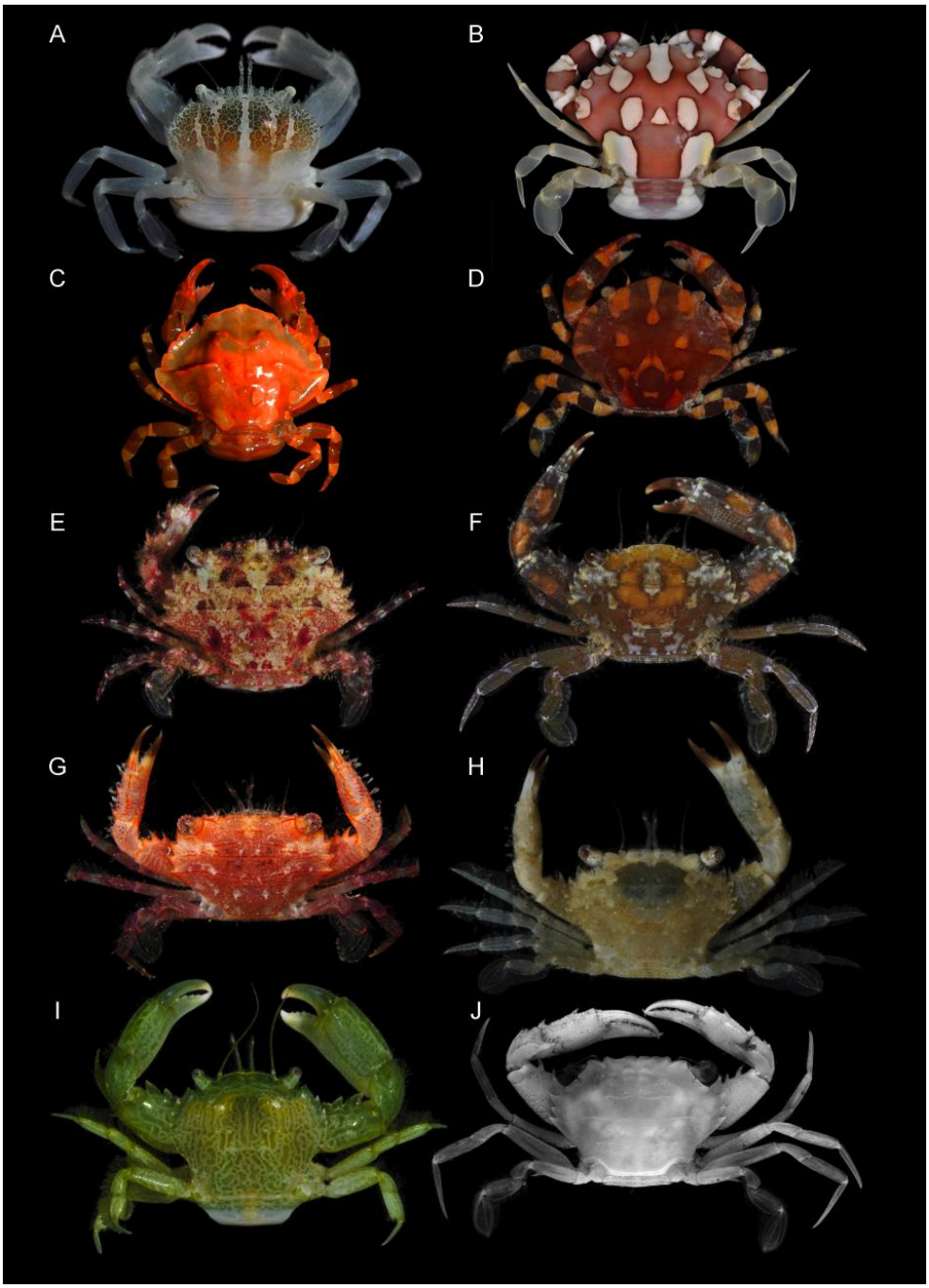

Figure 2-3. Representative symbiotic species from Thalamitinae. A) *Caphyra loevis* (UF 39060); B) *Lissocarcinus* cf. *laevis* (UF 39136); C) *Lissocarcinus holothuricola* (UF 30182); D) *Lissocarcinus orbicularis* (UF 23972); E) *Zygita murinae*, comb. nov. (UF 36721); F) *Trierarchus woodmasoni*, comb. nov. (UF 40079); G) *Trierarchus* cf. *cooperi* sp. A, comb. nov. (UF 16023); H) *Trierarchus* cf. *cooperi* sp. B, comb. nov. (UF 40100); I) *Trierarchus rotundifrons,* comb. nov. (UF 40067); J) *Trierarchus squamosus*, comb. nov. (USNM 102963, preserved specimen, grayscale, left frontal margin damaged).

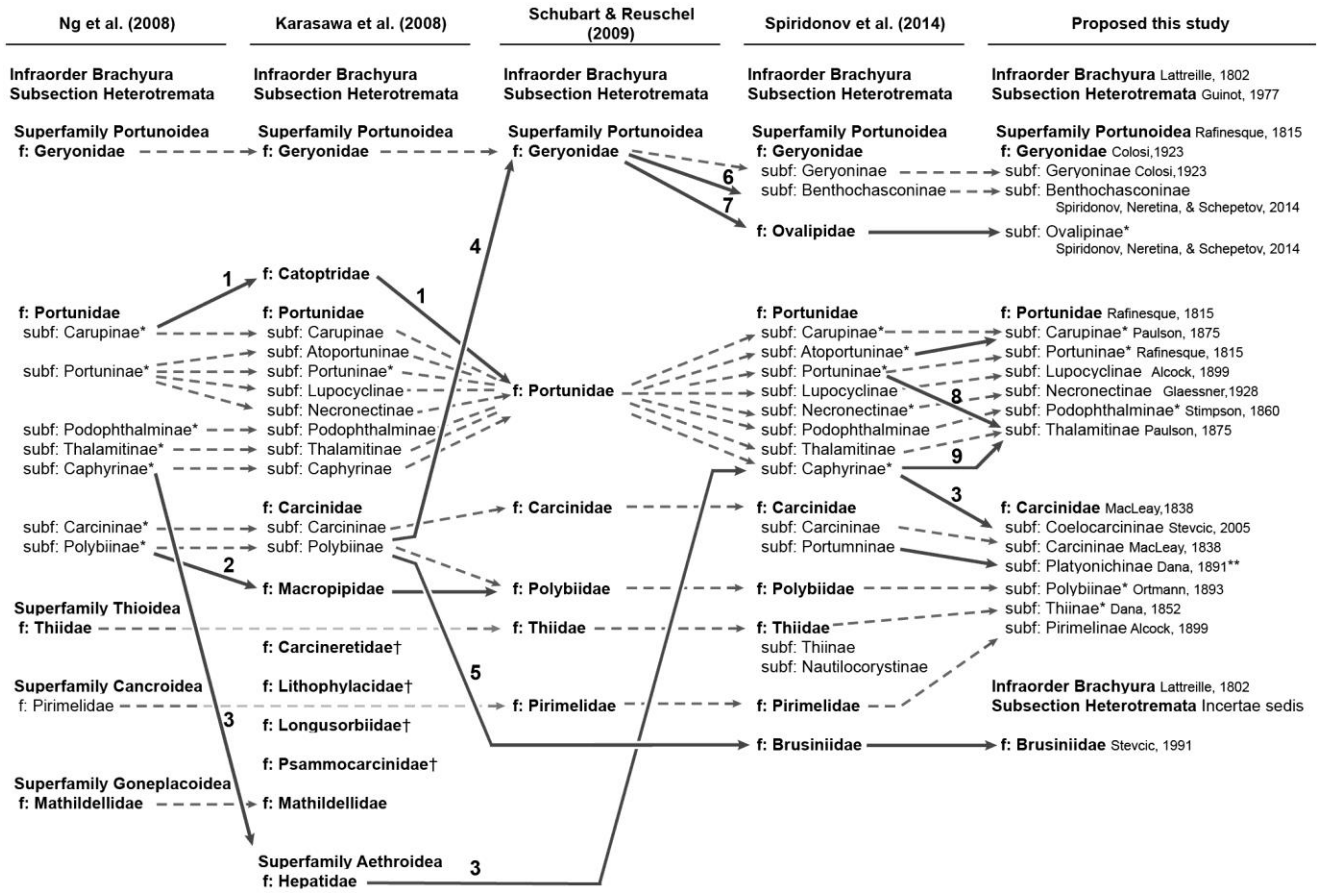

Figure 2-4. Summary of major recent changes to the classification of Portunoidea and a new proposed scheme. Arrows trace recognition of taxa between studies. Solid arrows highlight notable changes with numbers indicating the movement of specific genera: 1=*Catoptrus* and *Libystes*; 2=*Bathynectes*, *Macropipus*, and *Parathranites*; 3=*Coelocarcinus*; 4=Benthochchascon and *Ovalipes*; 5=*Brusinia* ; 6=*Benthochchascon*; 7=*Ovalipes*; 8=*Cronius*; 9=*Caphyra* and *Lissocarcinus*. *corresponding study suggests this subfamily needs reassessment given morphology, phylogenetic results or lack there of; **precedence noted by Davie at al. (2015b); † extinct clade. Figure modeled after Spiridonov et al. (2014, p. 419, Figure 8).

Figure 2-5. ML phylograms of Portunoidea based on analyses of single marker datasets of mitochondrial 16S rRNA and CO1. Support values appear above each relevant node and are based on 500 bootstrap replicate ML searches. A) ML phylogram of 163 portunoid taxa based on a 1105 bp alignment of partial 16S rRNA. B) ML phylogram of 148 portunoid taxa based on a 657 bp alignment of partial CO1.

Figure 2-6. ML phylograms of Portunoidea based on analyses of single marker datasets of nuclear 28S rRNA and H3. Support values appear above each relevant node and are based on 500 bootstrap replicate ML searches. A) ML phylogram of 66 portunoid taxa based on a 1224 bp alignment of partial 28S rRNA, B) ML phylogram of 123 portunoid taxa based on a 327 bp alignment of partial H3 sequence data.

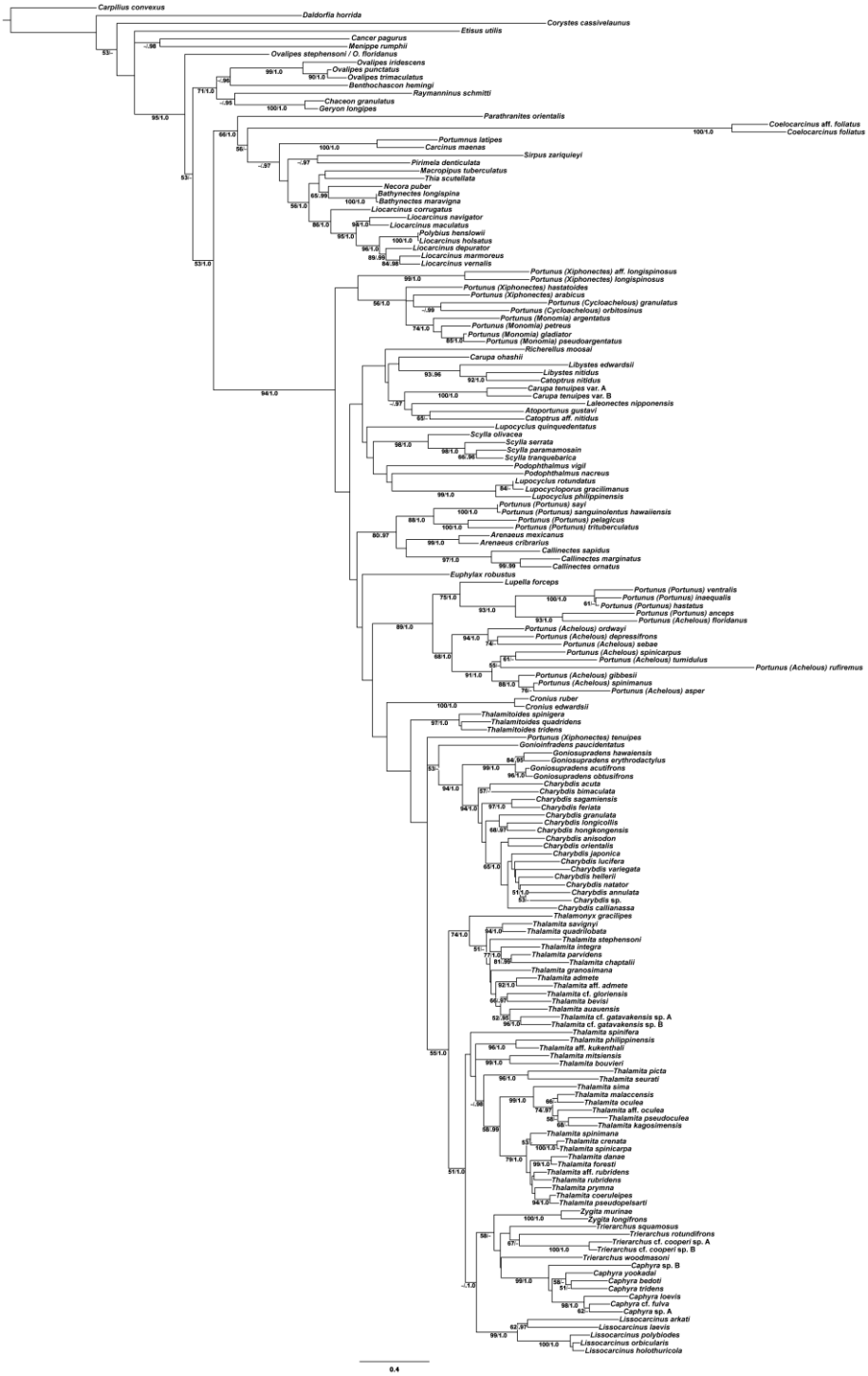

Figure 2-7. ML phylogram of Portunoidea based on analyses of 174 OTUs and a 3313 bp alignment of partial 16S rRNA, CO1, 28S rRNA, and H3 sequence data. Support values appear below each relevant node. Only significant values are reported with ML boostrap support appearing first (≥50%, based on 500 replicate searches), followed by BI posterior probabilities (≥0.95).

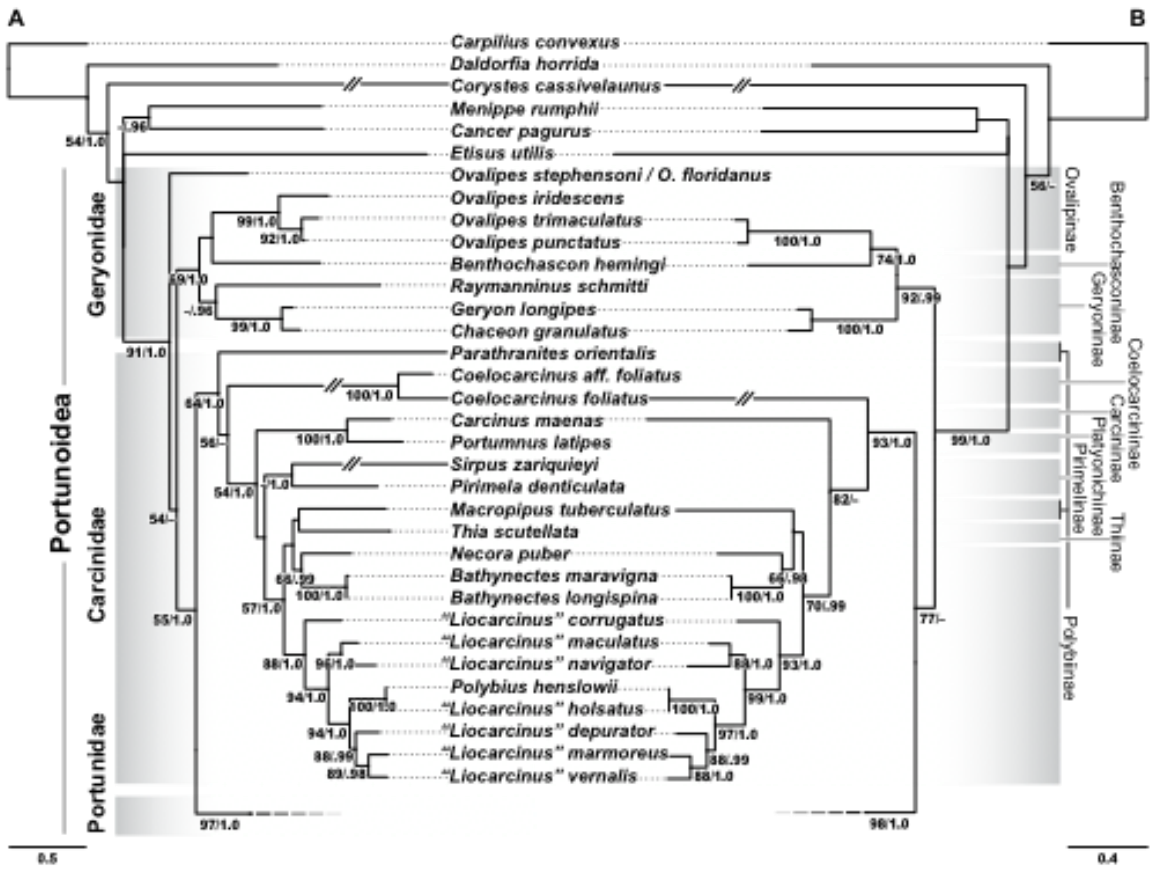

Figure 2-8. ML phylograms of Portunoidea based on analyses of 163 and 138 OTUs and a 3313 bp alignment of 16S rRNA, CO1, 28S rRNA, and H3 sequence data. Support values appear below each relevant node. Only significant values are reported with ML boostrap support appearing first (≥50%, based on 500 replicate searches), followed by BI posterior probabilities (≥0.95). A) ML phylogram based on analyses of 163 OTUs, each with at least 16S rRNA data, B) ML phylogram based on analyses of 138 OTUs, each with at least 16S rRNA and CO1 data. *Denotes nodes that topologically conflict with the corresponding BI majority consensus tree (see text and Figure 2-9B).

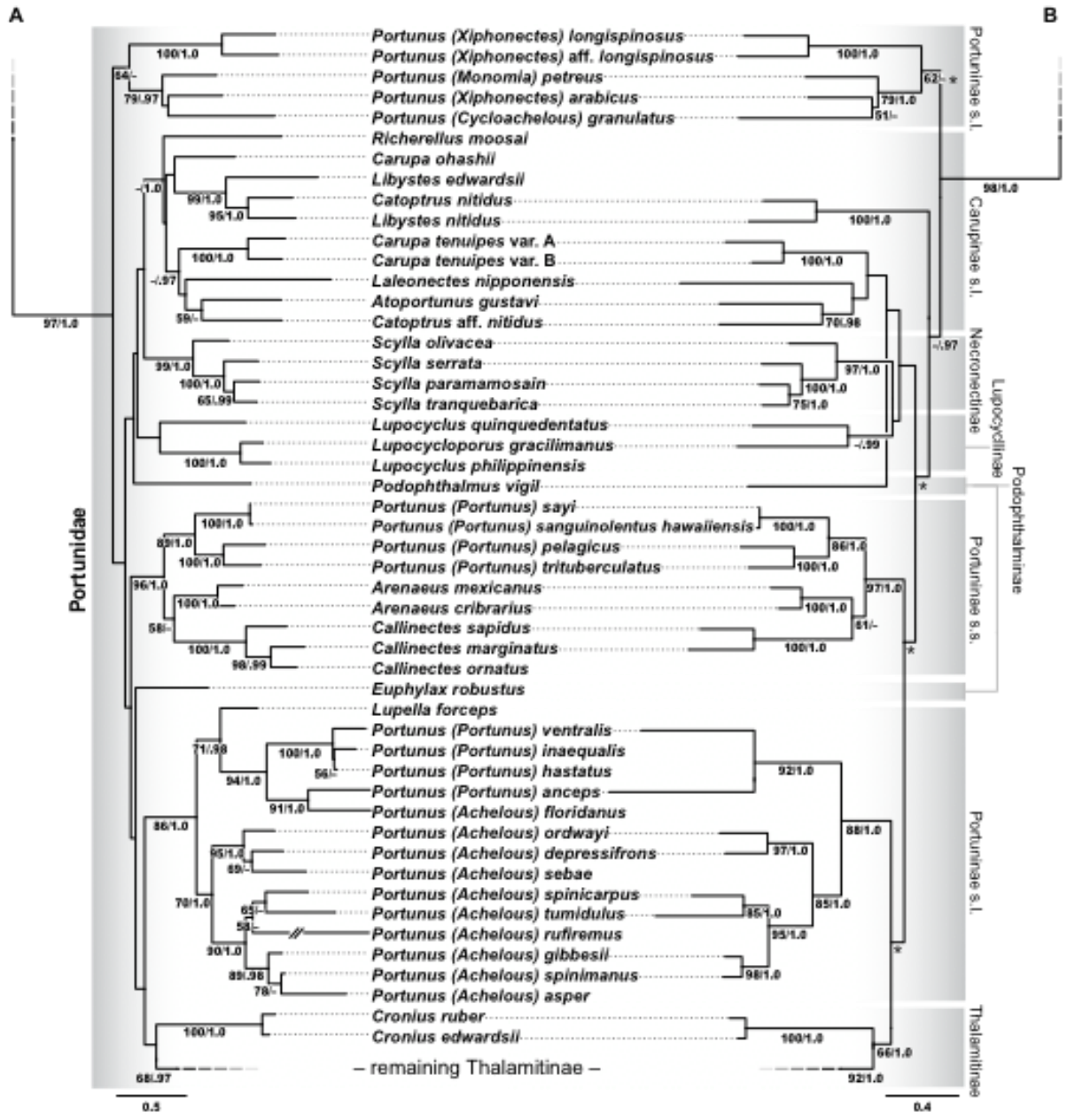

Figure 2-8. Continued.

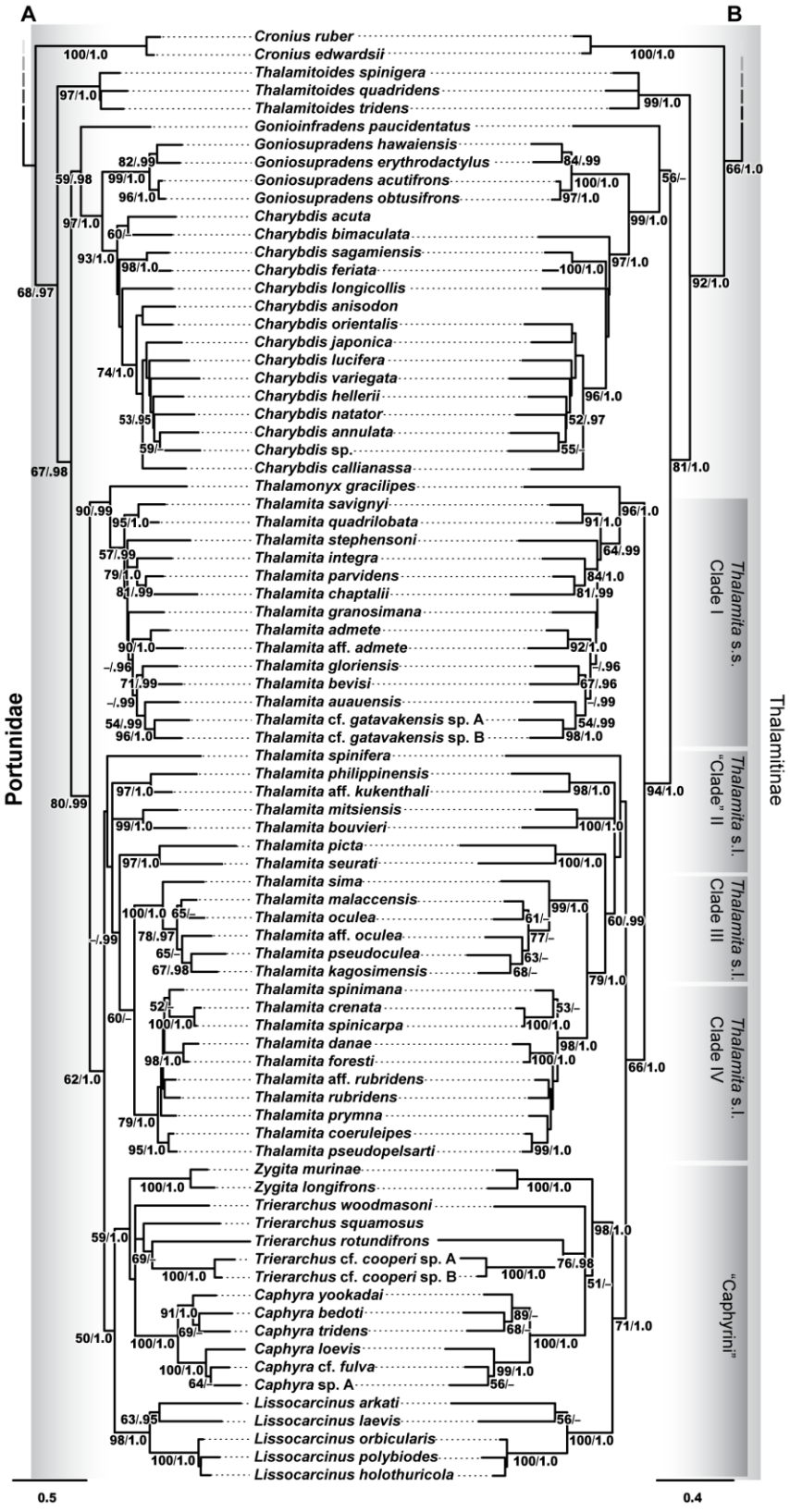

Figure 2-8. Continued.

Figure 2-9. Subsections of ML and BI topologies for Portunoidea based on analyses of 174 and 138 OTUs and a 3313 bp alignment of 16S rRNA, CO1, 28S rRNA, and H3 sequence data. A) A subsection of the 174 OTU ML phylogram representing the *Portunus* subgenera *Cycloachelous, Monommia, and Xiphonectes.* Support values appear below each relevant node. Only significant values are reported with ML boostrap support appearing first (≥50%, based on 500 replicate searches), followed by BI posterior probabilities (≥0.95). B) A subsection of the 138 OTU BI majority consensus tree conflicting topologically with the ML phylogram generated from the same concatenated dataset (see text and Figure 2-8B). BI posterior probabilities (≥0.95) appear below each relevant node.

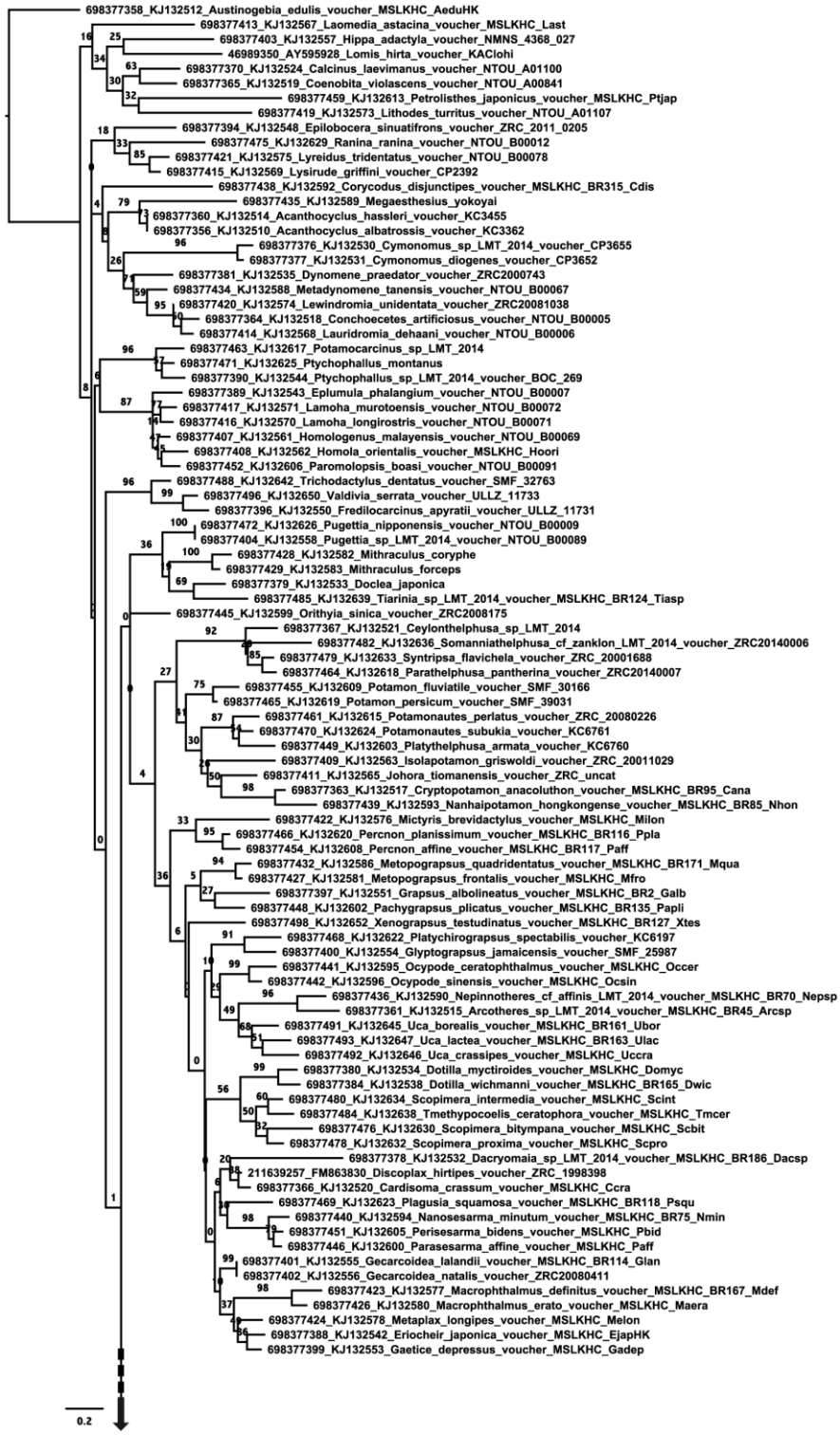

Figure 2-10. ML phylogram of *Brusinia profunda* and 308 mostly brachyuran taxa based on analyses of a 447 bp alignment of 16S rRNA sequence data. Support values appear above each relevant node and are based on 500 bootstrap replicate ML searches. Brusiniidae and Portunoidea are highlighted.

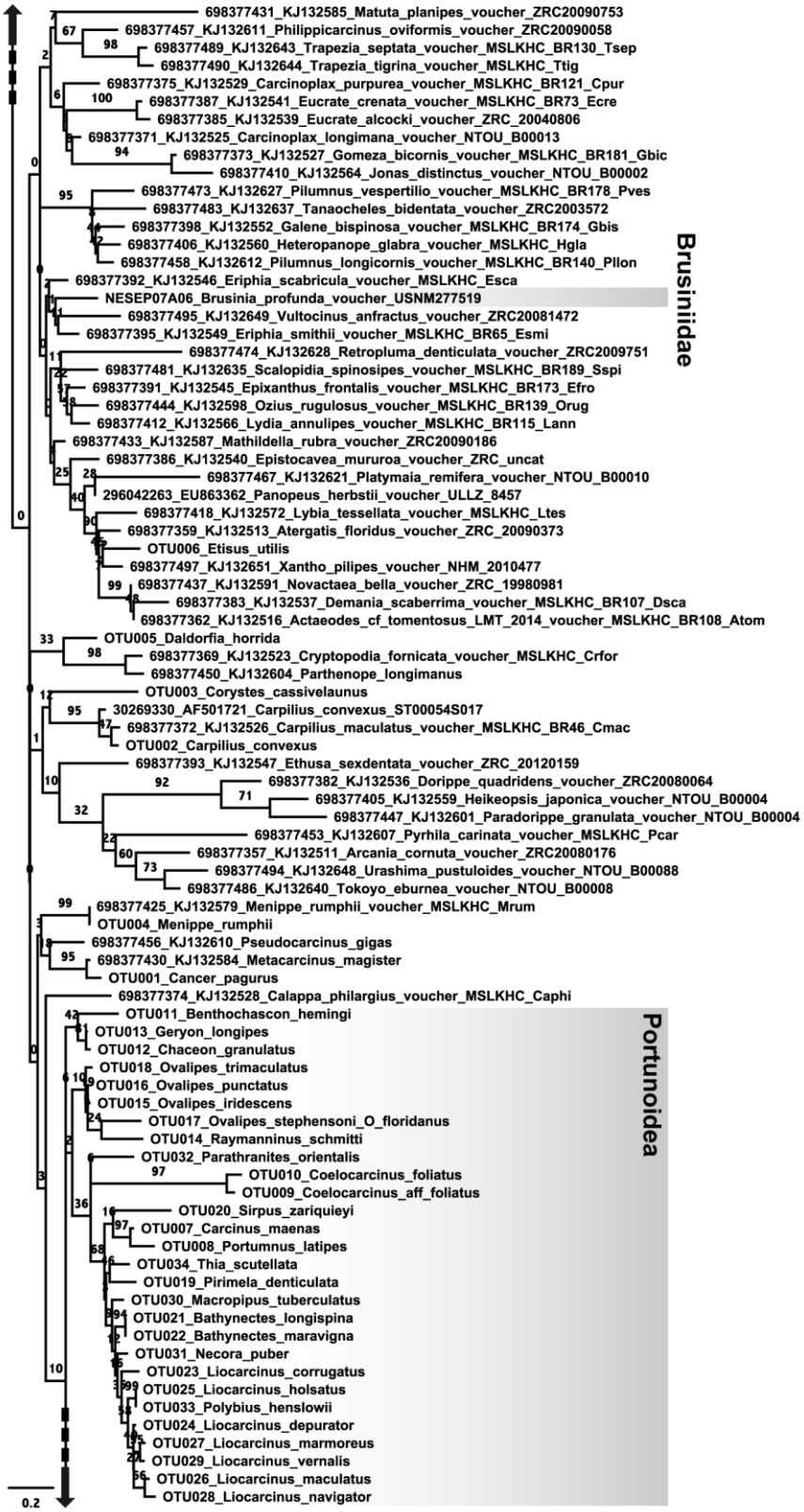

Figure 2-10. Continued.

Figure 2-10. Continued.

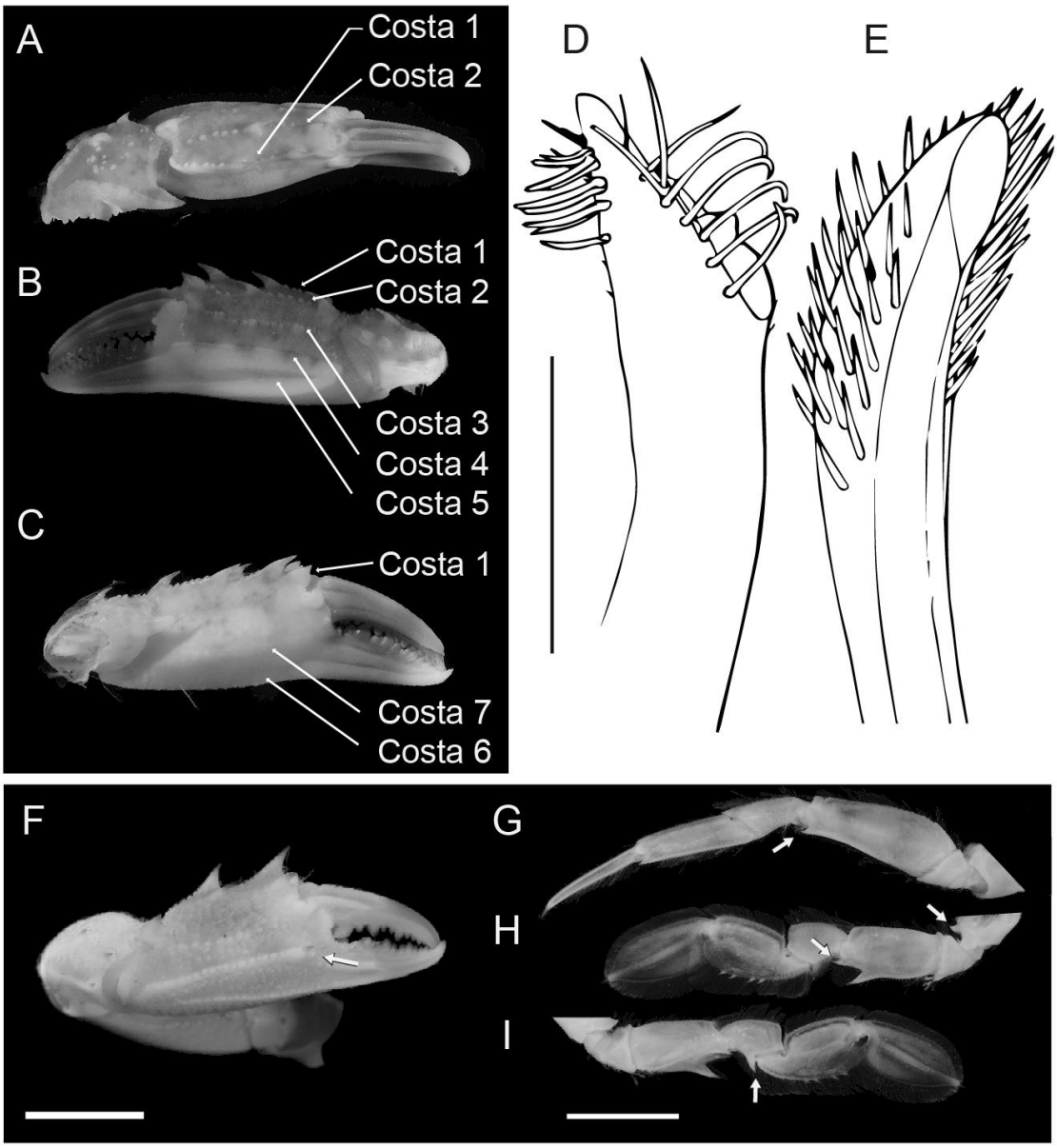

Figure 2-11. A selection of morphological features discussed in the Systematic Account. A-C) position of seven homologous costae found in Thalamitinae respectively depicted on the A) dorsal, B) outer and C) inner surfaces on the left cheliped of *Thalamita admete* (voucher UF7688A). D) Tip of the G1 for *Thalamonyx gracilipes* (scale bar = 0.1 mm; illustration modified from Stephenson & Rees 1967a, Figure 2H). E) Tip of the G1 for *Trierarchus demani* (illustration modified from Crosnier 1962, Figure 200). F) Outer cheliped surface for *Zygita longifrons* (voucher UF199). G) Fourth ambulatory leg of same *Z. longifrons*. H) dorsal surface of left natatory leg. I) ventral surface of natatory leg. Scale bars = 5 mm. Arrows indicate spines diagnostic of *Zygita* (see text).

CHAPTER 3
A REVIEW AND MOLECULAR ANALYSIS OF THE SYMBIOTIC GENUS *LISSOCARCINUS* (PORTUNIDAE: THALAMITINAE)

Introduction

Lissocarcinus Adams & White, 1849, is a small (9 species), charismatic genus of crabs belonging to the family Portunidae Rafinesque, 1815. These crabs are one of just a few lineages of portunids that live commensally with other organisms. Until recently, *Lissocarcinus* shared this distinction only with members of the genus *Caphyra*, together forming the subfamily Caphyrinae Paul'son, 1875. Recent molecular work (Chapter 2) has demonstrated that these genera are sister taxa and form a clade with two other genera that also appear to be symbiotic: *Trierarchus* Evans, 2016 and *Zygita* Evans, 2016. This clade in turn is nested within the subfamily Thalamitinae Paul'son, 1875. Collectively, these four genera exhibit significant morphological divergences from a typical portunid body plan, likely related to their symbiotic life style. That is, most portunids have a laterally streamlined carapace and paddle-shaped hind legs that together increase these crabs' efficiency at swimming and burying into soft sediment (Hartnoll, 1971; Bellwood, 2002). In contrast, *Lissocarcinus* as well as the other symbiotic lineages, are generally smaller, less streamlined and exhibit a more ovate or orbicular carapace. Also, their hind legs are variously modified to suit their commensal mode of life. Among *Lissocarcinus*, the sea cucumber symbiont *L. orbicularis* is by far the widest ranging, most commonly collected, and best studied species. It distribution extends from the Red Sea to the central Pacific. With the exception of this species, most members of *Lissocarcinus* are infrequently encountered, rarely collected and poorly represented in museum collections. The following provides a review and molecular analysis of this genus. This work was motivated by recent collections of rarely

collected species made by myself and other researchers from the Florida Museum of Natural History. Access to additional material from other institutions also made this work possible. Finally, sampling of *L. orbicularis* was sufficient enough to carry out a preliminary phylogeographic analysis of the species using mtDNA CO1 sequence data.

Materials and Methods

Vouchered Material

Morphological work was conducted on 177 vouchered *Lissocarcinus* specimens, from the following institutions: American Museum of Natural History, New York, USA (AMNH); Natural History Museum of Los Angeles County, Los Angeles, California, USA (NHMLAC); Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (UF); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC). Additional material referenced but not examined were from the following collections: Natural History Museum, London, UK (BNHM); Indian Museum, Kolkata, India (IMC); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Sequence data was generated for phylogenetic anlayses from some of this material (Table 3-1). Additionally, material for which only CO1 data was generated are indicated with an asterisk in the systematic account section.

Scanning Electron Microscopy

Male first gonopods (G1) were prepared for SEM work following the protocols of Felgenhauer (1987). Samples were cleaned of mucus and debris. Dehydration was carried out through a graded ethanol series and two washes in hexamethyldisilazane.

Specimens were then mounted and coated with 25 nm 60:40 gold:palladium using a Cressington Sputter Coater 108auto. A Leica Stereoscan 440 was used for image capture.

Illustrations and Photographs

Unless otherwise indicated photographs were captured by myself or used with permission from G. Paulay. Illustrations were reproduced with permission, are considered in the public domain, or were re-illustrated using Adobe Illustrator CS6.

Molecular Work and Analyses

Molecular work and phylogenetic analyses are outlined in Chapter 2. Briefly, sequence data for 16S rRNA, CO1, and H3 markers from *Lissocarcinus* and 16 thalamitine outgroup taxa was compiled from Chapter 2. This data was augmented with additional *Lissocarcinus* taxa and an approximately 365 bp fragment of 12S rRNA. Amplification of 12S rRNA was carried out using primers 12sf and 12 s1r (Buhay et al., 2007) following the protocol of Lasley et al. (2014). All resulting data were compiled into a single dataset for phylogenetic analyses. Sequence alignment was carried out using MAFFT v 7.123b (Katoh & Standley, 2013) under the E-INS-i setting. The resulting 2,484 bp alignment consisted of 26 taxa and four molecular markers (Table 3-1). Partitioned maximum likelihood (ML) phylogenetic analyses were carried using GARLI 2.0 (Zwickl 2006), and bayesian analyses (BI) were performed using MrBayes v3.2.5 (Ronquist et al., 2012). The best partitioning schemes were selected using the BIC criterion and a greedy search algorithm in Partitionfinder v.1.1.1 (Lanfear et al., 2012) (Table 3-2). ML analyses consisted of 100 independent searches and support values were assessed with 500 bootstrap replicate searches. BI analyses were run for 15 million generations, sampling every 10,000 generations, with an arbitrary burn-in of 3

million generations. Convergence was evaluated using Tracer v.1.6 (Rambaut et al., 2014). Phylogenetic analyses were carried out on the CIPRES Science Gateway (Miller et al., 2010).

In order to investigate the genetic diversity and species limits within *Lissocarcinus*, additional CO1 sequence data was generated, when possible, from multiple individuals of each species. This effort resulted in 85 additional CO1 sequences, including 57 sequences from *L. orbicularis* across its range. A neighbor-joining tree of all CO1 data was constructed using a K2P model and 500 bootstrap replicate searches in Geneious v. 7.1.8 (Kearse et al., 2012). Interspecific and intraspecific Kimura 2-parameter (K2P) genetic distances were calculated for all CO1 sequences using Species Identifier v.1.8 (Meier et al., 2006). Finally, phylogeographic analyses were also carried out on all 57 sequenced *L. orbicularis* specimens using a 568 bps portion of CO1 spanning only that region for which no sequence data was missing. Eleven CO1 sequences from the sister species *L. holothuricola* were also included. Haplotypes were mapped and a median-joining network constructed using the program PopART (Leigh & Bryant, 2015). Nucleotide and haplotype diversity as well as population pairwise Fst values were calculated using Arlequin 3.5 (Excoffier & Lischer, 2010).

Results and Discussion

Phylogenetic Results. Consistent with previous work (Chapter 2), phylogenetic analyses recovered strong support for a monophyletic *Lissocarcinus* composed of three well supported lineages (Figure 3-1 and 3-2). The first of these consists of four genetically distinct *Lissocarcinus laevis sensu lato* species (interspecific CO1 K2P distance ≥ 6.29%; Table 3-3) that can also be distinguished on morphological,

ecological, and distributional evidence as detailed below. A second lineage was comprised solely of *L. arkati* (intrageneric interspecific CO1 K2P distance ≥ 16.02%). The third lineage was composed of *L. holothuricola*, *L. orbicularis* and three genetically distinct *L. polyboides sensu lato* ESUs (interESU CO1 K2P distances 5.43-9.97%). The largest intraspecific CO1 K2P distance was 1.88% for *L. orbicularis*, the best sampled species (N=57). Though sampling for most lineages was limited, K2P intra- and interspecific distances did not overlap and interESU values were consistent with species-level divergence observed in other decapod taxa (e.g. see da Silva et al., 2011).

Phylogeographic analyses of *L. orbicularis* recovered significant genetic structure, with each of 13 haplotypes restricted to one of three geographic regions (Tables 3-4 and 3-5; Figure 3-3): the Western Indian Ocean Eastern Indian Ocean to Polynesia and Hawaii. The eleven *L. holothuricola* sequences had four haplotypes, including one shared between the Marquesas and Wake Island. *Lissocarcinus orbicularis* and *L. holothuricola* were deeply divergent, reciprocally monophyletic, and overlapped in range. However, no sequences are available for *L. holothuricola* from the Marshall Islands where the two species are known to be sympatric. Pairwise population Fst values between all four groups were all significant and ranged between 0.220 and 0.599 (Table 3-5). Although these results should be approach with some cuation–given that they are based on limited sampling of a single marker–the phylogeographic structure recovered for *L. orbicularis* is consistent with that reported for numerous other tropical marine invertebrates and fishes at either the intra- or interspecific level (e.g., Bowen et al. 2016).

Morphological Results. Molecular phylogenetic relationships largely support known morpho-groups in *Lissocarcinus*. Each of the three major genetic lineages recovered can be separated on the basis of male first gonopod (G1) morphology (see below). The four genetic lineages within *L. laevis s.l.* are also morphologically differentiated (Table 3-6, see also species diagnoses below), and are recognized as distinct species. At least two of these species cooccur in the Philippines, further supporting species status. Conversely, examination of *L. polybioides* failed to recover any morphological differences between the three genetic lineages. These lineages appear allopatric, sampled from Madagascar, Philippines, and Ryukyus only, but here taxon sampling is limited.

Here I also considered the three other nominal *Lissocarcinus* species, which were not examined (*L. boholensis*, *L. echinodisci*, and *L. ornatus*). The original description of *L. ornatus* Chopra, 1931, is very detailed and shows that it is a junior synonym of *L. orbicularis* (discussed below).

Finally, examination of the holotype, and only known specimen of *Lissocarcinus elegans* Boone, 1934 (AMNH-IZC00249978; 1♂; Tevaitoa, Raiatea Island, Society Islands; Figure 3-4)indicated that it is a species of *Caphyra* Guérin, 1832. Gross morphology and G1, shows this specimen to be very similar to *C. tridens* Richters, 1880 (compare Figure 3-4 to Crosnier, 1975b, Figure 3 a-n). The only clear distinction between the two is that the fifth pereopod is paddle-shaped in *L. elegans*, but styliform in *C. tridens*. However these paddle-shaped legs depicted in the original illustration of *L. elegans* are both missing from the type material (Figure 3-4). Finally, the *L. elegans* holotype was collected from “coral” in a geographic region where *C. tridens* is common.

Here I propose that *L. elegans* be moved to *Caphyra*. Future work should investigate whether this species is a junior synonym of *C. tridens*.

In summary, the present study finds that *Lissocarcinus* Adams & White, 1849, includes ten valid species, including one species complex (*L. polybioides s.l.*). Here I provide a systematic account and taxonomic key for of each of the ten species of *Lissocarcinus*.

Systematic Account

Family Portunidae Rafinesque, 1815

Subfamily Thalamitinae Paul'son, 1875

Lissocarcinus Adams & White, 1849

Figures 3-5 to 3-10.

- *Lissocarcinus* Adams & White,1847, in White: 126; *nomen nudum* (Direction 37).
- *Lissocarcinus* Adams & White, 1849: 45, type species: *Lissocarcinus polybioides* Adams & White, 1849, by monotypy; gender masculine (Opinion 73, Direction 37).
- = *Assecla* Streets, 1877: 110, type species *Assecla holothuricola* Streets, 1877, by monotypy; gender feminine.

Diagnosis. Carapace subcircular, slightly broader than long; typically smooth bearing only weakly or strongly developed epibranchial ridges, and sometimes numerous transverse, striated ridges (e.g., *L. arkati*). Anterolateral margin with five teeth or lobes (including outer orbital angle), sometimes poorly defined thus rendering margin nearly entire. Frontal margin one third to one half the width of carapace, more or less extended beyond the inner supra-orbital angles, and nearly entire or cut into two lobes or three acute teeth. One or two supraorbital fissures, sometimes poorly defined. Basal antennal joint short, lying obliquely, with a smooth or minutely-granulated ridge,

extending into the orbital hiatus such that the antennal peduncle and flagellum are completely excluded from orbit. Chelipeds short and stout, but a little longer than ambulatory legs. Cheliped merus typically smooth and lacking spines. Inner angle of cheliped carpus with a short, stout, and typically dull spine. Cheliped manus typically smooth or finely roughened; lacking well-developed spines; with no costae or with two costae on upper margin of manus that end bluntly, sometimes forming a dull spinule. Fifth pereopod typically with paddle-shaped propodus and dactylus; posterior margin of propodi always smooth, bearing no spines; dactyli sometimes lanceolate and more (in *L. holothuricola)* or less (in *L. orbicularis*) approaching styliform. Male first gonopods (G1) with a broad base and numerous subterminal bristles. Diagnosis modified from Leene (1938) and Apel & Spiridonov (1998).

Species included:

- *Lissocarcinus arkati* Kemp, 1923
- *Lissocarcinus boholensis* Semper, 1880
- *Lissocarcinus echinodisci* Derijard, 1968
- *Lissocarcinus holothuricola* (Streets, 1877)
- *Lissocarcinus laevis* Miers, 1886
- *Lissocarcinus* aff. *laevis* sp. nov. A
- *Lissocarcinus* aff. *laevis* sp. nov. B
- *Lissocarcinus* aff. *laevis* sp. nov. C
- *Lissocarcinus orbicularis* Dana, 1852
- = *Lissocarcinus pulchellus* Muller, 1887
  = *Lissocarcinus ornatus* Chopra, 1931, new synonymy;
- *Lissocarcinus polybioides* Adams & White, 1849
- Not *Lissocarcinus elegans* Boone, 1934 (= *Caphyra elegans* (Boone, 1934), comb. nov.)

Remarks. When present, costae on the cheliped manus of *Lissocarcinus* are morphologically consistent with the positionally homologous costae defined in Chapter 2 for all Thalamitinae taxa. Previous diagnoses of this genus (e.g., Leene, 1938) included the presence of two pairs of epibranchial ridges, based on the rarely collected *L.*

holothuricola. However, this interpretation is not supported here (discussed below) and like all other portunoids, no more than one pair of epibranchial ridges are present in any *Lissocarcinus* species.

***Lissocarcinus arkati* Kemp, 1923**

Figure 3-5 A-E.

- *Lissocarcinus arkati* Kemp, 1923: 405, pl.10, fig. 1; type locality: 20 fms mouth of Hugli River, India; syntypes: IMC C693/1 (2♀).

Material examined. 1♂, 1♀ ovig. (UF36296*) Espiritu Santo, Vanuatu, 2006.

Diagnosis. Carapace broader than long, somewhat flattened, with numerous transverse, striated ridges; epibranchial and other standard portunoid carapace ridges not readily apparent. Frontal margin comprised of two broad lobes separated by a smooth notch and not noticeably extending beyond well-defined inner orbital angles; with one well defined supraorbital fissure. Anterolateral border rounded and minutely cut into five distinct teeth. Posterior margin broader than frontal margin and approximately two-thirds the entire breadth. Cheliped meri granular, with numerous dull teeth or tubercles along the anterior border; dorsal and posterior distal surface granular and squamous. Outer margin of cheliped carpus with a stout spinule. Cheliped carpus and manus granular and squamous on upper and outer surface. Cheliped pollex and dactylus with well defined ridges. G1 broad, slightly curved, with a large subterminal lobe beginning halfway along its length on the outer border, extending and somewhat tapering towards tip; with bristles along inner and outer borders starting at the lobe, becoming dense at the subterminal end.

Color. Purplish red to brownish grey in hue. Live color is depicted here in an in situ photograph (Figure 3-5 C).

Ecology and distribution. This species is reported from muddy and sandy habitats at 10 to 65 meters from Hawaii, the tropical West Pacific, and the eastern and south-western Indian Ocean. It lives in association with echinoids, often *Astropyga radiata* (Spiridonov 1990, Nguyen, 2013).

Remarks The subterminal bristles of the G1 pictured here (Figure 3-5 D) were damaged and are not readily apparent (but see illustration by Crosnier, 1962; Figure 32). Nevertheless, the shape of G1 is species-specific.

Lissocarcinus boholensis Semper, 1880

- *Lissocarcinus boholensis* Semper, 1880: 60, 67; type locality: Bohol, Philippines; type material presumed lost.
- *Lissocarcinus boholensis*: Rathbun, 1910: 363.

Material examined. None.

Diagnosis. Carapace about as broad than long, somewhat flattened, and exhibiting numerous transverse, striated ridges on the anterior half that become obsolete posteriorly. Frontal margin triangular, comprised of two oblique lobes separated by a distinct notch, and extending substantially beyond the well-defined inner orbital angles. Anterolateral border with five, poorly-distinguished lobes. Posterior margin of carapace slightly concave and approximately half the entire breadth. Chelipeds stout and finely roughened. Cheliped manus with granular Costae 1, 2, and 3 (and possibly more). Cheliped pollex and dactlyi with well defined ridges. G1 not described. Diagnosis after Rathbun (1910) and Leene (1938).

Color. Unknown

Ecology and distribution. The only two recorded specimens of this species were collected from salps and are putative symbionts of these taxa. This species has

only been reported from Bohol, Philippines (holotype) and Koh Kut, Vietnam (Rathbun,1910).

Remarks. The additional record of Rathbun (1910) was based on a single immature female. This specimen was described in detail, but no illustrations were provided and it is unclear whether voucher material was retained. The description and validity of this species remains problematic. More material is needed to evaluate this species.

***Lissocarcinus echinodisci* Derijard, 1968**

Figure 3-5 F.

- *Lissocarcinus echinodisci* Derijard, 1968: 335, figs. 1-10; type locality: Toliara, Madagascar ; holotype: MNHN (1 ♂); paratypes MNHN (22 ♂, 12 ♀, 3 ♀ ovig.).

Material examined. None.

Diagnosis. Carapace about as broadlong, smooth, with minutely granular epibranchial ridges. Frontal margin extending forward beyond orbits and comprised of three subtly defined acute teeth formed by four concave margins. Inner orbital angle ill-defined or absent. One well defined supraorbital fissure. Anterolateral border with five moderately well-defined teeth that are swept forward and end acutely; first anterolateral tooth broadest, and subtly concave anteriorly. Cheliped carpus minutely granular on upper and outer margin. Cheliped manus with a spinule or tubercle on the outer proximal margin; lower surface faintly squamose. Cheliped dactylus with well-defined ridges. Fifth pereopod with lanceolate dactylus ending in a well developed spine. G1 long, slightly curved and generally bare or with minute spinules apically; distal inner border marked by a row of approximately 12 very long, straight, evenly-tapered,

bipinnate bristles; outer border bearing additional, short, subterminal bristles; with a well-developed subterminal membrane extending from the outer to inner border.

Color. Carapace reported to be off-white in color (“vieil ivoire”; Derijard, 1968) with longitudinal brown bands and spots. This coloration continues to a lesser extent onto the abdomen and pereopods.

Ecology and distribution. This species is currently only known from the Southwest coast of Madagascar and reported to live in association with the sand dollar *Echinodiscus auritus* (see Derijard, 1968).

Remarks. *Lissocarcinus echinodisci* is a distinct, well-described species, but it is known only from its original collection (38 specimens). Although it is similar to *L. polybiodes s.l.* in carapace shape, gonopod morphology, and color, its frontal margin is clearly different. The dactyli of the fifth pereopods are similar to that of *L. orbicularis*, and presumably aid in grasping their host. However, the original illustration of this structure (Derijard, 1968; Figure 6) suggest that this spine is curved outward and not inward as in *L. orbicularis.* If true, this modification may be unique to this species and could be adaptive for attaching to its echinoid host.

Lissocarcinus holothuricola **(Streets, 1877)**

Figure 3-6.

- *Assecla holothuricola* Streets, 1877: 111; type locality: Palmyra Atoll; holotype USNM 2302 (1 ♀, damaged).
- *Lissocarcinus holothuricola*: Leene, 1938: 5.

Material examined. Line Islands: Holotype: 1♀ (USNM 2302) Palmyra atoll; Wake: 4♂, 3♀ (NHMLAC PL0601-PL0607), 1958; 4 juv. (UF36080) with *Holothuria edulis*, depth ≤ 50 m, coll. S. Kim, 2009; 1♀ (UF8433*) lagoon, depth ≤ 1 m, coll. V.

Bonito, 2005; Marquesas**:** 1 juv. (UF40382*) with *Holothuria whitmaei*, depth ≤ 30 m, Ua Pou, coll. N. Evans, 2011; 1♂, 1♀ (UF30203*x2) with *Thelenota ananas*, depth ≤ 40 m, Fatu Hiva, coll. N. Evans, 2011; 5 juv. (UF29947) sand bottom, depth ≤ 28 m, Nuku Hiva, coll. N. Evans, 2011; 1 juv. (UF30031) with holothurian, depth ≤ 36 m, Nuku Hiva, coll. N. Evans, 2011; 2 juv. (UF30172) with holothurian, depth ≤ 25 m, Fatu Hiva, coll. N. Evans, 2011; 1♀ ovig. (UF30182*) with holothurian, depth ≤ 35 m, Fatu Hiva, coll. N. Evans, 2011; 1♂ (UF30190*) with holothurian, depth ≤ 40 m, Fatu Hiva, coll. N. Evans, 2011; 1♂, 1♀ (UF30235*x2) with holothurian, depth ≤ 40 m, Tahuata, coll. N. Evans, 2011; 1♂, 1 juv. (UF30253*) with holothurian, depth ≤ 30 m, Hiva Oa, coll. N. Evans, 2011; 1♂ (UF30302*) with holothurian, depth ≤ 20 m, Ua Pou, coll. N. Evans, 2011; 1♀? (UF30191*) with holothurian, depth ≤ 40 m, Fatu Hiva, coll. N. Evans, 2011; Marshall Islands: 1♀ (NHMLAC PL0611) Aniyaanii Island, Eniwetok Atoll; 1♂ (NHMLAC PL0619) stn. 572, Eniwetok Atoll; 2♂, 1♀ (NHMLAC PL0592-PL0596) stn. 160, Eniwetok Atoll, 1966.

Diagnosis. Carapace broader than long, with strongly developed, often keel-shaped epibranchial ridges; mesograstic ridges often present, sometimes robust, comprised of sculpted nodules; metagrastic ridges sometimes weakly present. Frontal margin sub-entire and broadly triangular. Inner supra-orbital angles poorly developed but always present. Two supraorbital fissures, sometimes poorly-defined and nearly merging into one another. Anterolateral border with five moderately well-defined lobes; last anterolateral lobe directed outward and bearing the distal end of the epibranchial ridge. Cheliped manus with a tubercle on the outer proximal margin; Costae 1 and 2 well-developed, but lacking spines; Costa 3 smooth but distinct. Cheliped pollex and

dactylus with well-defined ridges. Fifth pereopod with broad styliform (rarely narrowly lanceolate) dactylus, ending in a well-developed, inward-curved spine. G1 long, slightly curved and generally bare or with minute apical spinules, with a row of ~21 very long, straight, evenly tapered bristles along inner border to tip; outer border with additional, short subterminal bristles; with a relatively short, subterminal membrane extending from outer to inner border.

Color. This species presents a range of color patterns similar to its sister species *L. orbicularis* (compare Figures 3-6 B and 3-9 F-G). Of particular note, I found several male and female pairs on the orange-red sea cucumber *Thelenota ananas*, with males bright red and female bright orange, matching the colors of their host. Ayotte (2005) demonstrated that *L. orbicularis* will change its color during molting when moved to a different colored holothurian host.

Ecology and distribution. Like *L. orbicularis,* this species lives commensally on various holothurians, especially species of *Holothuria,* but also *Thelenota ananas.* Recent collections from the Marquesas Islands extend the range of this species from Wake Island, the Marshalls, and Line islands. Given the intensive sampling available for *L. orbicularis* from throughout the Indo-west Pacific, it is unlikely that *L. holothuricola* ranges much beyond what is currently known. The two species are known to coexist in the Marshall Islands.

Remarks. This rarely collected species was described from a single damaged female from Palmyra Atoll (Figure 3-6 A). Based on much new material I have provided a new diagnosis of the species. The original description indicates two pairs epibranchial ridges, however, all specimens have but a single ridge, which may, however, be

strongly keeled, ans this may be the source of this erroneous observation. It is most readily distinguished from *L. orbicularis* by the keeled epibranchial ridge and styliform fifth pereopod.

***Lissocarcinus laevis* Miers, 1886, sensu stricto**

Figure 3-7 A-G; Table 3-6.

- *Lissocarcinus laevis* Miers, 1886: 205, pl. 17, fig. 3 a,b; type locality: Celebes Sea, south of Mindanao, Indonesia; holotype: BNHM (1 ♀ ovig.)

Material examined. Philippines: 1♂ (UF41529*) reef slope, with *Cassiopeia*, depth ≤ 15 m, Calatagan, Luzon Island, coll. G. Paulay, 2014; 1♀ (UF41516*) reef slope, with Ceriantharia, depth ≤ 12 m, Calatagan, Luzon Island, coll. G. Paulay, 2014; 1♀ (UF41571*) patch reef sand flat, with *Heteractis aurora*, depth ≤ 12 m, Calatagan, Luzon Island, coll. G. Paulay, 2014; 1♀ (USNM 93069) Jolo Island, Albatross Expedition; 1♀ (UF41388*) reef slope, depth ≤ 30 m, Mabini, Luzon Island, coll. G. Paulay, 2014; 1♀ (UF41507) reef slope, depth ≤ 12 m, Calatagan, Luzon Island, coll. C. Pieotrowski, 2014; 1♀ ovig. (UF43176*) seagrass and reef, depth ≤ 7 m, Puerto Galera, Mindoro, coll. G. Paulay, 2015.

Diagnosis. Carapace broader than long; smooth, epibranchial ridges nearly absent, protogastric ridges faintly present. Frontal margin comprised of two broad, subtly-oblique, slightly-concave lobes separated by a smooth notch, and slightly or moderately extending beyond well-defined inner orbital angles. Two poorly defined supraorbital fissures. Anterolateral border with five moderately well-defined, blunt, rounded teeth; teeth one and five small, remaining teeth broad and subequal. Cheliped meri with a small tubercle on anterior distal border. Cheliped manus smooth with a dull tubercle on the outer proximal margin; pollex and dactylus sometimes with smoothly

defined ridges. Fifth pereopod with broad, paddle-shaped dactylus ending smoothly without a spine. G1 short, extremely stout and curved with a slightly flared tip; generally bare or with minute spinules towards tip, with a row of at least 30 well-developed, bipinnate bristles extending along the inner border to tip; outer surface otherwise bare; inner surface with minute spinules near tip; distinct lobe on subterminal outer surface of G1 opening bearing short papilliform setae that extend from the opening along the outer border.

Color Carapace and chelipeds patterned light red to brick red or brown over a dusky white background. Ambulatory legs similarly patterned on a somewhat transparent background (Figures 3-7 F, G).

Ecology and distribution. This species has been considered to be broadly distributed across the Indo-west Pacific from the Red Sea and Madagascar to Hawaii and the Marquesas Islands (e.g., see Stephenson, 1972; Spiridonov, 1990). The discovery of three additional cryptic species suggest that past records need to be reevaluated. Members of this species complex can live in sympatry. In the current study we can only confirm an Indo-Malay distribution for *L. laevis s.s.*, but this is based on very few specimens studied. Specimens examined here were collected in association with cerianthids and sea anemones, but one specimen was collected on the sedentary jellyfish *Cassiopeia*.

Remarks. The original description of *Lissocarcinus laevis* was thorough and provides sufficient information to distinguish this species from its three cryptic congeners described below. The original illustration of the holotype is provided here (Figure 3-7 A). Distinguishing characters of the four species are summarized in Table 3-

6. This species can be distinguished from the sympatric *Lissocarcinus* aff. *laevis* sp. nov. A by different color patterns, the presence of protogastric ridges, the presence of a small tubercle on the anterior distal border of the cheliped meri, and a G1 with a distinct lobe bearing papilliform setae at the terminal opening. A poorly illustrated gonopod by Edmondson (1954; Figure 7E, F) suggests this lobe may also be present in *Lissocarcinus* aff. *laevis* sp. nov. B.

***Lissocarcinus* aff. *laevis* sp. nov. A**

Figure 3-8 A-F; Table 3-6.

Material examined. Philippines: Intended holotype: 1♂ (UF42984*) sandy reef slope, in *Cerianthus* tube, depth ≤ 17 m, Puerto Galera, Mindoro, coll. G. Paulay, 2015; 1♀ (UF43311*) sandy reef slope, with *Actinodendron*, depth ≤ 4 m, Puerto Galera, Mindoro, coll. M. Daly, 2015; Mariana Islands: 1♂ (UF204*) with *Actinodendron*, depth ≤ 20 m, Guam Island, 1998; New Caledonia: 1♀ ovig. (UF39136*) sand bottom, with *Actinodendron*, depth ≤ 15 m, Surprise Island, coll. Antoine Gilbert, 2013.

Diagnosis. Carapace broader than long; smooth, epibranchial ridges and protogastric ridges absent. Frontal margin comprised of two broad, subtly oblique, slightly concave lobes separated by a smooth notch, and extending significantly beyond well-defined inner orbital angles. Two poorly defined supraorbital fissures. Anterolateral border with five moderately well-defined, blunt, rounded teeth; teeth one and five small, remaining teeth broad and subequal. Cheliped meri smooth, without a small tubercle on the anterior distal border. Cheliped manus smooth with a dull tubercle on the outer proximal margin; pollex and dactylus sometimes with smoothly defined ridges. Fifth pereopod with broad, paddle-shaped dactylus, ending smoothly without a spine. G1 short, extremely stout and curved with a slightly flared tip; generally bare or with minute

spinules towards apex, with a row of at least 30 well-developed bipinnate bristles extending along the inner border to tip; outer surface otherwise bare; inner surface with minute spinules especially near tip; without a distinct lobe on the subterminal outer surface of opening and bearing no papilliform setae.

Color. Carapace and chelipeds patterned light to dark red on a stark white background, but sometimes with yellow hues; yellow hues sometimes replace white background around mouth and infraorbital region, fading outwards. Ambulatory legs uniformly white to light yellow and only somewhat transparent (Figures 3-8 D, F.

Ecology and distribution. Specimens examined here are from the Philippines, Guam and New Caledonia. This species appears to live in sympatry with both *L. laevis s.s.* (in Philippines) and *Lissocarcinus* aff. *laevis* sp. nov. C (possibly in New Caledonia; see below). This species is also collected from cerianthids and sea anemones.

Remarks. Can be distinguished from the sympatric *Lissocarcinus laevis s.s.* by color pattern, absence of protogastric ridges, absence of a small tubercle on the anterior distal border of the cheliped meri, and a G1 without papilliform setae an a distinct lobe at the terminal opening (see Figure 3-8 A,B,D, Table 3-6).

***Lissocarcinus* aff. *laevis* sp. nov. B**

Figure 3-8 G-J; Table 3-6.

- = *Lissocarcinus laevis*: Edmondson, 1954, 230, fig. d-f.

Material examined. Intended holotype: Hawaiian Islands: 1♀ ovig. (UF37919*) *Halimeda* bed, depth ≤ 19 m, Black Rock, Maui Island, coll. P. Fiene, 2013; 1♂ (USNM 29663) Hawaii.

Diagnosis. Carapace broader than long; smooth; epibranchial ridges minutely granular, each extending approximately one third the width of carapace and gently

curving forward and then slightly backward toward the epibranchial region; protogastric ridges absent. Frontal margin comprised of two broad, level, slightly concave lobes separated by a smooth notch, and only slightly extending beyond well-defined inner orbital angles. Two poorly defined supraorbital fissures. Anterolateral border with five well-defined teeth, subtly directed forward; teeth one through four are broad and acutely pointed; tooth five narrow and sharp. Cheliped meri with a small tubercle on anterior distal border. Cheliped manus smooth with dull tubercle on outer proximal margin; pollex and dactylus sometimes with smoothly defined ridges. Fifth pereopod with broad, paddle-shaped dactylus ending smoothly without a spine.

Color. Carapace entirely dusky white (Figure 3-8 J) or with some purple marks (Edmondson 1954). Chelipeds patterned light to dark red on a dusky white background.

Ecology and distribution. This species is only known from the Hawaiian Islands. Though not reported to be symbiotic (based on dredged material; Edmondson, 1954), it has been observed in association with anemones, including *Heteractis malu* (Figure 3-8 J).

Remarks. This species is the most distinct among the four *Lissocarcinus laevis s.l.* species. The presence of a level frontal margin, granular epibranchial ridges and a narrow, sharp fifth anterolateral tooth are all unique among *L. laevis s.l.* species. A poorly illustrated gonopod by Edmondson (1954; Figure 7E, F) suggests that this species' G1 may be similar to that of *L. laevis s.s.*, but this could not be confirmed, as the only males examined for this study was missing both G1s.

***Lissocarcinus* aff. *laevis* sp. nov. C**

Figure 3-7 H-J; Table 3-6.

Material examined. Intended holotype: Papua New Guinea: 1♀ (UF2317*) with cerianthid, depth ≤ 10 m, Milne Bay Province; Marquesas Islands: 1♀ (USNM 149557) Nuku Hiva; 1♀ (USNM 149565); 1♀ (USNM 149566) Marquesas Islands; 1♀ (USNM 149567).

Diagnosis. Carapace broader than long; smooth; epibranchial ridges absent; protogastric ridges absent. Frontal margin comprised of two broad, subtly oblique, strongly concave lobes (each almost bilobed), separated by a smooth notch, and extending well beyond the well-defined inner orbital angles. Two poorly defined supraorbital fissures. Anterolateral border with five well-defined teeth, subtly directed forward; tooth one small and bluntly rounded; teeth two, three and four broad and acutely pointed; tooth five small and acutely pointed. Cheliped meri with small tubercle on antero-distal border. Cheliped manus smooth with a dull tubercle on outer proximal margin; pollex and dactylus sometimes with smoothly defined ridges. Fifth pereopod with broad, paddle-shaped dactylus ending smoothly without a spine.

Color. Unknown.

Ecology and distribution. Specimens examined here were from Papua New Guinea and the Marquesas Islands. This species has been observed in association with a cerianthid anemone.

Remarks. This species is genetically most similar to *Lissocarcinus laevis s.s.*, but the shape of the frontal lobes and anterolateral teeth are distinct from all other *L. laevis s.l.* species (see Figure 3-7 and Table 3-6).

***Lissocarcinus orbicularis* Dana, 1852**

Figure 3-9

- *Lissocarcinus orbicularis* Dana, 1852: 86, 288, pl. 18, fig. 1a-e; type locality: Insulas Vitienses (= Fiji); syntypes: MCZ CRU-4292 (2 ♂), see remarks below.
- = *Lissocarcinus pulchellus* Muller, 1887: 482, pl. 5, fig. 6; type locality: Trincomalee, Sri Lanka; type: presumed lost (1♀).
- = *Lissocarcinus ornatus* Chopra, 1931: 307, text-fig. 1&2, pl. 7 fig. 1; type locality: Cinque Isl., Andaman Arch.; holotype: IMC C1519/1 (1♂); new synonymy.

Material examined. 1♀ ovig. (UF14488*) reef slope, with *Actinopyga echinites*, depth ≤ 8 m, Nosy Be, Madagascar, coll. G. Paulay, 2008; 1♂ (UF39598*) with *Bohadschia*, depth ≤ 1 m, Magoodhoo Island, Maldives, coll. J. Moore, 2014; 1♂ (UF13421*) with *Bohadschia*, depth ≤ 7 m, Majuro Atoll, Marshall Islands, coll. F. Michonneau, 2008; 1♀ (UF39855*) with *Bohadschia*, depth ≤ 5 m, Carp Island, Palau, coll. A. Catches, 2014; 1♀? (UF10020*) reef flat, with *Bohadschia argus*, depth ≤ 2 m, Moorea Island, Society Islands, coll. G. Paulay, 2006; 1♀ (UF39732) with *Holothuria*, depth ≤ 2 m, Magoodhoo Island, Maldives, coll. J. Moore, 2014; 1♀ (UF39733) with *Holothuria*, depth ≤ 2 m, Magoodhoo Island, Maldives, coll. J. Moore, 2014; 1♀ (UF41378) reef slope, with *Holothuria atra*, depth ≤ 3 m, Maricaban Island, Philippines, coll. G. Paulay, 2014; 1♀? (UF21807*) fore reef, with *Holothuria atra*, depth ≤ 15 m, Ningaloo Reef, W. Australia, coll. R. Dixon, 2009; 1♀? (UF22498*) with *Holothuria atra*, depth ≤ 1 m, Ningaloo Reef, W. Australia, coll. R. Lasley, 2009; 1♀? (UF22583*) with *Holothuria atra*, depth ≤ 3 m, Ningaloo Reef, W. Australia, coll. R. Lasley, 2009; 1♀? (UF22763*) lagoon, with *Holothuria atra*, depth ≤ 7 m, Ningaloo Reef, W. Australia, coll. F. Michonneau, 2009; 1♀? (UF22764*) lagoon, with *Holothuria atra*, depth ≤ 7 m, Ningaloo Reef, W. Australia, coll. R. Lasley, 2009; 1♀? (UF22765*) lagoon, with *Holothuria atra*, depth ≤ 7 m, Ningaloo Reef, W. Australia, coll. R. Lasley, 2009; 1♀? (UF22768*) lagoon, with *Holothuria atra*, depth ≤ 7 m, Ningaloo Reef, W. Australia, coll.

R. Lasley, 2009; 1♂, 1♀, 1♀ ovig. (UF10927*x2) with *Holothuria fuscogilva*, depth ≤ 43 m, Negros Oriental, Philippines, coll. A. Kerr, 2006; 1♀ ovig. (UF32897*) reef slope, with *Holothuria isuga*, depth ≤ 14 m, Gulf of Tadjoura, Djibouti, coll. G. Paulay, 2012; 1♀? (UF9926*) reef slope, with *Holothuria whitmaei*, depth ≤ 23 m, Moorea Island, Society Islands, coll. C. McKeon, 2006; 1♀? (UF14266*) reef slope, with holothurian, depth ≤ 9 m, Nosy Kivindry, Madagascar, coll. G. Paulay, 2008; 1♀ (USNM 106625) with holothurian, Ifaluk atoll, Pacific Ocean; 1♀ (UF43299*) sandy reef slope, with holothurian, depth ≤ 4 m, Puerto Galera, Mindoro, Philippines, coll. C. Pieotrowski, 2015; 1♀? (UF3218*) with *Stichopus*, depth ≤ 10 m, Maui Island, Hawaiian Islands, coll. C. Pittman, 2002; 1♀? (UF4800*) reef slope, with *Stichopus*, depth ≤ 15 m, Oahu Island, Hawaiian Islands, coll. G. Paulay, 2006; 1♂ (UF2674) fringe reef, with *Stichopus chloronotus*, Viti Levu Island, Fiji, coll. G. Paulay, 1982; 1♀? (UF9884*) lagoon, with *Stichopus horrens*, depth ≤ 3 m, Moorea Island, Society Islands, coll. G. Paulay, 2006; 1♀? (UF13668*) reef flat, with *Thelenota ananas*, depth ≤ 3 m, Mayotte Island, Comoros Islands, coll. F. Michonneau, 2008; 1♀ (USNM 267078) with *Thelenota ananas*, Marshall Islands; 1♂ (USNM 1254590) with *Thelenota ananas*, Marshall Islands; 1♂ (USNM 1254591) with *Thelenota ananas*, Marshall Islands; 1♀ (UF9201) with *Thelenota ananas*, depth ≤ 5 m, Moorea Island, Society Islands, coll. G. Paulay; 1♀? (UF33481*) reef slope, with *Thelenota ananas*, depth ≤ 18 m, Moorea Island, Society Islands, coll. F. Michonneau, 2012; 1♂, 1♀ (UF31142*x2) with *Thelenota anax*, depth ≤ 20 m, Weno, Chuuk Island, Caroline Islands, coll. S. Kim, 2011; 1♀ ovig. (UF2088*) Cocos-Keeling Island, Australia, coll. L. Kirkendale, 1999; 1♀? (UF25926*) Heron Island, Australia, 2009; 3 juv. (UF32846*) reef slope, depth ≤ 8 m, Gulf of

Tadjoura, Djibouti, coll. G. Paulay, 2012; 1♀? (UF1922*) reef flat, Vilisites, Viti Levu Island, Fiji, coll. V. Bonito, 2001; 1♀ (UF8761*) reef slope, depth ≤ 15 m, Oahu Island, Hawaiian Islands, coll. G. Paulay, 2006; 3♂ (UF KOAST-10) depth ≤ 2 m, Kona, Hawaii Island, Hawaiian Islands, coll. N. Evans, 2013; 1♂ (UF KONA13-0016) depth ≤ 2 m, Kona, Hawaii Island, Hawaiian Islands, coll. N. Evans, 2013; 1♂ (UF KONA13-0048*) depth ≤ 2 m, Kona, Hawaii Island, Hawaiian Islands, coll. N. Evans, 2013; 1♀ ovig. (UF KONA13-0049*) depth ≤ 2 m, Kona, Hawaii Island, Hawaiian Islands, coll. N. Evans, 2013; 1♀? (UF8340*) depth ≤ 12 m, Maui Island, Hawaiian Islands, coll. C. Pittman, 2003; 1♂ (NHMLAC 16901) Watamu, Kenya; 1♂, 1♀ (UF14018*) sandflat, depth ≤ 3 m, Nosy Be, Madagascar, coll. F. Michonneau, 2008; 1♀ (UF39599) depth ≤ 1 m, Magoodhoo Island, Maldives, coll. J. Moore, 2014; 1♀ (UF186*) patch reef, depth ≤ 5 m, Guam Island, Mariana Islands, coll. L. Kirkendale, 1999; 2♂, 1♀ ovig. (UF26572) lagoon, depth ≤ 4 m, Guam Island, Mariana Islands, coll. F. Michonneau, 2010; 1♀ ovig. (UF40068*) depth ≤ 3 m, Guam Island, Mariana Islands, coll. A. Catches, 2014; 1♂ (UF40071*) depth ≤ 3 m, Guam Island, Mariana Islands, coll. A. Catches, 2014; 1♀? (UF4032*) reef flat, depth ≤ 1 m, Guam Island, Mariana Islands, coll. G. Paulay, 2003; 1♂ (NHMLAC PL0590) Engebi Is. , Eniwetok Atoll , Marshall Islands, 1957; 1♂ (NHMLAC PL0591) Engebi Is. , Eniwetok Atoll , Marshall Islands, 1961; 1♀ (NHMLAC PL0597) stn. 160, Eniwetok Atoll , Marshall Islands, 1966; 1♂ (NHMLAC PL0608) stn. GA64-29a, Eniwetok Atoll , Marshall Islands; 3♀ (NHMLAC PL0598-PL0600) stn. JWK 210, Eniwetok Atoll , Marshall Islands; 2♀ (NHMLAC PL0609-PL0610) Gugegwe Isand, Kwajalein Atoll, Marshall Islands; 1♂, 2♀ (NHMLAC PL0612-PL0614) Eniwetok Atoll , Marshall Islands, 1968; 3♂, 1♀ (NHMLAC PL0615-PL0618) stn. 160, Eniwetok Atoll ,

Marshall Islands; 1♀? (UF13427*) lagoon, depth ≤ 5 m, Majuro Atoll, Marshall Islands, coll. F. Michonneau, 2008; 1♂ (UF38879*) sand bottom, depth ≤ 3 m, Ile des Pins, New Caledonia, coll. N. Evans, 2013; 1♂ (UF38893*) sand bottom, depth ≤ 3 m, Ile des Pins, New Caledonia, coll. N. Evans, 2013; 1♂ (UF39125*) depth ≤ 3 m, Surprise island, New Caledonia, coll. N. Evans, 2013; 1♀? (UF5410*) reef slope, depth ≤ 10 m, Muscat, Oman, coll. G. Paulay, 2004; 1♀, 2♀ ovig., 1 juv. (UF39940*) depth ≤ 2 m, Lighthouse, Palau, coll. A. Catches, 2014; 1♀ ovig. (UF2297*) depth ≤ 10 m, Milne Bay Province, Papua New Guinea, coll. G. Paulay, 1998; 1♀ (UF38583*) Madang Province, Papua New Guinea, coll. B. Chen, 2012; 1♀? (UF2307*) fringing reef, depth ≤ 3 m, Milne Bay Province, Papua New Guinea, coll. G. Paulay, 1998; 1♀, 1♀ ovig. (UF10225*x2) Moorea Island, Society Islands, coll. G. Paulay, 2006; 1♂ (UF15429*) reef slope, Moorea Island, Society Islands, coll. S. McKeon, 2008; 1♂ (UF15741*) lagoon, depth ≤ 15 m, Moorea Island, Society Islands, coll. J. Poupin, 2008; 1♀? (UF16245*) reef flat, depth ≤ 2 m, Moorea Island, Society Islands, coll. V. Ivanenko, 2008; 1♀? (UF19443*) reef flat, depth ≤ 3 m, Zanzibar, Tanzania, coll. T. Werner, 2009; 1♂, 1♀ (ZRC NERMS072*) Espiritu Santo, Vanuatu, 2006; 1♀? (UF7491*) depth ≤ 2 m, Rotua Island, Vanuatu, coll. C. Meyer, 2005; 1♀ (USNM 41079) Saya de Malha, Indian Ocean; 1♀? (UF20494*) Europa Island, Iles Eparses, 2009; 1♀? (UF20495*) Europa Island, Iles Eparses, 2009; 1♀? (UF20496*) Europa Island, Iles Eparses, 2009.

Diagnosis. Carapace broader than long; smooth; typically with weakly developed epibranchial ridges. Frontal margin sub-entire and ranging from broadly triangular to smoothly rounded. Inner supra-orbital angle poorly developed to nearly absent. Two supraorbital fissures, sometimes poorly defined and nearly merging into

one another. Anterolateral border with five poorly distinguished lobes often coalescing to form a nearly entire margin. Cheliped manus with a tubercle on the outer proximal margin; Costae 1 and 2 present but typically smooth and weakly developed. Cheliped pollex and dactylus smooth or with well-defined ridges. Fifth pereopod with lanceolate dactylus ending in a well-developed, inward curved spine. G1 long, slightly curved and generally bare or with minute spinules towards tip, with a row of approximately 21 very long, straight, evenly-tapered bipinnate bristles extending along the inner border to tip; outer border bearing additional short, subterminal bristles; with a relatively short subterminal membrane extending from outer to inner border.

Color. During molting this species can modify its color to match its host (Ayotte, 2005). Most commonly it is white to beige and patterned with black spots, or black to deep red patterned with white spots (Figure 3-9 F and G). Sometimes it can be found in red hues, especially when found in association with *Thelenota ananas* (Figure 3-9 H).

Ecology and distribution. This holothurian symbiont is wide ranging across the Indo-west Pacific from the Red Sea to Hawaii. Phylogeographic results presented above show modest genetic structure.

Remarks. This species can be confused with *L. holothuricola*, but typically has a much smoother carapace and always exhibits lanceolate (not stylifom) dactyli on the fifth pereopods (compare Figures 3-9 and 3-6).

The original description of *L. ornatus* Chopra, 1931 reveals that species to be a junior synonym of *L. orbicularis*. Described from a single specimen from the Andaman Islands (Indian Ocean), Chopra (1931) distinguished his species from *L. orbicularis* mostly by a concave frontal margin. However, Chopra's detailed illustration of the

holotype clearly depicts a malformed *L. orbicularis* (reproduced here in Figure 3-9 D). It is not uncommon for the frontal margin of *L. orbicularis* to be malformed and to exhibit a similar shape (Sankarankutty & Thomas, 1963; personal observation).

Lissocarcinus polybioides Adams & White, 1849, species complex

Figure 3-10.

- *Lissocarcinus polybioides* Adams & White, 1849: 46, pl. 11 fig. 5; type locality: “Eastern Seas”; holotype: BNHM 47.21 (1 ♀).
- = *Portunus polybioides* Adams & White,1847, in White: 25; *nomen nudum*
- = *Lissocarcinus polybioides* Adams & White,1847, in White: 26; *nomen nudum*
- = *Lissocarcinus polybiodes* (misspelling) Ng et al., 2008.

Material examined. Japan: 1♀ (UF27181*) soft bottom, with *Protoreaster nodosus*, depth ≤ 25 m, Toukamuri, Okinawa, Japan, coll. N. Evans, 2010; 1♂ (UF27186*) soft bottom, with *Protoreaster nodosus*, depth ≤ 25 m, Toukamuri, Okinawa, Japan, coll. N. Evans, 2010; 3♂, 4♀ ovig., 1juv. (UF35245*) soft bottom, depth ≤ 25 m, Toukamuri, Okinawa, Japan, coll. N. Evans, 2010; Madagascar: 1♀ ovig. (UF12527*) lagoon, depth ≤ 25 m, Nosy Tanikely, coll. G. Paulay, 2008.

Diagnosis. Carapace about as broader as long; smooth, with weakly developed epibranchial ridges. Frontal margin triangular, comprised of two oblique lobes separated by a distinct notch, and extending well beyond well-defined inner orbital angles. Two supraorbital fissures. Anterolateral border with five teeth, weakly to moderately defined, swept forward, and ending acutely; first anterolateral tooth broadest and subtly concave anteriorly. Cheliped carpus with a spinule or tubercle on the upper proximal margin. Cheliped manus with a spinule or tubercle on the outer proximal margin. Cheliped manus with Costae 1 and 2; Costa 2 sometimes terminating distally in a sharp spine.

Cheliped pollex and dactylus smooth. Fifth pereopod with paddle-shaped dactylus ending in a small spine. G1 long, slightly curved, generally bare or with minute spinules towards tip, with a row of approximately 19 very long, straight, evenly tapered bipinnate bristles extending along the inner border to tip; outer border bearing additional short subterminal bristles; with a well developed subterminal membrane extending from outer border to inner border.

Color. Typically pale white or light in hue with subtle or no patterning (Figure 3-10 B).

Ecology and distribution. This species is distributed across the Indo-west Pacific, but genetic data suggests that it may be an allopatric complex of deeply-differentiated lineages. Specimens from Madagascar, Philippines, and Ryukyus fall into different lineages. Several specimens examined here were associated with *Protoreaster* sea stars, but Stephenson (1972) reported that it can sometimes be found associated with “madreporian corals”.

Remarks. This species complex can be distinguished from other *Lissocarcinus* based on the overall shape of its smooth carapace and the shape of its frontal lobes (Figure 3-10). However, no clear morphological distinctions were found between the three genetic lineages (compare holotype and specimens from 3 localities in Figure 3-10). The only subtle distinction was an overall smoother carapace and chelipeds in the Philippine specimen (UF42958), but only one specimen was available from this locality. Further work is need to revise this species complex.

Key to species of *Lissocarcinus* Adams & White, 1849.

1. Carapace with numerous transverse, striated ridges.....2

   Carapace without transverse, striated ridges.....3

2. (1) Frontal margin not noticeably extending beyond inner orbital angles; posterior margin of carapace approximately two-thirds as long as carapace width ..... *Lissocarcinus arkati*

   Frontal margin markedly extending beyond inner orbital angles; posterior margin of carapace approximately half as long as carapace width..... ..... *Lissocarcinus boholensis*

3. (2) Carapace about as broad as long; anterolateral border with acute teeth; G1 bearing a well developed subterminal membrane from outer to inner border 4

   Carapace broader than long; anterolateral border with lobes, broad teeth, or nearly entire; G1 subterminal membrane relatively short, poorly developed, or absent 5

4. (3) Frontal margin comprised of three subtle acute teeth; one well defined supraorbital fissure; fifth pair of pereopods with lanceolate dactyli ending in a well-developed spine .... *Lissocarcinus echinodisci*

   Frontal margin comprised of two oblique lobes separated by a distinct notch; two supraorbital fissures; fifth pair of pereopods with paddle-shaped dactyli ending in a small spine ....*Lissocarcinus polybiodes* spp. complex

5. (3) Frontal margin sub-entire and broadly triangular or smoothly rounded; anterolateral carapace border nearly entire or with lobes 6

   Frontal margin comprised of two broad lobes separated by a notch; anterolateral carapace border with moderately well defined, though often dull, teeth 7

6. (5) Epibranchial ridges moderately to strongly developed, sometimes appearing keeled; fifth pair of pereopods with broad styliform dactyli..... .....*Lissocarcinus holothuricola*

   Epibranchial ridges nearly absent or weakly to moderately developed; Fifth pair of pereopods with lanceolate dactyli ....*Lissocarcinus orbicularis*

7. (5) Frontal lobes level and not extending well beyond inner orbital angles; minutely granular epibranchial ridges present; last anterolateral tooth narrower than all others and sharp ....*Lissocarcinus* aff. *laevis* sp. nov. B

Frontal lobes subtly oblique and extending beyond inner orbital angles; epibranchial ridges absent; last anterolateral tooth not narrower or sharper than others.....8

8. (7) Frontal lobes significantly concave, each almost bilobed; anterolateral teeth two through five acute ....*Lissocarcinus* aff. *laevis* sp. nov. C

Frontal lobes subtly concave; all anterolateral teeth blunt and rounded.....9

9. (8) Protogastric ridges faint, but present; cheliped meri with a small tubercle on antero-distal border; G1 with a distinct lobe present on subterminal outer surface of opening with papilliform setae that continue forward along outer boarder. Live color light red to brick red and brown on a dusky white background ..... *Lissocarcinus laevis s.s.*

Protogastric ridges not present; cheliped meri without a small tubercle on antero-distal border; G1 without a distinct lobe on the subterminal outer surface of opening, nor with papilliform setae; Live color light to dark red on a stark white background, sometimes with yellow hues ....*Lissocarcinus* aff. *laevis* sp. nov. A

Table 3-1. Taxon sampling and operational taxonomic unit (OTU) composition of sequence data used for phylogenetic analyses.

Taxon	OTU ID	Voucher ID	16S rRNA Genbank #	CO1 Genbank #	H3 Genbank #	12S rRNA Genbank #	Locality
Cronius ruber (Lamarck, 1818)	OTU-01	UF26364 / *UF25995	KT365546	*KT365725	KT425008	XXXXXXXX	United States, Florida
Gonioinfradens paucidentatus (A. Milne-Edwards, 1861)	OTU-02	UF5109 / *UF30184	KT365547	KT365726	*KT588216	XXXXXXXX	Palau / *Marquesas Islands
Goniosupradens obtusifrons (Leene, 1937)	OTU-03	UF16599	KT365544	KT365720	KT425007	XXXXXXXX	Australia, Lizard Island
Charybdis natator (Herbst, 1794)	OTU-04	UF3707 / *UF21403	KT365543	KT365719	*KT424998	*XXXXXXXX	Taiwan / *Australia, Ningaloo Reef
Thalamitoides quadridens A. Milne-Edwards, 1869	OTU-05	UF18495 / *UF15637	KT365588	*KT365792	KT425017	XXXXXXXX	French Polynesia
Thalamonyx gracilipes A. Milne-Edwards, 1873	OTU-06	UF 3784-A	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	Hawaii, Maui Island
Thalamita integra Dana, 1852	OTU-07	UF 587 / *UF 22085	KT365578	*KT365770	*KT425028	*XXXXXXXX	Saipan / *Australia, Ningaloo Reef
Thalamita admete (Herbst, 1803)	OTU-08	UF 7688-A / *UF 16971	KT365562	*KT365749	*KT425014	*XXXXXXXX	Oman / *Australia, Lizard Island
Thalamita picta Stimpson, 1858	OTU-09	UF 161	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	Guam
Thalamita sima H. Milne Edwards, 1834	OTU-10	UF35869	KT365619	KT365786	XXXXXXXX	XXXXXXXX	Australia, Darwin
Thalamita prymna (Herbst, 1803)	OTU-11	UF16749	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	Australia, Lizard Island
Thalamita crenata Ruppell, 1830	OTU-12	UF8950 / *UF17752	KT365572	KT365763	*KT424991	*XXXXXXXX	Hawaii, Oahu Island / *Australia, Tannum Sands
Zygita murinae (Zarenkov, 1971)	OTU-13	UF36525	KT365615	KT365776	KT425018	XXXXXXXX	Saudi Arabia, Farasan Banks

* Marks second specimens in multi-specimen OTUs.

Table 3-1. Continued.

Taxon	OTU ID	Voucher ID	16S rRNA Genbank #	CO1 Genbank #	H3 Genbank #	12S rRNA Genbank #	Locality
Trierarchus woodmasoni (Alcock, 1899)	OTU-14	UF4114-A	KT365624	KT365791	KT425026	XXXXXXXX	Guam
Caphyra cf. *fulva*	OTU-15	UF11748	KT365529	KT365696	KT424990	XXXXXXXX	Indo Pacific, Unknown
Caphyra tridens Richters, 1880	OTU-16	UF15907	KT365532	KT365701	KT425003	XXXXXXXX	French Polynesia, Moorea Island
Lissocarcinus arkati Kemp, 1923	OTU-17	UF36296-A	KT365549	KT365729	KT425045	XXXXXXXX	Vanuatu, Espiritu Santo
Lissocarcinus aff. *laevis* sp. nov. C	OTU-18	UF2317	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	Papua New Guinea, Alotau
Lissocarcinus laevis Miers, 1886*, s.s.*	OTU-19	UF41571	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	Philippines, Luzon Island
Lissocarcinus aff. *laevis* sp. nov. A	OTU-20	UF204	KT365550	KT365730	XXXXXXXX	XXXXXXXX	Guam
Lissocarcinus aff. *laevis* sp. nov. B	OTU-21	UF37919	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	Hawaii, Maui Island
Lissocarcinus polybiodes Adams and White, 1849	OTU-22	UF35245-A	KT365602	KT365733	KT424994	XXXXXXXX	Japan, Okinawa Island
Lissocarcinus polybiodes Adams and White, 1849	OTU-23	UF42958	NA	XXXXXXXX	NA	NA	Philippines, Mindoro
Lissocarcinus polybiodes Adams and White, 1849	OTU-24	UF12527	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	Madagascar, Nosy Be
Lissocarcinus orbicularis Dana, 1852	OTU-25	UF15741 / *UF15429	KT365552	KT365732	*KT425032	*XXXXXXXX	French Polynesia, Moorea Island
Lissocarcinus holothuricola (Streets, 1877)	OTU-26	UF30203	KT365551	KT365731	KT425041	XXXXXXXX	Marquesas Islands

Table 3-2. Best scoring partition schemes for the concatenated molecular dataset.

Marker	Marker Subset	Alignment positions	Model for ML Runs	Model for BI Runs	Partition ID (both analyses)
CO1	Codon Pos. 1	1-657\3	TrNef+G	SYM+I	1
	Codon Pos. 2	2-657\3	F81+I	F81+I	2
	Codon Pos. 3	3-657\3	TrN+I+G	HKY+I+G	3
16S rRNA + tRNA-LEU + NADH1	ND1 Codon Pos. 1	658-1060\3	HKY+I+G	HKY+I+G	4
	ND1 Codon Pos. 2	659-1060\3	HKY+I+G	HKY+I+G	4
	ND1 Codon Pos. 3	660-1060\3	TrN+I+G	HKY+I+G	3
	tRNA-LEU Codon Pos. 1	1061-1129\3	HKY+I+G	HKY+I+G	4
	tRNA-LEU Codon Pos. 2	1062-1129\3	TIM+I+G	HKY+I+G	5
	tRNA-LEU Codon Pos. 3	1063-1129\3	HKY+I+G	HKY+I+G	4
	16S rRNA	1130-1776	TIM+I+G	HKY+I+G	5
12S rRNA	Partial fragment	1777-2156	TIM+I+G	HKY+I+G	5
H3	Codon Pos. 1	2158-2484\3	TrNef	JC	7
	Codon Pos. 2	2159-2484\3	TrNef	JC	7
	Codon Pos. 3	2157-2484\3	GTR+G	GTR+G	6

Table 3-3. Kimura 2-parameter (K2P) genetic distances for 658 bps of mtDNA CO1 sequence data from 10 distinct *Lissocarcinus* lineages.

Species	N	Average intraspecific K2P distance	Greatest intraspecific K2P distance	Average interspecific K2P distance	Smallest interspecific K2P distance	Smallest distance from
Lissocarcinus arkati	1	NA		17.13%	16.02%	*Lissocarcinus holothuricola*
Lissocarcinus holothuricola	11	0.22%	0.49%	8.77%	5.43%	*Lissocarcinus polybiodes (Madagascar)*
Lissocarcinus laevis s.s.	5	0.61%	0.92%	18.95%	6.29%	*Lissocarcinus* aff. *laevis* sp. nov. C
Lissocarcinus aff. *laevis* sp. nov. A	4	0.36%	0.61%	19.66%	7.65%	*Lissocarcinus* aff. *laevis* sp. nov. B
Lissocarcinus aff. *laevis* sp. nov. B	1	NA	NA	18.15%	7.65%	*Lissocarcinus* aff. *laevis* sp. nov. A
Lissocarcinus aff. *laevis* sp. nov. C	1	NA	NA	17.76%	6.29%	*Lissocarcinus laevis s.s.*
Lissocarcinus orbicularis	57	0.47%	1.88%	12.74%	5.64%	*Lissocarcinus holothuricola*
Lissocarcinus polybiodes (Philippines)	1	NA	NA	11.99%	9.97%	*Lissocarcinus orbicularis*
Lissocarcinus polybiodes (Okinawa)	3	0.11%	0.15%	11.35%	9.10%	*Lissocarcinus polybiodes (Madagascar)*
Lissocarcinus polybiodes (Madagascar)	1	NA	NA	8.54%	5.43%	*Lissocarcinus holothuricola*

Table 3-4. Genetic diversity indices for *Lissocarcinus orbicularis* based on 568 bps of CO1.

Population	N	Unique haplotypes	Nuclotide diversity	Haplotype diversity
Hawaii	6	4	0.006455	0.8
EIO-WP	39	7	0.00182	0.7126
Western Indian Ocean	12	2	0.000293	0.1667
Lissocarcinus holothuricola	11	4	0.002113	0.7636
Total	68	17	0.019841	0.8753

EIO-WP= Eastern Indian Ocean – West Pacific.

Table 3-5. Population pairwise FST values.

Populations:	Hawaii	Indo-Pacific	EIO-WP
Indo-Pacific	0.25704*		
EIO-WP	0.59905*	0.47986*	
Lissocarcinus holothuricola	0.22066*	0.26713*	0.54366*

* $p<0.05$; EIO-WP= Eastern Indian Ocean – West Pacific.

Table 3-6. Summary of distinguishing features in *Lissocarcinus laevis s.l. species*

Morphology	*L. laevis s.s*	*L.* aff. *laevis* sp. nov. A	*L.* aff. *laevis* sp. nov. B	*L.* aff. *laevis* sp. nov. C
Angle of frontal lobes	Subtly oblique,	Subtly oblique,	Level,	Subtly oblique,
Shape of frontal lobes	slightly concave	slightly concave	slightly concave	markedly concave
Position of frontal lobes	Extending well beyond inner orbital angles	Extending well beyond inner orbital angles	Not extending well beyond inner orbital angles	Extending well beyond inner orbital angles
Carapace ridges	Protogastric, faint	None	Epibranchial, long, minutely granular	None
Cheliped meri with a small tubercle on the antero-distal border	Yes	No	Yes	Yes
Anterolateral teeth	All blunt, rounded; one and five smallest	All blunt, rounded; one and five smallest	Teeth 1-4 broad, acutely pointed; tooth 5 narrow and sharp	Tooth 1 small, blunt, rounded; teeth 2-4 broad, acute; tooth 5 small, acute
G1: lobe present on subterminal outer surface of opening with papilliform setae	Yes	No	Lobe present; papilliform setae unconfirmed*	Unknown
Carapace and cheliped color	Patterned, light red to brick red and brown on a dusky white background	Patterned light to dark red on a stark white background, but sometimes with yellow hues	dusky white or with some purple marks*; chelipeds patterned light to dark red on dusky white background	Unknown
Ambulatory leg color	Patterned with colors similar to carapace on a somewhat transparent background	Uniformly white to yellow and somewhat transparent to opaque	Unknown	Unknown
Known distribution	Indonesia, Philippines Islands (confirmed), possibly across the Indo-Pacific	Philippines, Guam, New Caledonia	Hawaiian Islands	Papua New Guinea, Marquesas Islands

*Based on Edmondson (1954).

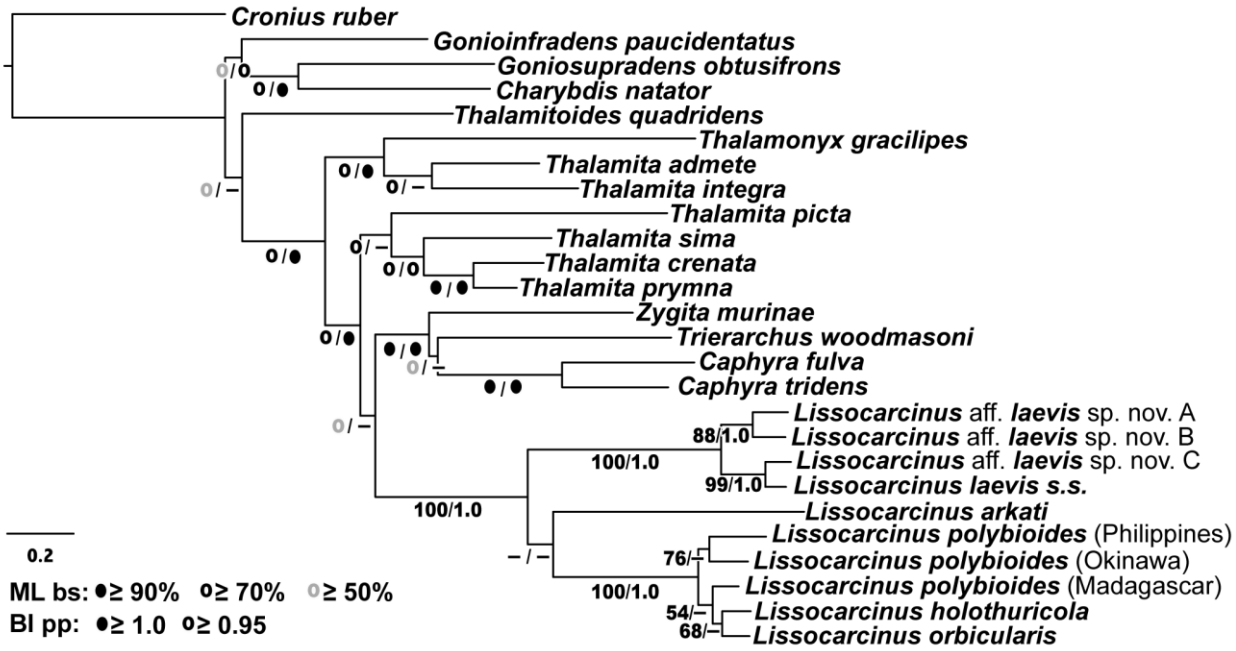

Figure 3-1. ML phylogram of 10 *Lissocarcinus* and 16 outgroup taxa based on analyses of 2484 bps of partial 16S rRNA, CO1, 12S rRNA, and H3 sequence data. Significant values reported with ML boostrap support first (≥50%, based on 500 replicate searches), followed by BI posterior probabilities (≥0.95).

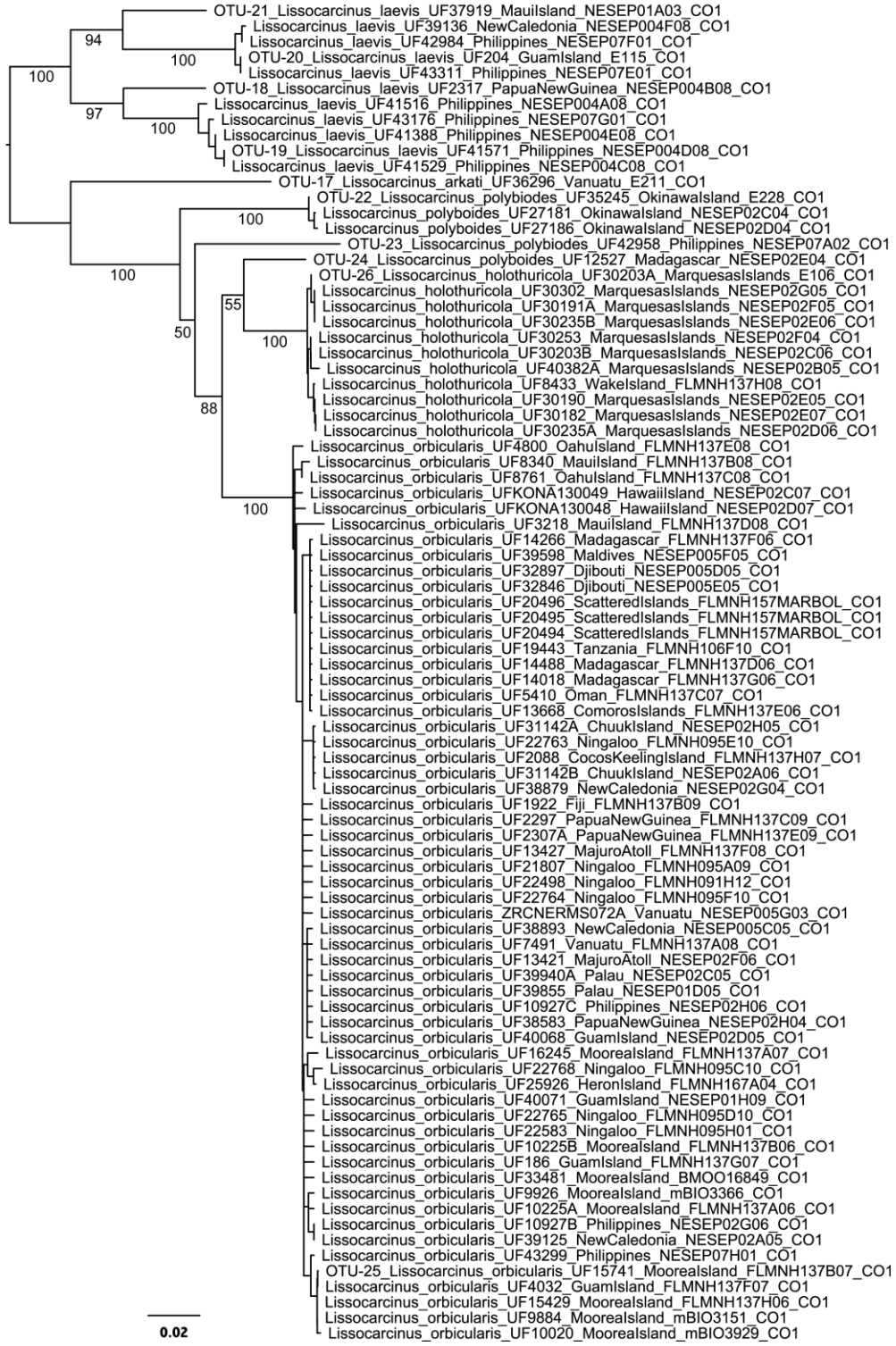

Figure 3-2. NJ topology (K2P model) of 657 bps of CO1 sequence data from 85 *Lissocarcinus* specimens. Bootstrap support values are based on 500 replicates; values greater than 50% are displayed.

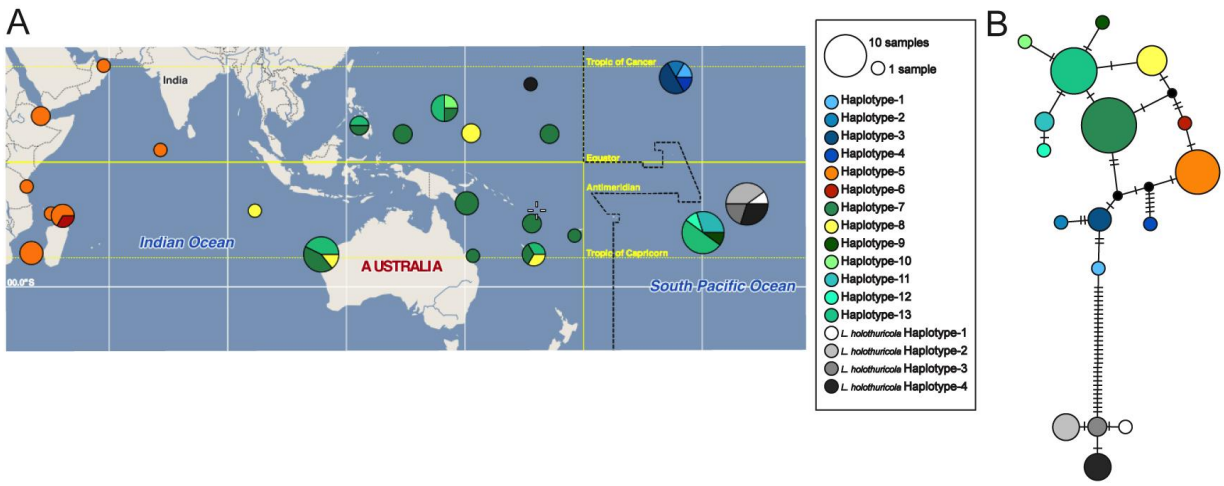

Figure 3-3. *Lissocarcinus orbicularis* and *L. holothuricola* CO1 (568 bps) haplotype diversity and distribution. A) CO1 haplotype distribution for 57 *L. orbicularis* (colored) and 11 *L. holothuricola* (grey scale) specimens. B) median-joining network for the same haplotypes (colors matching A and legend).

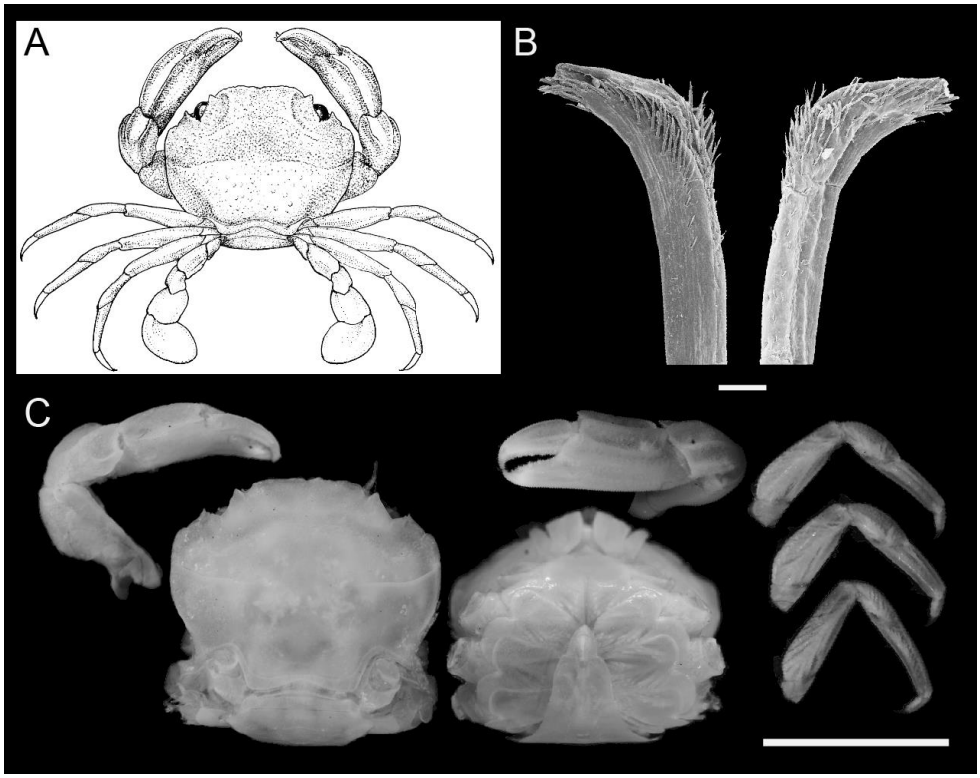

Figure 3-4 Holotype and original illustration of *Caphyra elegans* (Boone, 1934), comb. nov. (holotype: AMNH-IZC00249978). A) illustration from the original description of *Lissocarcinus elegans* Boone, 1934 (Plate 16). B) G1 outer (left) and inner (right) terminal surface of right G1 from holotype. C) composite photograph of all remaining material of holotype; left cheliped and body depicted in two views.

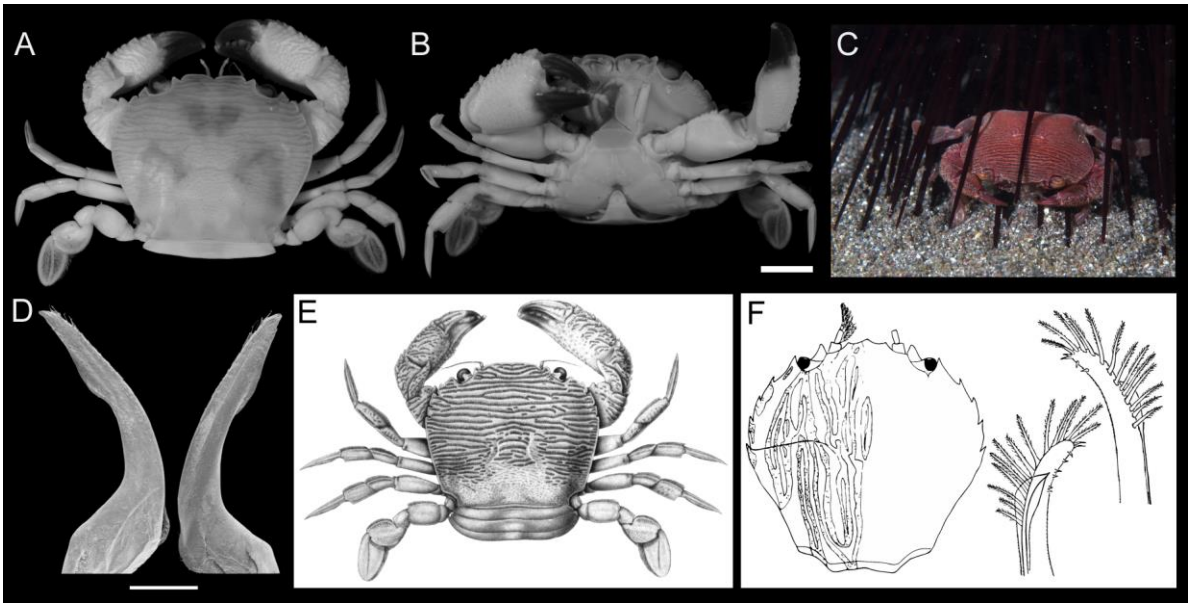

Figure 3-5. Morphology and live color of *Lissocarcinus arkati* Kemp, 1923, and original illustrations of type material for *L. arkati* and *L. echinodisci* Derijard, 1968. A) dorsal view of *L. arkati* (UF36296 A). B) ventral view; same specimen (scale= 5 mm). C) In situ photo graph of *L. arkati* on an urchin (C. Gloor; Lembeh, Indonesia, 2015; no voucher retained). D) inner and outer surface, respectively, of left G1 of *L. arkati* (scale= 1mm; UF36296 A). E) holotype illustration from the original description of *L. arkati* (Kemp, 1923) (Plate 10, Figure 1). F) holotype of *L. echinodisci* Derijard, 1968, re-illustrated from original description (Figures 1 and 9, Derijard, 1968); depicts carapace and outer and inner terminal surface of left G1, respectively.

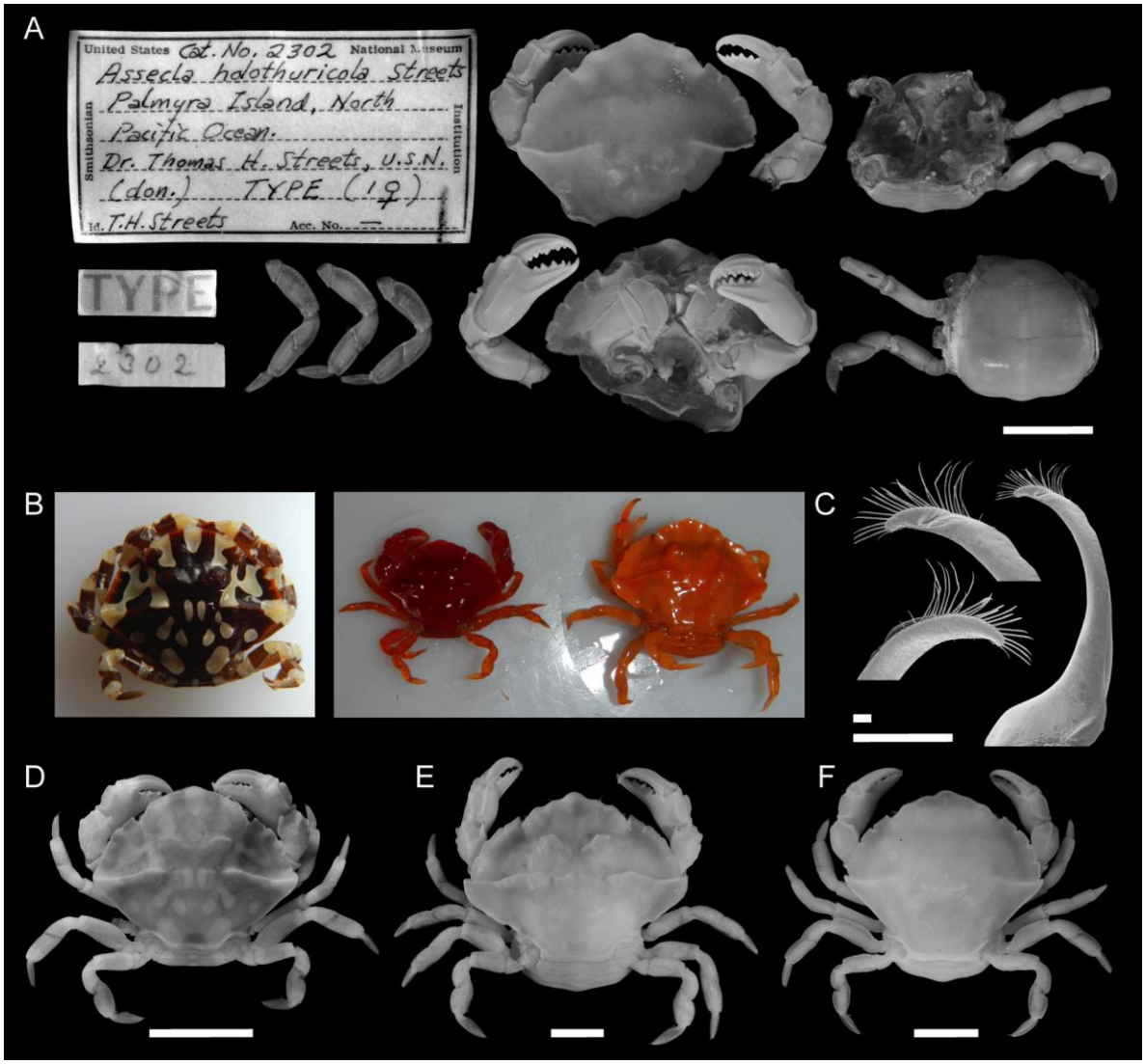

Figure 3-6. Holotype and additional material of *Lissocarcinus holothuricola* (Streets, 1877). A) holotype of *L. holothuricola* (USNM 2302, Palmyra Island). B) live color (UF30302, singleton; UF30203, pair). C) right G1 outer (top), inner (bottom) terminal surface, entire outer surface (right) (lower scale =1 mm) (UF30235-A). D) UF30302 (Marquesas Islands). E) UF30235-B (Marquesas Islands). F) NHMLAC PL0594 (Eniwetok Atoll). Scale= 5 mm for A) and D) through F).

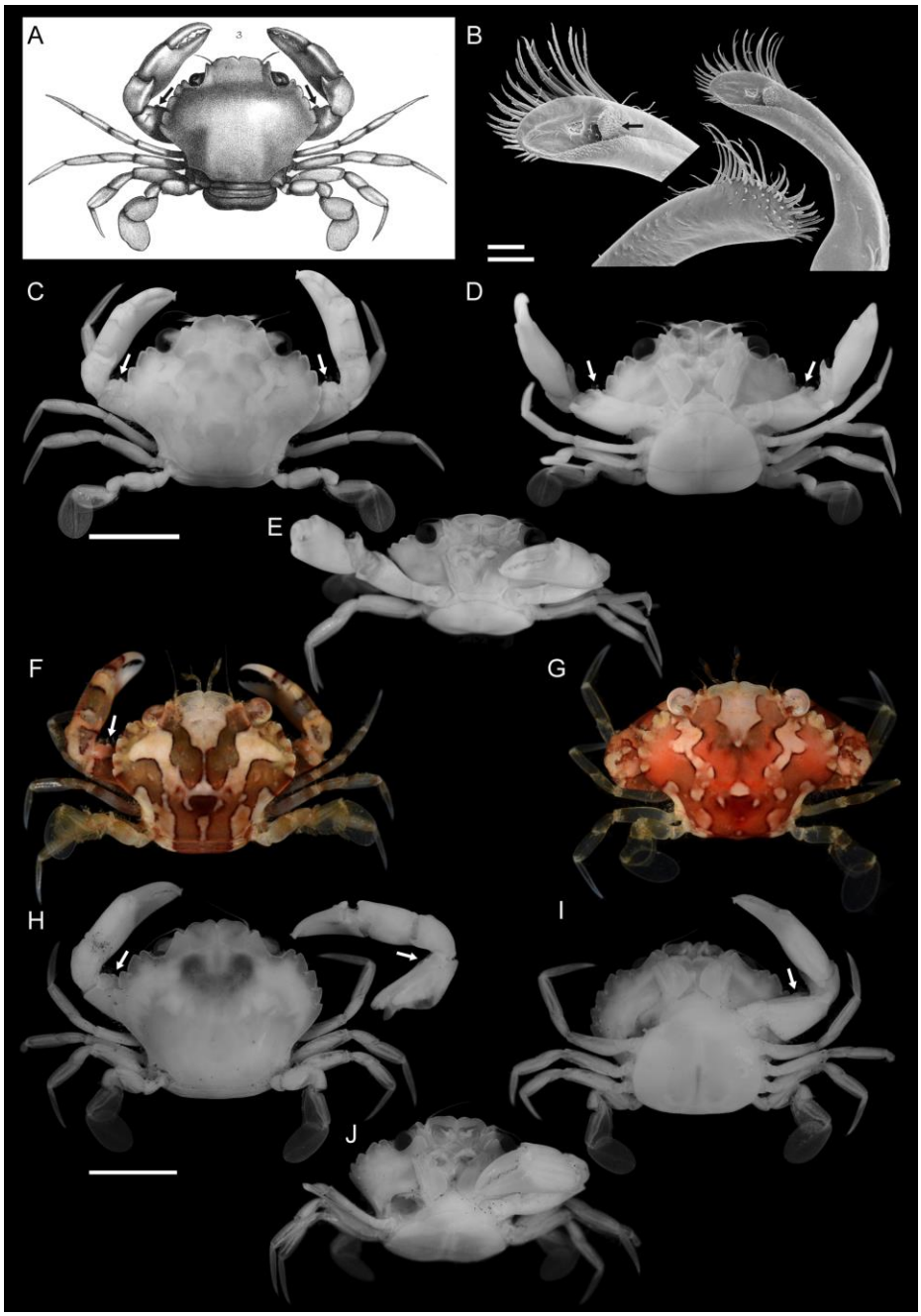

Figure 3-7. Illustration, morphology and live color of *Lissocarcinus laevis* Miers, 1886, *s.s.* and *L.* aff. *laevis* sp. nov. C. A) holotype illustration from original description of *L. laevis* Miers, 1886 (Plate 17, Figure 3a). B) right G1 of *L. laevis s.s.* (UF41529); outer (top) and inner (bottom) terminal surface, respectively (upper scale= 100 µm), entire outer surface (right) (lower scale= 200 µm). C) through E) *L. laevis s.s.* (UF41571; scale= 5 mm). F) *L. laevis s.s.* live color (UF-dPHIL_01943a). G) *L. laevis s.s.* live color (UF-dPHIL_03210a). H) through J) *L.* aff. *laevis* sp. nov. C. (UF2317; scale= 5 mm).

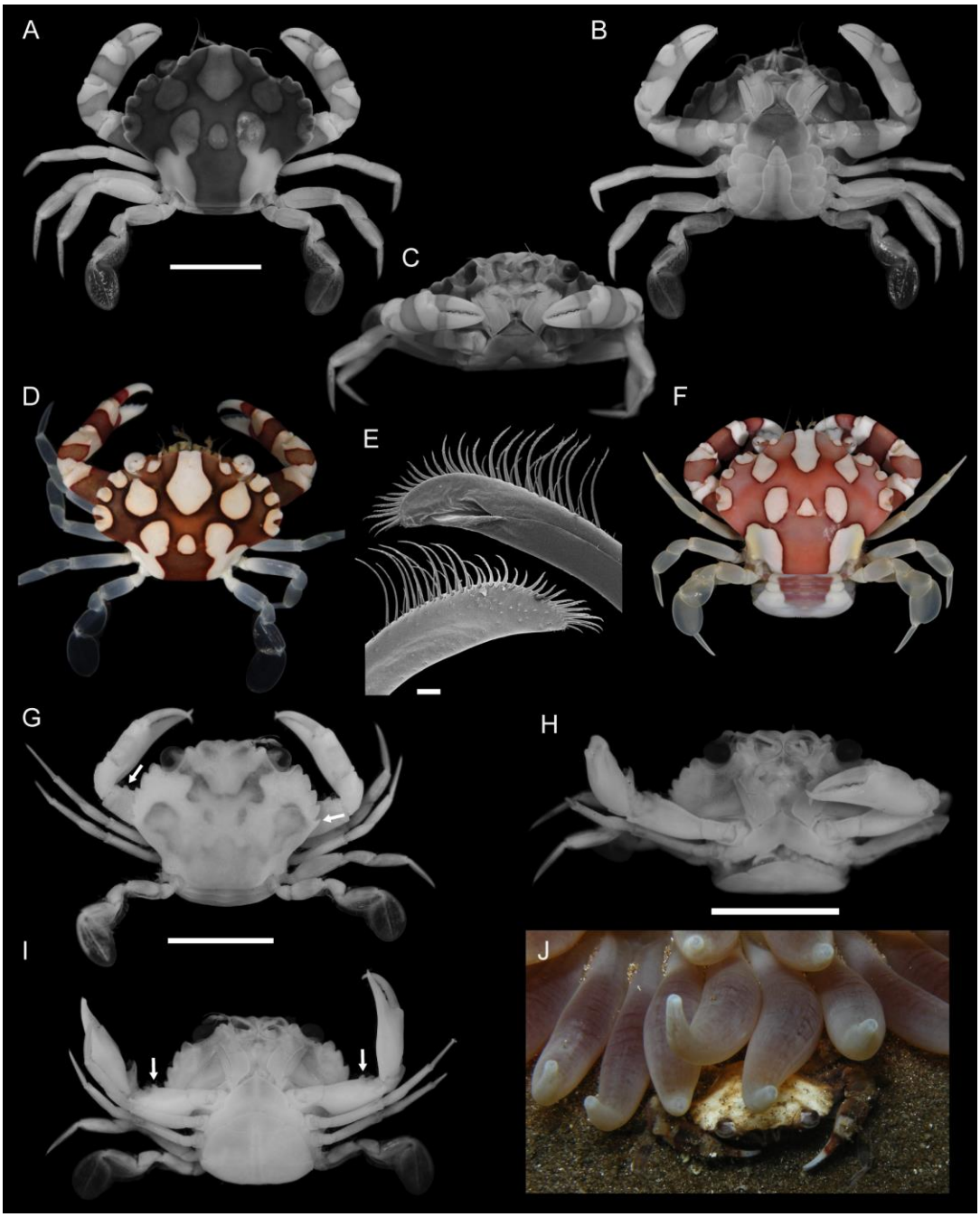

Figure 3-8. Morphology and live color of *Lissocarcinus* aff. *laevis* sp. nov. A and *L.* aff. *laevis* sp. nov. B. A) through C) *L.* aff. *laevis* sp. nov. A (UF42984; scale= 5 mm). D) live color *L.* aff. *laevis* sp. nov. A (UF42984) E) right G1 of *L. laevis* sp. nov. A (UF42984); inner (top) and outer (bottom) terminal surface, respectively (scale= 100 µm). F) live color *L.* aff. *laevis* sp. nov. A (UF39136). G) through I) *L.* aff. *laevis* sp. nov. B (UF37919; scales= 5 mm). J) In situ photo graph of *L.* aff. *laevis* sp. nov. B under *Heteractis malu* (C. Pitmann; Maalaea Bay, Maui Island, 2011; no voucher retained).

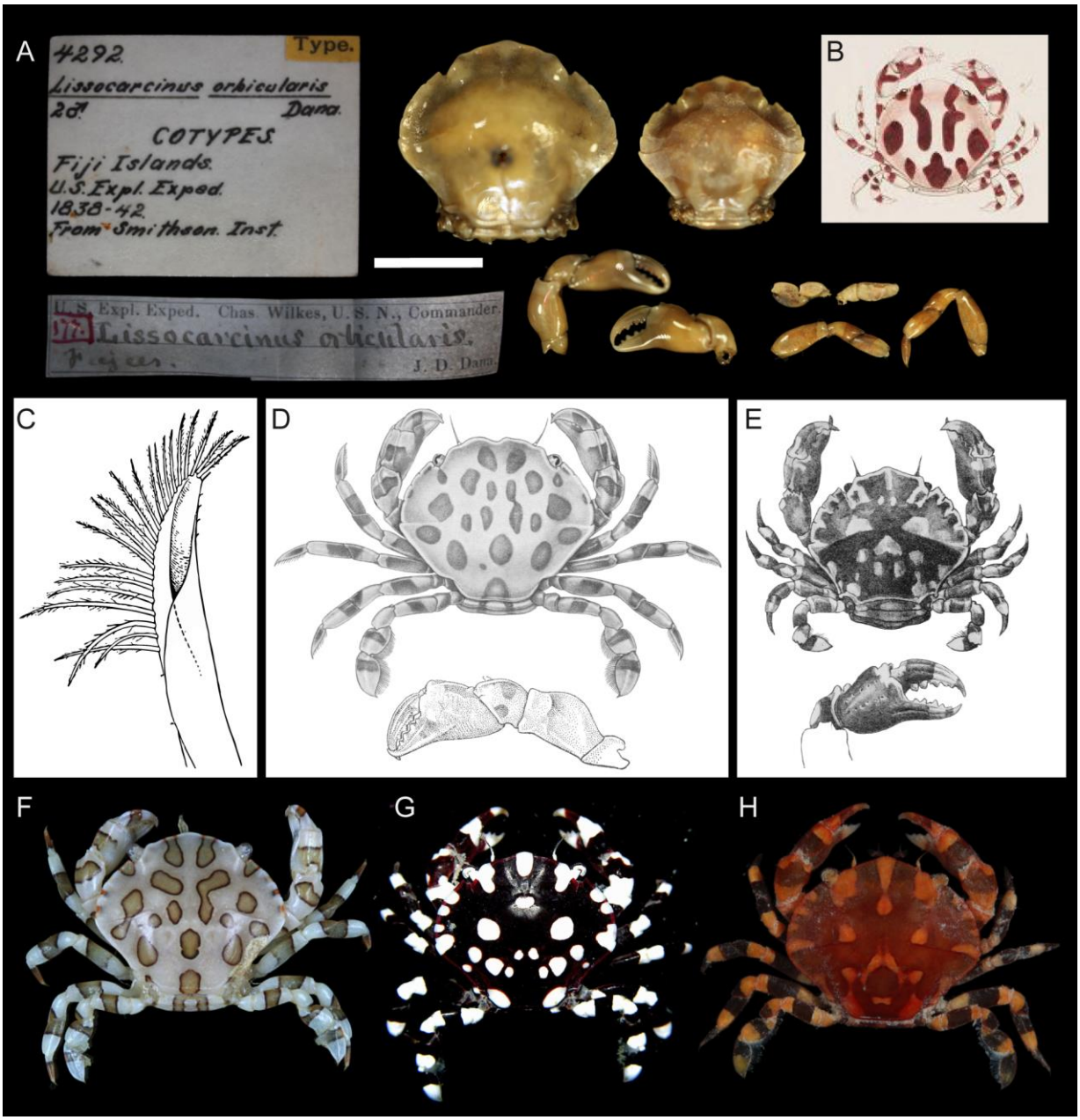

Figure 3-9. Syntype and additional material and illustrations of *Lissocarcinus orbicularis* Dana, 1852. A) composite photograph of remaining syntype material (MCZ CRU-4292; 2 ♂; scale= 5 mm). B) type illustration from original description (Plate 18, Figure 1a). C) left G1 outer surface for *L. orbicularis*; re-illustrated from Forest & Guinot (1961; Figure 15b). D) holotype illustration from the original description of *L. ornatus* Chopra, 1931 (Plate 7, Figure 1; text Figure 1). E) holotype illustration from original description of *L. pulchellus* Muller, 1887 (Plate 5, Figure 6). F) through H) live color (UF15741, UF16245, UF23972, respectively).

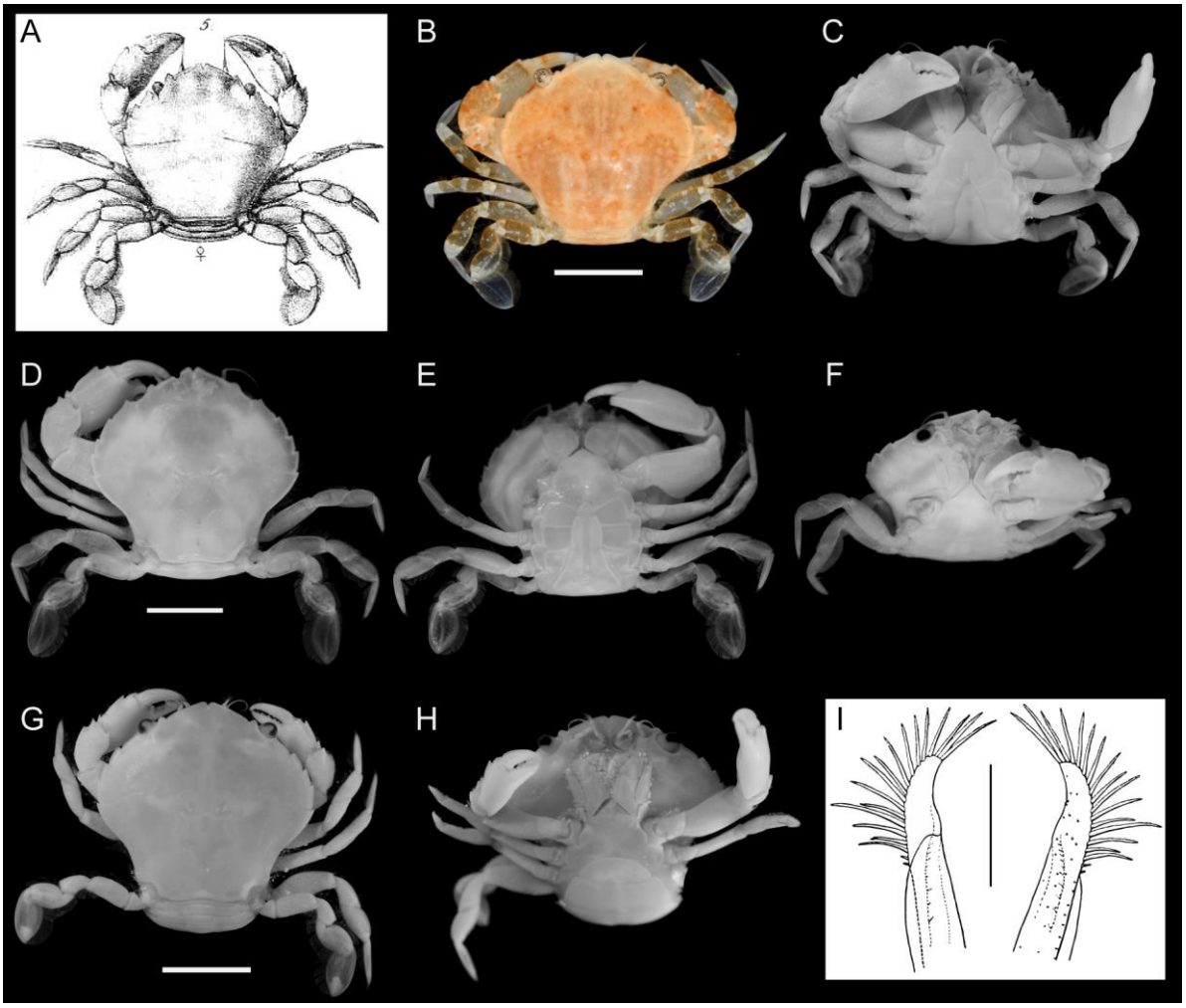

Figure 3-10. Holotype illustration and additional material of *Lissocarcinus polybioides* Adams & White, 1849, species complex. A) holotype illustration from original description (Plate 11, Figure 5). B) and C) live color and ventral surface *L. polybioides*, Mindoro, Philippines (UF42958). D) through F) *L. polybioides*, Okinawa, Japan (UF35245-A). G) and H) *L. polybioides*, Nosy Be, Madagascar (UF12527). I) G1 outer and inner terminal surface, respectively; re-illustrated from Stephenson & Campbell (1959; Figure 2H; scale= 500 µm). Specimen scales= 5 mm

CHAPTER 4
MORPHOLOGICAL DISPARITY IN CARAPACE SHAPE AND THE EMERGENCE OF SYMBIOTIC SWIMMING CRABS (PORTUNIDAE)

Introduction

Commonly referred to as “swimming crabs”, members of the Family Portunidae are known for being much better at swimming than any other group of brachyuran crabs. This fact can been attributed to a number of morphological adaptations typical of the group, including a broader, more laterally streamlined carapace and modified, paddle-shaped posterior legs (Cochran, 1935; Hartnoll, 1971). Yet members of the portunid tribe Caphyrini exhibit a divergent morphology and ecology that suggests they have abandoned this natatory lifestyle. Compared with most portunids, these crabs are smaller, rounder, less streamlined and many have nearly or completely lost the paddle shape of their posterior legs. Not surprisingly, they are generally poor at swimming and have adopted a more sedentary lifestyle. They are also unique among portunids for living in symbioses with algae, echinoderm, sea anemones and soft corals. Recent molecular phylogenetic work (Chapter 2) has revealed that Caphyrini evolved within the genus *Thalamita* s.l. *Thalamita* is a diverse lineage of free-living portunid crabs common in tropical reefs. Thalamitinae thus provides an interesting system to study the origin of novel morphological diversity (i.e. disparity).

Theory on body-size evolution predicts that miniaturization can generate substantial morphological novelty and facilitate ecological divergence, including symbiosis (Hanken & Wake, 1993). Caphyrini and some *Thalamita* species are among the smallest portunid taxa. Phylogenetic and morphological investigations of Thalamitinae can be used to assess how functionally significant morphology evolved leading up to and following a major ecological divergence. Here I use a geometric

morphometric approach to investigate the evolution of carapace shape and size change across Thalamitinae. Specifically, I explore whether considerable, quantifiable, morphological change occurred before, during or after changes in body-size and whether this corresponded to the emergence of the symbiotic clade Caphyrini.

Materials and Methods

Vouchered Material

Morphological work was conducted on 995 specimens, from 103 of the 107 Thalamitinae OTUs included in the phylogenetic analyses (Table 4-1, 4-3): Natural History Museum of Los Angeles County, Los Angeles, California, USA (NHMLAC); Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (UF); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC).

Molecular Work and Analyses

For this study a molecular dataset was constructed for 107 Thalamitinae taxa and 417 sequences of CO1, 16S rRNA, H3, and 12S rRNA; including 153 generated for this study (Table 4-1). Sequence alignments were carried out using MAFFT v7.123b (Katoh & Standley, 2013) under the E-INS-i setting or, for rRNA sequences, with Guidance2 as outlined in Chapter 2. The resulting concatenated alignment was 2,484 bps in length. Substitution models and partition schemes (Table 4-2) were selected using the BIC criterion and a greedy search algorithm in Partitionfinder v.1.1.1 (Lanfear et al., 2012). Partitioned maximum likelihood (ML) phylogenetic analyses were carried using GARLI 2.0 (Zwickl 2006), and bayesian analyses (BI) were performed using MrBayes v3.2.5 (Ronquist et al., 2012). ML analyses consisted of 300 independent

searches, and support values for the best scoring topology were assessed with 500 bootstrap replicate searches. BI analyses were run for 25 million generations, sampling every 10,000 generations, with an arbitrary burn-in of 5 million generations. Convergence was evaluated using Tracer v.1.6 (Rambaut et al., 2014) and by confirming that the standard deviation of split frequencies was less than 0.01. Phylogenetic analyses were carried out on the CIPRES Science Gateway (Miller et al., 2010).

A total of 519 CO1 or 16S rRNA sequences were used to confirm morphological identification of over half of the 995 specimens examined (see Table 4-1). Barcode data was frequently used to correctly identify hard to distinguish species (e.g., *Thalamita chaptalii* vs. *T. parvidens*) or ESUs (e.g., *T. picta* species complex). ESU assignments were made using the software ABGD (Puillandre et al., 2011), with a barcode gap distinction of 2% K2P divergence (analyses not shown). These results were used to guide morphological identification, but some morphologically distinct species were recognized even when this genetic threshold was not met (e.g., the complex *T. pelsarti, T. prymna*, and *T. tenuipes*).

Geometric Morphometric Analyses

For each specimen the carapace was photographed and the coordinates of 18 homologous landmark (Figure 4-1) were captured using the program tpsDig2. Geometric morphometric (GMM) analyses were performed on the resulting dataset using MorphoJ v1.06d (Klingenberg, 2011). Because of object symmetry, a Procrustes fit was performed with reflection. Asymmetry was not significant, nor were any significant outlier shape configurations detected. The symmetric component of shape was used to generate a covariance matrix and perform a principal component analysis.

Relevant PC axes were plotted against one another to generate two-dimensional theoretical morphospaces. The same analyses were performed on a second dataset, generated from the first, consisting of OTU-averaged shape coordinates. From these analyses a theoretical phylomorphospace (Sidlauskas, 2008) was generated using relevant PC axes and incorporated the ML topology, trimmed to include the 103 taxa for which GMM data was available. Phylomorphospace mapping included a 10,000 replicate permutation test for phylogenetic signal in the shape data. As a null hypothesis, this test simulates the absence of a phylogenetic signal in shape data by permuting values across all terminal taxa of the provided phylogeny. Centroid size and the first three PC axes were also each plotted on the 103 taxa topology using unweighted squared change parsimony implemented in Mesquite v3.10 (Maddison & Maddison, 2016).

Results and Discussion

Phylogenetic Results. ML and BI phylogenetic analyses of 107 Thalamitinae taxa recovered consistent topologies (Figures 4-2 and 4-3) that demonstrated improved resolution and support values relative to that recovered in Chapter 2. Results confirm the monophyly of Caphyrini and provide greater resolution at several nodes.

Geometric Morphometric Results. Greater than 90% of carapace shape disparity was explained by the first three PC axes. PC1 accounted for 67% of this variance while PC2 and PC3 accounted for 17% and 7%, respectively. The range of carapace shape disparity explained by each PC axis is illustrated in Figure 4-4. For each PC axis, the minimum values incorporate carapace shapes present in Caphyrini. Theoretical morphospaces generated from the first three PC axes each reveal that Caphyrini taxa are more widely distributed than, but always share some overlap with,

Thalamita s.l. clades. However, the Caphyrini taxa most frequently overlapping with *Thalamita* include *Trierachus* and *Zygita* species. Symbiotic associations in these two genera have are thought to be facultative (Chapter 2). Theoretical phylomorphospace projections of PC axes based on PCA of taxon averaged shape values (Figures 4-8 to 4-10) are similar to the morphospace projections, with Caphyrini taxa occupying a significantly great range of phylomorphospace, frequently solely occupied by the clade. The permutation test (10,000 replicates) for phylogenetic signal in the PC axes was significant ($p < 0.0001$), indicating that shape values are not independent from the provided phylogeny. Values for each of the three PC axes were also reconstructed on the ML topology using squared change parsimony (Figures 4-11 to 4-13) and revealed similar results to that of phylomorphospace projections. That is, each PC axes revealed a greater level of disparity in carapace shape for Caphyrini than its sister *Thalamita s.l.* clades. Finally, parsimony reconstruction of carapace size (as centroid size) revealed that *Thalamita s.l.* is dominated by small taxa and Caphyrini is not considerably smaller (or larger) than its sister *Thalamita* lineages (Figure 4-14). However, this size reconstruction also clearly depicts the emergence of a single large-sized clade within the *Thalamita s.l.*, here termed *Thalamita* clade 4.

Concluding Remarks. Morphological disparity is an important measure of biodiversity and understanding its evolutionary dynamics is a major macroevolutionary research agenda (Jablonski, 2000). Though debate persists about the relative importance of adaptive and non-adaptive modes of evolution (e.g., Rundell & Price, 2009; Weins, 2011), it is clear that considerable morphological disparity can accumulate

during an evolutionary radiation and that ecology can significantly influence this process (Erwin 2007; Glor, 2010; Losos, 2011; Monteiro and Nogueira, 2011; Price et al., 2011).

The present study contributes to this debate, revealing that a greater level of morphological diversity is present in symbiotic than more diverse and older non-symbiotic Thalamitinae lineages. These results suggest that transition from a free-living to symbiotic lifestyle was characterized by a greater, and likely more rapid, accumulation of morphological disparity than in non-symbiotic lineages.

Further analyses (e.g., with model-based phylogenetic comparative methods) may be able to better test this pattern, but the results presented here are compelling. Future work may also benefit from considering how allometry has influenced the evolution of shape. The investigation of allometric patterns in geometric morphometric data is complicated, because analyses are neither straightforward nor easy to implement in existing geometric morphometric software packages. However, this area has received renewed attention both empirically and theoretically (see discussion Klingenberg, 2016). New methods are increasingly implemented in the R program geomorph (e.g., v.3.03 release September, 2016; Adams et al., 2013). Data presented here seems quite amenable to these analyses, but their implementation was beyond the scope of the present study.

Table 4-1. Taxon sampling for molecular and geometric morphometric (GMM) analyses.

Taxon	OTU ID	CO1	16S rRNA	H3	12S rRNA	Voucher IDs	GMM Specimen Count	DNA Barcoded specimens
Clade: Caphyrini								
Caphyra bedoti	CH3OTU-002	KT365695	KT365591	KT425019	XXXXXXXX	ZRC-NERM026	1	2
Caphyra holocarinata	CH3OTU-005	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF39105	2	2
Caphyra loevis	CH3OTU-001	KT365696	KT365529	KT424990	XXXXXXXX	UF11748	6	5
Caphyra loevis	CH3OTU-003	KT365697	KT365592	KT425009	XXXXXXXX	ZRC-NERM025	13	5
Caphyra sp. A	CH3OTU-009	KT365699	KT365531	NA	XXXXXXXX	UF5061-A	1	1
Caphyra sp. C	CH3OTU-008	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF21835	1	1
Caphyra tridens	CH3OTU-006	KT365701	KT365532	KT425003	XXXXXXXX	UF15907	7	6
Caphyra yookadai	CH3OTU-007	KT365702	KT365593	KT424993	XXXXXXXX	ZRC-NERM023	1	2
Lissocarcinus aff. laevis sp. A	CH3OTU-032	KT365730	KT365550	XXXXXXXX	XXXXXXXX	UF204	4	4
Lissocarcinus aff. laevis sp. B	CH3OTU-035	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF37919	2	1
Lissocarcinus aff. laevis sp. C	CH3OTU-033	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF2317	5	1
Lissocarcinus arkati	CH3OTU-030	KT365729	KT365549	KT425045	XXXXXXXX	UF36296-A	2	1
Lissocarcinus holothuricola	CH3OTU-031	KT365731	KT365551	KT425041	XXXXXXXX	UF30203	27	11
Lissocarcinus laevis	CH3OTU-034	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF41571	6	5
Lissocarcinus orbicularis	CH3OTU-036	KT365732	KT365552	KT425032	XXXXXXXX	UF15741 / UF15429	65	32
Lissocarcinus polyboides	CH3OTU-037	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF12527	1	1
Lissocarcinus polybioides	CH3OTU-038	KT365733	KT365602	KT424994	XXXXXXXX	UF35245-A	11	4

XXXXXXXX = newly generated sequences for this chapter, GenBank number TBD; NA = no sequence available

Table 4-1. Continued.

Taxon	OTU ID	CO1	16S rRNA	H3	12S rRNA	Voucher IDs	GMM Specimen Count	DNA Barcoded specimens
Trierarchus cooperi sp. A	CH3OTU-054	KT365760	KT365570	KT424996	XXXXXXXX	UF16152	11	9
Trierarchus cooperi sp. B	CH3OTU-055	KT365761	KT365571	KT425029	XXXXXXXX	UF16949	13	6
Trierarchus rotundifrons	CH3OTU-004	KT365698	KT365530	KT424989	XXXXXXXX	UF4079 / UF4057	15	4
Trierarchus squamosus	CH3OTU-102	NA	KU737571	NA	NA	USNM102963	1	1
Trierarchus woodmasoni	CH3OTU-104	KT365791	KT365624	KT425026	XXXXXXXX	UF4114-A	15	9
Zygita longifrons	CH3OTU-071	KT365773	KT365613	KT425002	XXXXXXXX	UF7343	12	2
Zygita murinae	CH3OTU-075	KT365776	KT365615	KT425018	XXXXXXXX	UF36525	4	2
Clade: *Charybdis*								
Charybdis acuta	CH3OTU-010	XXXXXXXX	KT365594	KT425049	XXXXXXXX	UF13466	1	1
Charybdis annulata	CH3OTU-012	KT365708	KT365595	KT425027	XXXXXXXX	UF22076	1	1
Charybdis bimaculata	CH3OTU-013	KT365709	KT365596	KT425036	XXXXXXXX	ZRC-NERM019	NONE	1
Charybdis callianassa	CH3OTU-014	KT365710	KT365537	KT425035	XXXXXXXX	ZRC-NERM003	NONE	1
Charybdis feriatus	CH3OTU-016	KT365712	KT365538	KT425051	XXXXXXXX	UF3739	1	1
Charybdis hellerii	CH3OTU-018	KT365715	KT365540	KT424999	XXXXXXXX	UF11430	2	1
Charybdis japonica	CH3OTU-019	KT365716	XXXXXXXX	KT425042	XXXXXXXX	ZRC-NERM006	NONE	1
Charybdis lucifera	CH3OTU-020	KT365718	KT365542	KT425034	XXXXXXXX	UF7684 / UF7667	8	2
Charybdis natator	CH3OTU-021	KT365719	KT365543	KT424998	XXXXXXXX	UF3707 / UF21403	2	2

Table 4-1. Continued.

Taxon	OTU ID	CO1	16S rRNA	H3	12S rRNA	Voucher IDs	GMM Specimen Count	DNA Barcoded specimens
Charybdis orientalis	CH3OTU-023	KT588225	KT588234	KT781074	XXXXXXXX	USNM112062	1	1
Charybdis variegata	CH3OTU-024	KT365723	KT365600	KT425043	XXXXXXXX	ZRC-NERM032	NONE	1
Charybdis longicollis	CH3OTU-025	KT365717	KT365541	KT425054	XXXXXXXX	UF3179	2	1
Charybdis sagamiensis	CH3OTU-026	KT365721	KT365598	XXXXXXXX	XXXXXXXX	UF29479	1	1
Clade: Cronius								
Cronius edwardsii	CH3OTU-027	KT588227	XXXXXXXX	XXXXXXXX	XXXXXXXX	USNM112311 / USNM1254607	2	2
Cronius ruber	CH3OTU-028	KT365725	KT365546	KT425008	XXXXXXXX	UF25995 / UF26364	3	2
Clade: *Gonioinfradens*								
Gonioinfradens paucidentata	CH3OTU-029	KT365726	KT365547	KT588216	XXXXXXXX	UF5109 / UF30184	3	1
Clade: Goniosupradens								
Charybdis acutifrons	CH3OTU-011	KT365707	KT365535	KT425033	XXXXXXXX	UF17047 / UF7114	3	2
Charybdis erythrodactyla	CH3OTU-015	KT365711	KT365597	XXXXXXXX	XXXXXXXX	UF1398	1	1
Charybdis hawaiensis	CH3OTU-017	KT365714	KT365539	KT425023	XXXXXXXX	UF25871	2	1
Charybdis obtusifrons	CH3OTU-022	KT365720	KT365544	KT425007	XXXXXXXX	UF16599	1	1
Clade: *Thalamita s.s*								
Thalamita admete s.s.	CH3OTU-041	KT365749	KT365562	KT425014	XXXXXXXX	UF7688-A / UF16971	69	44
Thalamita aff. admete sp. A	CH3OTU-039	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF12308	10	7

Table 4-1. Continued.

Taxon	OTU ID	CO1	16S rRNA	H3	12S rRNA	Voucher IDs	GMM Specimen Count	DNA Barcoded specimens
Thalamita aff. admete sp. B	CH3OTU-040	KT365748	KT365561	KT424995	XXXXXXXX	UF17745 / UF17744	19	12
Thalamita aff. gatavakensis	CH3OTU-092	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	USNM274270-A	4	2
Thalamita aff. integra	CH3OTU-066	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF8598	23	2
Thalamita auauensis	CH3OTU-046	KT365750	KT365563	KT425022	XXXXXXXX	UF12320	21	1
Thalamita bevisi	CH3OTU-048	KT365751	KT365564	KT425048	XXXXXXXX	UF197	18	4
Thalamita bilobata	CH3OTU-049	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF3384	6	3
Thalamita chaptalii	CH3OTU-052	KT365758	KT365568	KT425047	XXXXXXXX	UF13103 / UF206	25	12
Thalamita difficilis	CH3OTU-047	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	USNM1226914	2	2
Thalamita gatavakensis	CH3OTU-060	KT365767	KT365576	KT424997	XXXXXXXX	UF16649	6	6
Thalamita gatavakensis	CH3OTU-061	KT365766	KT365575	KT424992	XXXXXXXX	UF17486 / UF17469	15	16
Thalamita gloriensis	CH3OTU-062	KT365779	KT365582	KT425038	XXXXXXXX	UF25902	4	3
Thalamita granosimana	CH3OTU-064	KT365769	KT365577	KT425005	XXXXXXXX	UF24790	15	9
Thalamita integra	CH3OTU-067	KT365770	KT365578	KT425028	XXXXXXXX	UF22085 / UF587	23	20
Thalamita iranica	CH3OTU-068	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF36855	1	1
Thalamita margaritimana	CH3OTU-073	NA	XXXXXXXX	NA	XXXXXXXX	USNM41108-A	2	1
Thalamita parvidens	CH3OTU-078	KT365757	KT365567	KT425037	XXXXXXXX	UF17595	25	13
Thalamita pilumnoides	CH3OTU-082	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF22623	6	5

Table 4-1. Continued.

Taxon	OTU ID	CO1	16S rRNA	H3	12S rRNA	Voucher IDs	GMM Specimen Count	DNA Barcoded specimens
Thalamita platypenis	CH3OTU-084	NA	KT365617	NA	XXXXXXXX	USNM151091	5	2
Thalamita poissonii	CH3OTU-085	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF7581	15	4
Thalamita quadrilobata	CH3OTU-091	KT365782	KT365585	KT425015	XXXXXXXX	UF14254 / UF14608	18	15
Thalamita savignyi	CH3OTU-094	KT365784	KT365618	KT425061	XXXXXXXX	UF7689-A	14	9
Thalamita spiceri	CH3OTU-083	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF40175	8	7
Thalamita stephensoni	CH3OTU-103	KT365790	KT365623	KT425059	XXXXXXXX	UF17070	10	5
Clade: *Thalamita* clade 2								
Thalamita aff. mitsiensis	CH3OTU-044	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF33748	1	1
Thalamita aff. spinifera	CH3OTU-100	KT365788	KT365621	KT425001	XXXXXXXX	UF33379	8	5
Thalamita bouvieri	CH3OTU-050	KT365752	KT365565	KT425016	XXXXXXXX	UF24801 / UF17562	12	7
Thalamita cf. macropus	CH3OTU-042	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	ZRC-NERMS066	8	1
Thalamita imparimana	CH3OTU-065	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	ZRC-NERMS075-A	8	2
Thalamita kukenthali	CH3OTU-079	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF574	2	2
Thalamita mitsiensis	CH3OTU-074	XXXXXXXX	KT365580	KT425053	XXXXXXXX	UF190 / UF21937	14	12
Thalamita philippinensis	CH3OTU-070	KT365772	KT365579	KT425006	XXXXXXXX	UF24920	11	8
Thalamita picta sp. A	CH3OTU-081	KT365778	KT365581	KT425013	XXXXXXXX	UF24881	19	21
Thalamita picta sp. B	CH3OTU-080	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF161	13	7

Table 4-1. Continued.

Taxon	OTU ID	CO1	16S rRNA	H3	12S rRNA	Voucher IDs	GMM Specimen Count	DNA Barcoded specimens
Thalamita seurati sp. A	CH3OTU-095	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF10717	5	3
Thalamita seurati sp. B	CH3OTU-096	KT365785	KT365587	KT425004	XXXXXXXX	UF12832	3	4
Thalamita spinifera	CH3OTU-058	XXXXXXXX	XXXXXXXX	NA	NA	USNM127104 / USNM29626-A	9	4
Clade: *Thalamita* clade 3								
Thalamita aff. sexlobata	CH3OTU-045	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	ZRC-NERMS073	2	1
Thalamita kagosimensis	CH3OTU-069	KT365771	KT365612	KT425011	XXXXXXXX	ZRC-NERMS063	2	2
Thalamita oculea	CH3OTU-077	KT365777	KT365616	KT425044	XXXXXXXX	ZRC-NERM056	4	4
Thalamita plicatifrons	CH3OTU-072	KT365774	KT365614	KT425010	XXXXXXXX	ZRC-NERM040	7	3
Thalamita pseudoculea	CH3OTU-089	KT365754	KT365610	KT425050	XXXXXXXX	UF13877	15	6
Thalamita pseudopoissoni	CH3OTU-076	KT365755	KT365609	KT425055	XXXXXXXX	UF5051	2	2
Thalamita sexlobata	CH3OTU-097	NA	XXXXXXXX	XXXXXXXX	XXXXXXXX	USNM274296	2	1
Thalamita sima	CH3OTU-098	KT365786	KT365619	XXXXXXXX	XXXXXXXX	UF35869	27	6
Clade: *Thalamita* clade 4								
Thalamita aff. rubridens	CH3OTU-043	KT365756	KT365566	KT425021	XXXXXXXX	UF25803	5	4
Thalamita cerasma	CH3OTU-051	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF39852	11	2
Thalamita coeruleipes	CH3OTU-053	KT365759	KT365569	KT425057	XXXXXXXX	UF3232	24	13
Thalamita crenata	CH3OTU-056	KT365763	KT365572	KT424991	XXXXXXXX	UF8950 / UF17752	42	7

Table 4-1. Continued.

Taxon	OTU ID	CO1	16S rRNA	H3	12S rRNA	Voucher IDs	GMM Specimen Count	DNA Barcoded specimens
Thalamita danae	CH3OTU-057	KT365764	KT365573	KT425031	XXXXXXXX	UF25992 / UF22114	31	9
Thalamita foresti	CH3OTU-059	KT365765	KT365574	KT425040	XXXXXXXX	UF2222	11	3
Thalamita pelsarti	CH3OTU-087	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	ZRC-NERM013 / UF41408	1	2
Thalamita prymna	CH3OTU-086	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF16749	12	4
Thalamita pseudopelsarti	CH3OTU-090	KT365781	KT365584	KT425039	XXXXXXXX	UF16218	11	8
Thalamita rubridens	CH3OTU-093	KT365783	KT365586	KT425060	XXXXXXXX	UF7700	2	1
Thalamita spinicarpa	CH3OTU-099	KT365787	KT365620	KT425012	XXXXXXXX	UF36225	6	2
Thalamita spinimana	CH3OTU-101	KT365789	KT365622	XXXXXXXX	XXXXXXXX	UF36209 / UF39973	18	2
Thalamita tenuipes	CH3OTU-088	XXXXXXXX	KT365583	KT425025	XXXXXXXX	UF7819 / UF14613	3	3
Clade: *Thalamitoides*								
Thalamitoides quadridens	CH3OTU-105	XXXXXXXX	KT365588	KT425017	XXXXXXXX	UF18495	1	1
Thalamitoides spinigera	CH3OTU-106	KT365793	KT365625	XXXXXXXX	XXXXXXXX	UF32881	1	1
Thalamitoides tridens	CH3OTU-107	KT365794	KT365626	XXXXXXXX	XXXXXXXX	UF18231 / UF39860	1	1
Clade: *Thalamonyx*								
Thalamonyx gracilipes	CH3OTU-063	XXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXX	UF3784-A	16	7

Table 4-2. Best scoring partition schemes for the concatenated molecular dataset

Marker	Marker Subset	Alignment positions	Model for ML Runs	Partition ID	Model for BI Runs	Partition ID
CO1	Codon Pos. 1	1-657\3	TrNef+I+G	1	SYM+I+G	1
	Codon Pos. 2	2-657\3	F81+I	2	F81+I	2
	Codon Pos. 3	3-657\3	TrN+I+G	3	GTR+I+G	3
16S rRNA + tRNA-LEU + NADH1	ND1 Codon Pos. 1	658-1061\3	TrN+I+G	4	HKY+I+G	4
	ND1 Codon Pos. 2	659-1061\3	TrN+G	5	GTR+G	5
	ND1 Codon Pos. 3	660-1061\3	TrN+I+G	3	GTR+I+G	3
	tRNA-LEU Codon Pos. 1	1062-1130\3	TrN+G	5	HKY+I+G	4
	tRNA-LEU Codon Pos. 2	1063-1130\3	TrN+I+G	6	GTR+I+G	6
	tRNA-LEU Codon Pos. 3	1064-1130\3	TrNef+I+G	1	SYM+I+G	1
	16S rRNA	1131-1750	K81uf+I+G	7	GTR+I+G	7
12S rRNA	Partial fragment	1751-2116	TrN+I+G	6	GTR+I+G	6
H3	Codon Pos. 1	2118-2444\3	TrNef+I	9	SYM+I+G	1
	Codon Pos. 2	2119-2444\3	TrNef+I	9	GTR+G	8
	Codon Pos. 3	2117-2444\3	GTR+G	8	JC+I	9

Table 4-3. Vouchered specimens used for geometric morphometric analyses (GMM)

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-001	*Caphyra fulva*	UF11748, PL0744; UF28483A, PL0793; UF28483B, PL0794; UF38855, PL1218; UF38880, PL1213; UF38885, PL1216
CH3OTU-002	*Caphyra bedoti*	UF5061B, PL0767
CH3OTU-003	*Caphyra loevis*	UF6377, PL1219; UF38851A, PL0706; UF38876A, PL0795; UF38876F, PL0800; UF38876H, PL0802; UF38876B, PL0796; UF38876C, PL0797; UF38876D, PL0798; UF38876E, PL0799; UF38881, PL1215; UF39063A, PL1229; UF39063B, PL1230; UF39377, PL1214
CH3OTU-004	*Trierarchus rotundifrons*	UF4079, PL0725; UF5085, PL1154; UF38849, PL1155; UF40038, PL1156; UF40067A, PL1160; UF40070A, PL1161; UF40070B, PL1162; UF40109A, PL1157; UF40109B, PL1158; UF40109C, PL1159; UF40143A, PL1149; UF40143B, PL1150; UF40143C, PL1151; UF40143D, PL1152; UF40143E, PL1153
CH3OTU-005	*Caphyra holocarinata*	UF39105, PL1220; UFex.38876G, PL0801
CH3OTU-006	*Caphyra tridens*	UF9605A, PL1227; UF10130, PL1224; UF10138, PL1223; UF15865, PL1226; UF15907, PL0735; UF15910, PL1225; UF15932, PL1222
CH3OTU-007	*Caphyra alata*	UF14468, PL1221
CH3OTU-008	*Caphyra sp. C*	UF21835, PL0786
CH3OTU-009	*Caphyra sp. A*	UF5061A, PL0766
CH3OTU-010	*Charybdis acuta*	UF13466, PL0137
CH3OTU-011	*Charybdis acutifrons*	UF7114, PL0136; UF17047, PL0186; UF27220, PL0185
CH3OTU-012	*Charybdis annulata*	UF22076, PL0235
CH3OTU-015	*Charybdis erythrodactyla*	UF1398, PL0176
CH3OTU-016	*Charybdis feriata*	UF3739, PL0182
CH3OTU-017	*Charybdis hawaiensis*	UF25871, PL0165; USNM25377, PL1020
CH3OTU-018	*Charybdis hellerii*	UF11430A, PL0187; UF11430B, PL0188
CH3OTU-020	*Charybdis lucifera*	UF217, PL0147; UF7613A, PL0141; UF7613B, PL0142; UF7667, PL0198; UF7668, PL0143; UF7684, PL0146; UF7701, PL0145; UF7702, PL0138
CH3OTU-021	*Charybdis natator*	UF2614, PL0190; UF3707, PL0181
CH3OTU-022	*Charybdis obtusifrons*	UF16599, PL0199
CH3OTU-023	*Charybdis orientalis*	USNM112062, PL0634

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-025	*Charybdis longicollis*	UF3179A, PL0139; UF3179B, PL0140
CH3OTU-026	*Charybdis sagamiensis*	UF29479, PL0177
CH3OTU-027	*Cronius edwardsii*	USNM112311, PL0628; USNM1254607, PL0630
CH3OTU-028	*Cronius ruber*	UF25995, PL0192; UF26364, PL0172; UF31724, PL0202
CH3OTU-029	*Gonioinfradens paucidentatus*	UF1411A, PL0183; UF1411B, PL0184; UF5109, PL0170
CH3OTU-030	*Lissocarcinus arkati*	UF36296A, PL0919; UF36296B, PL0920
CH3OTU-031	*Lissocarcinus holothuricola*	USNM2302, PL0685; UF8433, PL0841; UF29947, PL0836; UF30031, PL0872; UF30172, PL0875; UF30182, PL0868; UF30190, PL0871; UF30203B, PL0879; UF30203A, PL0878; UF30235A, PL0876; UF30235B, PL0877; UF30253B, PL0874; UF30253A, PL0873; UF30302, PL0870; UF36080, PL0857; UF40382A, PL0839; UF40382B, PL0840; NHMLAC_PL0592, PL0592; NHMLAC_PL0593, PL0593; NHMLAC_PL0594, PL0594; NHMLAC_PL0595, PL0595; NHMLAC_PL0596, PL0596; NHMLAC_PL0601, PL0601; NHMLAC_PL0602, PL0602; NHMLAC_PL0603, PL0603; NHMLAC_PL0604, PL0604; NHMLAC_PL0605, PL0605; NHMLAC_PL0606, PL0606; NHMLAC_PL0607, PL0607; NHMLAC_PL0611, PL0611; NHMLAC_PL0619, PL0619
CH3OTU-032	*Lissocarcinus aff.laevis.sp.A*	UF204, PL0237; UF39136, PL0935; UF42984, PL0805; UF43311, PL0808
CH3OTU-033	*Lissocarcinus aff.laevis.sp.C*	UF2317, PL0936; USNM149557, PL0483; USNM149565, PL0934; USNM149566, PL0932; USNM149567, PL0931
CH3OTU-034	*Lissocarcinus laevis*	UF41388, PL0940; UF41507, PL0942; UF41516, PL0939; UF41529, PL0938; UF41571, PL0941; UF43176, PL0806
CH3OTU-035	*Lissocarcinus aff.laevis.sp.B*	USNM29663, PL0693; UF37919, PL0937

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-036	*Lissocarcinus orbicularis*	NHMLAC_PL0597, PL0597; NHMLAC_PL0612, PL0612; NHMLAC_PL0613, PL0613; NHMLAC_PL0614, PL0614; UF186, PL0846; UF2088, PL0949; UF2297, PL0943; UF2674, PL0851; UF8761, PL0950; UF10225A, PL0834; UF10225B, PL0835; UF10927B, PL0863; UF10927C, PL0864; UF10927A, PL0862; UF13421, PL0845; UF14018A, PL0848; UF14018B, PL0849; UF14488, PL0865; UF15429, PL0850; UF15741, PL0740; NHMLAC16901, PL0620; UF26572A, PL0946; UF26572B, PL0947; UF26572C, PL0948; UF31142A, PL0832; UF31142B, PL0833; UF32846, PL0867; UF32897, PL0842; UF38583, PL0838; UF38879, PL0843; UF38893, PL0847; UF39125, PL0837; UF39598, PL0855; UF39599, PL0856; UF39732, PL0853; UF39733, PL0854; UF39855, PL0844; UF39940A, PL0858; UF39940B, PL0859; UF39940C, PL0860; UF39940D, PL0861; UF40068, PL0866; UF40071, PL0831; USNM41079, PL0453; UF41378, PL0852; UF43299, PL0807; USNM106625, PL0454; NHMLAC168701, PL0621; USNM267078, PL0455; USNM1254590, PL0452; USNM1254591, PL0451; NHMLAC_PL0590, PL0590; NHMLAC_PL0591, PL0591; NHMLAC_PL0598, PL0598; NHMLAC_PL0599, PL0599; NHMLAC_PL0600, PL0600; NHMLAC_PL0608, PL0608; NHMLAC_PL0609, PL0609; NHMLAC_PL0610, PL0610; NHMLAC_PL0615, PL0615; NHMLAC_PL0616, PL0616; NHMLAC_PL0617, PL0617; NHMLAC_PL0618, PL0618; UFKOAST-10A, PL0952; UFKOAST-10B, PL0953; UFKOAST-10C, PL0954; UFKONA13-0016, PL0955; UFKONA13-0048, PL0951; UFKONA13-0049, PL0945; ZRCNERMS072A, PL0718; ZRCNERMS072B, PL0719
CH3OTU-037	*Lissocarcinus aff.polybiodes*	UF12527, PL0929
CH3OTU-038	*Lissocarcinus polybiodes*	UF27186, PL0930; UF35245B, PL0921; UF35245C, PL0922; UF35245D, PL0923; UF35245E, PL0924; UF35245G, PL0926; UF35245H, PL0927; UF35245I, PL0928; UF42958, PL0809; UF27181, PL0286; UF35245A, PL0207
CH3OTU-039	*Thalamita aff.admete.sp.B*	USNM2225, PL0082; USNM3390, PL0093; UF3628, PL0221; UF8592, PL0220; UF8788, PL1198; UF12212, PL1205; UF12308, PL1199; UF12310, PL1200; UF37967, PL0964; USNM102957, PL0095
CH3OTU-040	*Thalamita aff.admete.sp.A*	UF168A, PL0218; UF15751, PL1208; UF16827, PL0217; UF17013, PL0215; UF17738, PL0219; UF17744, PL0903; UF17745, PL0216; USNM33364B, PL0460; USNM33364C, PL0461; UF39941, PL1210; UF39942, PL1217; UF39960, PL1211; UF39987, PL1212; UF40120A, PL1209; UF40128, PL0904; USNM46352, PL0102; USNM48332, PL0079; USNM111733, PL0456; ZRCNERMS098A, PL1207

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-041	*Thalamita admete*	UF220, PL0404; UF1653, PL0426; UF2028, PL0227; UF2272, PL0421; UF4139A, PL0391; UF4139B, PL0392; UF4139C, PL0393; UF5856, PL1203; UF7582A, PL1202; UF7605A, PL0402; UF7605B, PL0403; UF7620A, PL0394; UF7688A, PL0161; UF7690, PL0413; UF7699A, PL0407; UF7699B, PL0408; UF7775, PL0223; UF7833, PL0388; UF8434, PL1193; UF9957, PL0425; UF12852, PL0222; UF14201, PL1206; UF16763, PL0390; UF16971, PL0224; UF17217, PL0422; UF23943, PL1194; UF24054, PL0423; UF25446, PL0226; UF25470, PL0396; UF25551, PL0424; UF25915, PL0225; UF26944, PL1204; UF26945, PL0228; UF26950A, PL0398; UF26950B, PL0399; UF26950C, PL0400; UF26950D, PL0401; USNM33364A, PL0459; UF34320A, PL0419; UF34320B, PL0420; UF38894, PL0405; UF38895, PL1201; UF38899, PL0397; UF39005, PL0414; UF39082, PL0412; UF39140, PL0410; UF39141, PL0418; UF39142, PL0416; UF39853, PL0395; UF39943, PL0406; UF40031, PL0415; UF40111, PL0417; UF40125, PL0389; UF40142, PL0411; USNM41105A, PL0457; USNM41105B, PL0458; USNM96915A, PL0492; USNM111922A, PL0096; USNM111922B, PL0097; USNM111922C, PL0098; USNM111922D, PL0099; USNM111930A, PL0083; USNM112243, PL0080; USNM127096, PL0081; USNM149608, PL0085; USNM267062, PL0545; Ufex.10489, PL0819; ZRCNERMS060A, PL1192; ZRCNERMS079A, PL0409; ZRCNERMS089, PL1197; ZRCNERMS100, PL1191
CH3OTU-042	*Thalamita macropus*	USNM45886A, PL0484; USNM45886B, PL0485; USNM45886C, PL0486; USNM45886D, PL0487; USNM45886E, PL0488; USNM45886F, PL0489; USNM45886G, PL0490; USNM45886H, PL0491
CH3OTU-043	*Thalamita aff.rubridens*	UF25803, PL0210; UF43314A, PL1027; UF43314B, PL1028; USNM274297, PL0672; USNM274298, PL0673
CH3OTU-044	*Thalamita mitsiensis*	UF33748, PL0774
CH3OTU-045	*Thalamita aff.sexlobata*	ZRCNERMS073A, PL1102; ZRCNERMS073B, PL1103
CH3OTU-046	*Thalamita auauensis*	UF12320A, PL0732; UF12320B, PL0733; USNM29602A, PL0493; USNM29602B, PL0494; USNM29602C, PL0495; USNM29602D, PL0496; USNM29602E, PL0497; USNM29602F, PL0498; USNM29602G, PL0499; USNM29602H, PL0500; USNM29602I, PL0501; USNM29602J, PL0502; USNM29602K, PL0503; USNM29602L, PL0504; USNM29602M, PL0505; USNM29602N, PL0506; USNM29602O, PL0507; USNM29602P, PL0508; USNM29602Q, PL0509; USNM29602R, PL0510; USNM29602S, PL0511; USNM29602T, PL0512
CH3OTU-047	*Thalamita difficilis*	USNM274272A, PL0999; USNM1226914, PL0544
CH3OTU-048	*Thalamita bevisi*	UF197, PL0726; UF2324, PL0911; UF4087, PL0813; UF11640A, PL0908; UF11640B, PL0909; UF11640C, PL0910; USNM12343, PL0478; UF36041, PL0283; USNM56039, PL0479; USNM94009A, PL0476; USNM94009B, PL0477; USNM99129, PL0094; USNM111650, PL0480; USNM111801A, PL0471; USNM111801B, PL0472; USNM111802, PL0470; USNM149654A, PL0475; USNM1226915, PL0474; USNM1226916, PL0473

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-049	*Thalamita bilobata*	UF3384, PL1039; UF39858, PL1036; UF39904, PL1037; UF39967, PL1038; UF39968, PL1035; UF39976, PL1034
CH3OTU-050	*Thalamita bouvieri*	UF1925, PL0781; UF14197, PL0710; UF14609, PL0811; UF14617, PL1231; UF16873, PL0780; UF17562, PL0729; UF24064, PL0709; UF24801, PL0750; UF29225, PL1112; UF41652, PL0782; USNM123228A, PL0546; USNM123228B, PL0547; USNM274274A, PL1004
CH3OTU-051	*Thalamita cerasma*	UF185, PL1104; UF35219A, PL0324; UF35219B, PL0325; UF35219C, PL0326; UF39825, PL0321; UF39834, PL0322; UF39852, PL0317; UF39899, PL0320; UF39900, PL0318; UF39902, PL0323; UF39969, PL0319
CH3OTU-052	*Thalamita chaptalii*	UF206A, PL0753; UF206B, PL0754; UF206C, PL0755; UF206D, PL0756; UF206E, PL0757; UF206F, PL0758; UF206G, PL0759; UF206H, PL0760; UF206I, PL0761; UF206J, PL0762; UF206K, PL0763; UF206L, PL0764; UF13103, PL0238; UF14010, PL0976; USNM32855G, PL0555; UF39917, PL0975; UF40073, PL0973; UF43255, PL0972; UF43256, PL0974; USNM112082, PL0565; USNM149653A, PL0566; USNM149653B, PL0567; USNM1254587, PL0068; ZRCNERMS094, PL0970; ZRCNERMS095, PL0971
CH3OTU-053	*Thalamita coeruleipes*	UF211, PL0358; UF2704, PL0353; UF3232, PL0350; UF5090B, PL0371; UF9892, PL0364; UF11322, PL0201; UF12795, PL0369; UF16969, PL0365; UF39030, PL0368; UF39117, PL0367; UF39123, PL0366; UF39854, PL0361; UF39894, PL0362; UF39895, PL0351; UF39896, PL0363; UF39898A, PL0349; UF40033, PL0355; UF40040, PL0352; UF40049, PL0356; UF40074, PL0357; UF40117, PL0359; UF40127, PL0360; UF40144A, PL0354; UF41677, PL0370; ZRCNERMS077, PL0777
CH3OTU-054	*Trierarchus cooperi.sp.A*	UF10498A, PL1137; UF10498B, PL1138; UF15608, PL1143; UF16023, PL1141; UF16041, PL1132; UF16152, PL0768; UF18087, PL1142; UF23673, PL1139; UF23708, PL1130; UF23802, PL1131; UF30165A, PL1140
CH3OTU-055	*Trierarchus cooperi.sp.B*	UF1242, PL1128; UF16949, PL0728; UF40069, PL1134; UF40100, PL1129; UF40154A, PL1124; UF40154B, PL1125; UF40154C, PL1126; UF40154D, PL1127; UF40174, PL1133; USNM41125B, PL1007; USNM41125A, PL1006; UF41423, PL1135; ZRCNERMS067, PL1136
CH3OTU-056	*Thalamita crenata*	UF8950, PL0313; UF17752, PL0275; UF19983, PL0196; UF33049, PL0274; UF36197, PL0271; UF36989, PL0272; UF38252, PL0273; UF39965, PL0316; UF39970, PL0267; UF39972, PL0315; UF40007, PL0266; UF40008, PL0263; UF40009, PL0260; UF40010, PL0261; UF40011, PL0262; UF40012, PL0264; UF40013, PL0265; UF40052, PL0269; UF40053, PL0268; UF40126, PL0314; UF40160, PL0270; USNM41099, PL0124; USNM73090A, PL0106; USNM73090B, PL0107; USNM73090C, PL0108; USNM73090D, PL0109; USNM111783, PL0123; USNM112051, PL0126; USNM112328, PL0125; USNM1254594A, PL0110; USNM1254594B, PL0111; USNM1254594C, PL0112; USNM1254594D, PL0113; USNM1254595A, PL0114; USNM1254595B, PL0115; USNM1254595C, PL0116; USNM1254595D, PL0117; USNM1254595E, PL0118; USNM1254596A, PL0119; USNM1254596B, PL0120; USNM1254596C, PL0121; USNM1254596D, PL0122; ZRCNERMS078, PL0776

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-057	*Thalamita danae*	UF7165, PL0204; UF22114, PL0193; USNM23879, PL0104; UF25440, PL0331; UF25731, PL0332; UF25992, PL0168; UF29426, PL0913; UF29427, PL0336; UF36206A, PL0915; UF36206B, PL0916; UF36212A, PL0334; UF36212B, PL0335; UF36222, PL0333; UF36274, PL0917; UF36279, PL0918; UF36283, PL0906; UF36289, PL0914; UF39966, PL0340; UF39971, PL0338; UF40014, PL0339; UF41429, PL0337; USNM64682A, PL0128; USNM64682B, PL0129; USNM96910, PL0103; USNM111774A, PL0131; USNM111774B, PL0132; USNM111959, PL0127; USNM112329A, PL0133; USNM112329B, PL0134; USNM112329C, PL0135; USNM149656, PL0130
CH3OTU-058	*Thalamita spinifera*	USNM29626A, PL0991; USNM29626C, PL0993; USNM29626H, PL0998; USNM29626B, PL0992; USNM29626D, PL0994; USNM29626E, PL0995; USNM29626F, PL0996; USNM29626G, PL0997; USNM127104, PL0683
CH3OTU-059	*Thalamita foresti*	UF2222, PL0194; UF14902, PL0912; USNM41100, PL0466; USNM111716, PL0467; USNM111756, PL0105; USNM111855, PL0468; USNM111856, PL0465; USNM1254597A, PL0462; USNM1254597B, PL0463; USNM1254597C, PL0464; USNM1254598, PL0469
CH3OTU-060	*Thalamita gatavakensis*	UF16594, PL0830; UF16649, PL0765; UF21527, PL0978; UF27203, PL0979; UF27683, PL0977; Ufex.2532, PL0717
CH3OTU-061	*Thalamita gatavakensis*	UF3399, PL0982; UF13997, PL0988; UF17377, PL0989; UF17435, PL1022; UF17469, PL0211; UF17486, PL0738; UF22283, PL0986; UF24660, PL0980; UF24915, PL1023; UF25003, PL0984; UF25530, PL0981; UF25765, PL1024; UF25974, PL0990; UF33494, PL0983; UF33750, PL0985; UF43265, PL0987
CH3OTU-062	*Thalamita gloriensis*	UF16660, PL1196; UF25902, PL0737; USNM111578, PL0674; ZRCNERMS099, PL1195
CH3OTU-063	*Thalamita gracilipes*	UF3784A, PL1163; UF3784B, PL1164; UF3784C, PL1165; UF3784D, PL1166; UF15202, PL1171; UF15203, PL1167; UF35884, PL1174; UF42972, PL1170; USNM106601A, PL1000; USNM274299A, PL0694; USNM274299B, PL0695; USNM274300, PL0727; ZRCNERMS074A, PL1172; ZRCNERMS074B, PL1173; UFUSNM127103A, PL1168; UFUSNM127103B, PL1169
CH3OTU-064	*Thalamita granosimana*	UF14200, PL1046; UF24790, PL0752; UF41384, PL1045; UF42366A, PL1043; UF42366B, PL1044; UF42832, PL1047; UF43118, PL1048; UF43188, PL1049; USNM111941, PL0656; USNM111956A, PL0686; USNM274276A, PL1001; USNM274276B, PL1002; USNM274276C, PL1003; USNM274283B, PL0585; Ufex.40319, PL0713
CH3OTU-065	*Thalamita imparimana*	USNM112077, PL0659; USNM112133, PL0675; ZRCNERMS069A, PL1118; ZRCNERMS069B, PL1119; ZRCNERMS075A, PL1120; ZRCNERMS075B, PL1121; ZRCNERMS075C, PL1122; ZRCNERMS075D, PL1123

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-066	*Thalamita aff.integra*	UF8598B, PL0899; UF8598A, PL0898; USNM13867, PL0513; UF35898A, PL0900; UF35898B, PL0901; UF35898C, PL0902; USNM1254600A, PL0525; USNM1254600B, PL0526; USNM1254600C, PL0527; USNM1254600D, PL0528; USNM1254600E, PL0529; USNM1254601A, PL0530; USNM1254601B, PL0531; USNM1254601C, PL0532; USNM1254601D, PL0533; USNM1254602A, PL0534; USNM1254602B, PL0535; USNM1254602C, PL0536; USNM1254602D, PL0537; USNM1254602E, PL0538; USNM1254603A, PL0539; USNM1254603B, PL0540; USNM1254603C, PL0541; USNM1254603D, PL0542
CH3OTU-067	*Thalamita integra*	UF587A, PL0741; UF587B, PL0742; UF587C, PL0743; UF7166A, PL0890; UF7166B, PL0891; UF7703, PL0892; USNM18862, PL0517; UF21395, PL0880; UF21941, PL0869; UF21942, PL0882; UF22085, PL0307; UF22505, PL0881; UF32741, PL0889; UF32745, PL0888; UF32754, PL0810; UF36034A, PL0893; UF36034B, PL0894; UF36034C, PL0895; UF39914, PL0886; UF39964, PL0887; UF40072, PL0884; UF40129, PL0885; UF40131, PL0883; UF41592, PL0896; UF43284, PL0962; USNM111994, PL0522; USNM112112A, PL0515; USNM112112B, PL0516; USNM125499A, PL0523; USNM125499B, PL0524; USNM150737A, PL0514; USNM274278A, PL0518; USNM274278B, PL0519; USNM274278C, PL0520; USNM274278D, PL0521; Ufex.40319, PL0773
CH3OTU-068	*Thalamita iranica*	UF36855, PL1105
CH3OTU-069	*Thalamita kagosimensis*	USNM48364, PL0482; ZRCNERMS063, PL0149
CH3OTU-070	*Thalamita philippinensis*	UF17393, PL1145; UF24920, PL0212; UF25822, PL1146; UF26826, PL1144; UF43266, PL1148; UF43277, PL1147; USNM112000A, PL0665; USNM112000B, PL0666; USNM112139, PL0670; USNM112238, PL0663; USNM274287A, PL1012; USNM274288A, PL1010; USNM274288B, PL1011
CH3OTU-071	*Zygita longifrons*	UF189, PL0827; UF196, PL0825; UF199, PL0287; UF1237, PL0822; UF7343, PL0230; UF33284, PL0284; UF34275, PL0229; UF35635, PL0231; USNM48862, PL0622; USNM1294238, PL0961; USNM1294239, PL0960; USNM112418, PL0564; USNM125870, PL0481
CH3OTU-072	*Thalamita malaccensis*	ZRCNERMS059A, PL1094; ZRCNERMS059B, PL1095; ZRCNERMS059C, PL1096; ZRCNERMS059D, PL1097; ZRCNERMS059E, PL1098; USNM274290A, PL0647; USNM274290B, PL0648
CH3OTU-073	*Thalamita margaritimana*	USNM41108A, PL0100; USNM41108B, PL0101; USNM41110, PL0668
CH3OTU-074	*Thalamita mitsiensis*	UF190, PL0213; UF13884, PL0789; UF16419, PL0815; UF16852, PL1187; UF16875, PL1186; UF16923, PL0783; UF20202, PL1183; UF21937, PL0821; UF25229A, PL1175; UF25229B, PL1176; UF25229C, PL1177; UF25229D, PL1178; UF25929, PL0816; UF26664, PL1184; UF26751, PL1181; UF26968, PL1189; UF27192, PL1188; UF39857, PL1182; UF39958, PL1185; USNM274279, PL0679; ZRCNERMS081, PL1179; ZRCNERMS087, PL1180

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-075	*Zygita murinae*	UF36525, PL0232; UF36526, PL0820; UF36528, PL0829; UF36721, PL0288
CH3OTU-076	*Thalamita pseudopoissoni*	UF5051, PL0746; UF27180, PL1101
CH3OTU-077	*Thalamita oculea*	UF5243, PL1100; USNM41128, PL0657; USNM274280A, PL1008; USNM274280B, PL1009
CH3OTU-078	*Thalamita parvidens*	UF17558, PL0233; UF17561, PL0967; UF17595, PL0151; UF21795, PL0965; UF21796, PL0812; USNM32855A, PL0549; USNM32855B, PL0550; USNM32855C, PL0551; USNM32855D, PL0552; USNM32855E, PL0553; USNM32855F, PL0554; USNM32855H, PL0556; USNM32855I, PL0557; USNM32855J, PL0558; USNM32855K, PL0559; USNM32855L, PL0560; USNM32855M, PL0561; USNM32855N, PL0562; UF41377, PL0897; UF41385B, PL0792; UF41385A, PL0791; UF42828, PL0969; UF43273, PL0968; UF43274, PL0966; USNM112191, PL0563; USNM274281A, PL0588; USNM274283A, PL0584; USNM274283C, PL0586; USNM274283D, PL0587; USNM274284A, PL0589
CH3OTU-079	*Thalamita kukenthali*	UF574, PL1106; USNM274289, PL0667
CH3OTU-080	*Thalamita picta.sp.B*	UF177A, PL1054; UF269, PL1056; UF1518, PL0787; UF8344, PL1053; UF10089, PL1055; USNM18429, PL0638; UF30126A, PL1050; UF30126B, PL1051; UF30187, PL0779; UF40026, PL1058; UF40145, PL1057; USNM77787A, PL0660; USNM77787B, PL0661; USNM77787C, PL0662
CH3OTU-081	*Thalamita picta.sp.A*	UF6291, PL1071; UF10479, PL1065; UF10486, PL1074; UF10489A, PL0818; UF12783, PL1063; UF12784, PL1061; UF12946, PL1062; UF13752, PL1072; UF16591, PL1070; UF17026, PL1073; UF22160, PL1060; UF24881, PL0751; UF26967, PL1064; UF29425, PL1066; UF39311, PL0784; UF39322, PL1059; USNM105337A, PL0681; USNM105337B, PL0682; USNM150734, PL0684; ZRCNERMS061A, PL1067; ZRCNERMS080, PL1068; ZRCNERMS085, PL1069
CH3OTU-082	*Thalamita pilumnoides*	UF13615, PL1235; UF17357, PL1233; UF21925, PL1236; UF21939, PL1232; UF22535, PL0788; UF22623, PL1234
CH3OTU-083	*Thalamita spiceri*	UF8040, PL1239; UF30108, PL1240; UF40075, PL0708; UF40103, PL1241; UF40135, PL1245; UF40136, PL1237; UF40148, PL1244; UF40149, PL1242; UF40150, PL1243; UF40175, PL1238
CH3OTU-084	*Thalamita, Platypenis*	USNM151091A, PL0721; USNM151091B, PL0722; USNM151091C, PL0723; USNM151092B, PL1019; USNM151092A, PL1018
CH3OTU-085	*Thalamita poissonii*	USNM54225A, PL0073; USNM54225B, PL0074; USNM1254588A, PL0075; USNM1254588B, PL0076; USNM1254589A, PL0077; USNM1254589B, PL0078; UF7581, PL1107; USNM106038A, PL0581; USNM106038B, PL0582; USNM106038C, PL0583; USNM112320A, PL0569; USNM112320B, PL0570; USNM173078, PL0568; USNM1254605A, PL0579; USNM1254605B, PL0580
CH3OTU-086	*Thalamita prymna*	UF16749, PL0379; UF39892, PL0381; UF39893, PL0380; UF40034, PL0372; UF40050, PL0373; UF40051, PL0384; UF40058, PL0383; UF40064, PL0374; UF40076, PL0375; UF40077, PL0385; UF40106, PL0376; UF40110, PL0377; UF40133, PL0378; UF40155, PL0382
CH3OTU-087	*Thalamita pelsarti*	UF41408, PL0308

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-088	*Thalamita tenuipes*	UF7819, PL0282; UF14613, PL0234; UF36384, PL0707; UF38032, PL0304
CH3OTU-089	*Thalamita pseudoculea*	UF5093A, PL1099; UF13877, PL0731; USNM274291F, PL0701; USNM274291H, PL0703; USNM274291A, PL0696; USNM274291B, PL0697; USNM274291C, PL0698; USNM274291D, PL0699; USNM274291E, PL0700; USNM274291G, PL0702; USNM274291I, PL0704; USNM274291J, PL0705; USNM274292A, PL0088; USNM274292B, PL0089; USNM1254592, PL0090; USNM1254593A, PL0091; USNM1254593B, PL0092
CH3OTU-090	*Thalamita pseudopelsarti*	UF77, PL0344; UF154, PL0343; UF6710, PL0342; UF7344, PL0346; UF8307, PL0281; UF16218, PL0341; UF24536, PL0280; UF26576, PL0348; UF26662, PL1025; UF26665, PL0347; UF39674, PL1026; UF42867, PL0963; UF218, PL0345
CH3OTU-091	*Thalamita quadrilobata*	UF2252, PL0295; UF3814, PL0294; UF12512, PL0301; UF14254, PL0303; UF14608, PL0289; UF14980, PL0291; UF17429, PL0285; UF17513, PL0300; UF17531, PL0302; UF17560, PL0299; UF24744, PL0290; UF24746, PL0298; UF32840, PL1041; UF32843, PL0803; UF33749, PL0293; UF36720, PL0296; UF36747, PL0292; UF37076, PL0297; UF38255, PL1040; UF43156, PL1042; USNM274294A, PL0649; USNM274295A, PL0687
CH3OTU-092	*Thalamita richeri*	UF431, PL1108; USNM274270A, PL0653; USNM274270B, PL0654; USNM274270C, PL0655
CH3OTU-093	*Thalamita rubridens*	UF156, PL0306; UF7700, PL0305
CH3OTU-094	*Thalamita savignyi*	UF7604, PL0905; UF7607, PL0907; UF7689A, PL0386; UF7689B, PL0387; UF7698, PL0236; USNM8988A, PL0086; USNM8988B, PL0087; UF32752, PL1031; UF35899, PL1030; UF36651, PL1029; UF36653, PL0790; UF36706, PL1032; UF36833, PL0775; UF36893, PL1033; UF40348, PL0785
CH3OTU-095	*Thalamita seurati.sp.A*	UF194, PL0824; UF10487A, PL1077; UF10487B, PL1078; UF10487C, PL1079; UF10487D, PL1080; UF10718, PL1075; UF10717, PL0823
CH3OTU-096	*Thalamita seurati.sp.B*	UF12832, PL0206; UF12834, PL0828; UF12958, PL0826; UF30109, PL1076
CH3OTU-097	*Thalamita sexlobata*	USNM112236, PL0642; USNM274296A, PL0639; USNM274296C, PL0641

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-098	*Thalamita sima*	USNM1254527, PL0001; USNM1254528, PL0002; USNM1254529, PL0003; USNM1254530, PL0004; USNM1254531, PL0005; USNM1254532, PL0006; USNM1254533, PL0007; USNM1254534, PL0008; USNM1254535, PL0009; USNM1254536, PL0010; USNM1254537, PL0011; USNM1254538, PL0012; USNM1254539, PL0013; USNM1254540, PL0014; USNM1254541, PL0015; USNM1254542, PL0016; USNM1254543, PL0017; USNM1254544, PL0018; USNM1254545, PL0019; USNM1254546, PL0020; USNM1254547, PL0031; USNM1254548, PL0021; USNM1254549, PL0022; USNM1254550, PL0032; USNM1254551, PL0023; USNM1254552, PL0024; USNM1254553, PL0025; USNM1254554, PL0026; USNM1254555, PL0027; USNM1254557, PL0033; USNM1254558, PL0028; USNM1254560, PL0035; USNM1254561, PL0034; USNM1254562, PL0038; USNM1254563, PL0036; USNM1254564, PL0029; USNM1254565, PL0040; USNM1254567, PL0041; USNM1254568, PL0042; USNM1254569, PL0043; USNM1254570, PL0044; USNM1254571, PL0045; USNM1254573, PL0047; USNM1254574, PL0048; USNM1254575, PL0049; USNM1254576, PL0050; USNM1254577, PL0051; USNM1254578, PL0052; USNM1254579, PL0053; USNM1254580, PL0054; USNM1254581, PL0055; USNM1254583, PL0057; USNM18510B, PL0063; USNM18510A, PL0062; USNM26265, PL0060; UF35869, PL0720; UF36191, PL0734; USNM57489, PL0059; USNM61936, PL0061; USNM112078, PL0058; USNM1254584A, PL0066; USNM1254584B, PL0067; USNM1254585B, PL0065; USNM1254585A, PL0064; USNM1254586A, PL0069; USNM1254586B, PL0070; USNM1254586C, PL0071
CH3OTU-099	*Thalamita spinicarpa*	UF36226, PL0309; UF36227, PL0310; UF36265, PL0311; UF36282, PL0312; USNM274285, PL0669; UF36225, PL0171
CH3OTU-100	*Thalamita aff.spinifera*	UF33379, PL0748; UF33380, PL1113; UF33381, PL1115; Ufex.5243, PL0716; ZRCNERMS065, PL1114; USNM111864, PL0664; USNM149637A, PL1005; USNM149639A, PL0680; ZRCNERMS062A, PL1116; ZRCNERMS062B, PL1117
CH3OTU-101	*Thalamita spinimana*	UF27228, PL0279; UF36209, PL0189; UF36218, PL0328; UF36223, PL0329; UF36230, PL0327; UF36231, PL0278; UF36266A, PL0276; UF36266B, PL0277; UF39826, PL0248; UF39835, PL0258; UF39836, PL0259; UF39876, PL0251; UF39883, PL0257; UF39975, PL0330; UF39977, PL0247; UF39978, PL0254; UF39979, PL0253; UF39981, PL0249; UF39982, PL0255; UF39983, PL0252; UF40005, PL0256; UF40006, PL0250
CH3OTU-102	*Trierarchus squamosus*	USNM102963, PL0677
CH3OTU-103	*Thalamita stephensoni*	UF13574, PL1111; UF14108, PL1109; UF17067, PL1110; UF17070, PL0730; USNM123229A, PL0651; USNM123229B, PL0652; Ufex.11315A, PL0714; Ufex.11315B, PL0715; Ufex.40319A, PL0711; Ufex.40319B, PL0712

Table 4-3. Continued.

OTU ID	Species	GMM specimen voucher and photo (PL) ID numbers
CH3OTU-104	*Trierarchus woodmasoni*	UF180, PL0817; UF4110, PL0778; UF4114A, PL0770; UF4114B, PL0771; UF4114C, PL0772; UF14009, PL1090; UF35650, PL1093; UF40029, PL1089; UF40037, PL1085; UF40079, PL1092; UF40098, PL1088; UF40152A, PL1081; UF40152B, PL1082; UF40152C, PL1083; UF40152D, PL1084; UF40156A, PL1086; UF40156B, PL1087; UF43271, PL1091
CH3OTU-105	*Thalamitoides quadridens*	UF1962, PL0203
CH3OTU-106	*Thalamitoides spinigera*	UF32881, PL0159
CH3OTU-107	*Thalamitoides tridens*	UF18231, PL0152

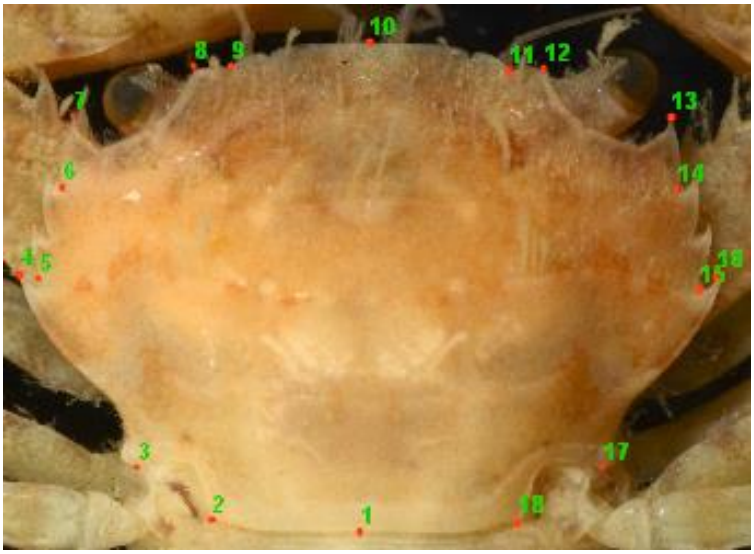

Figure 4-1. Eighteen landmarks used for quatification of carapace shape.

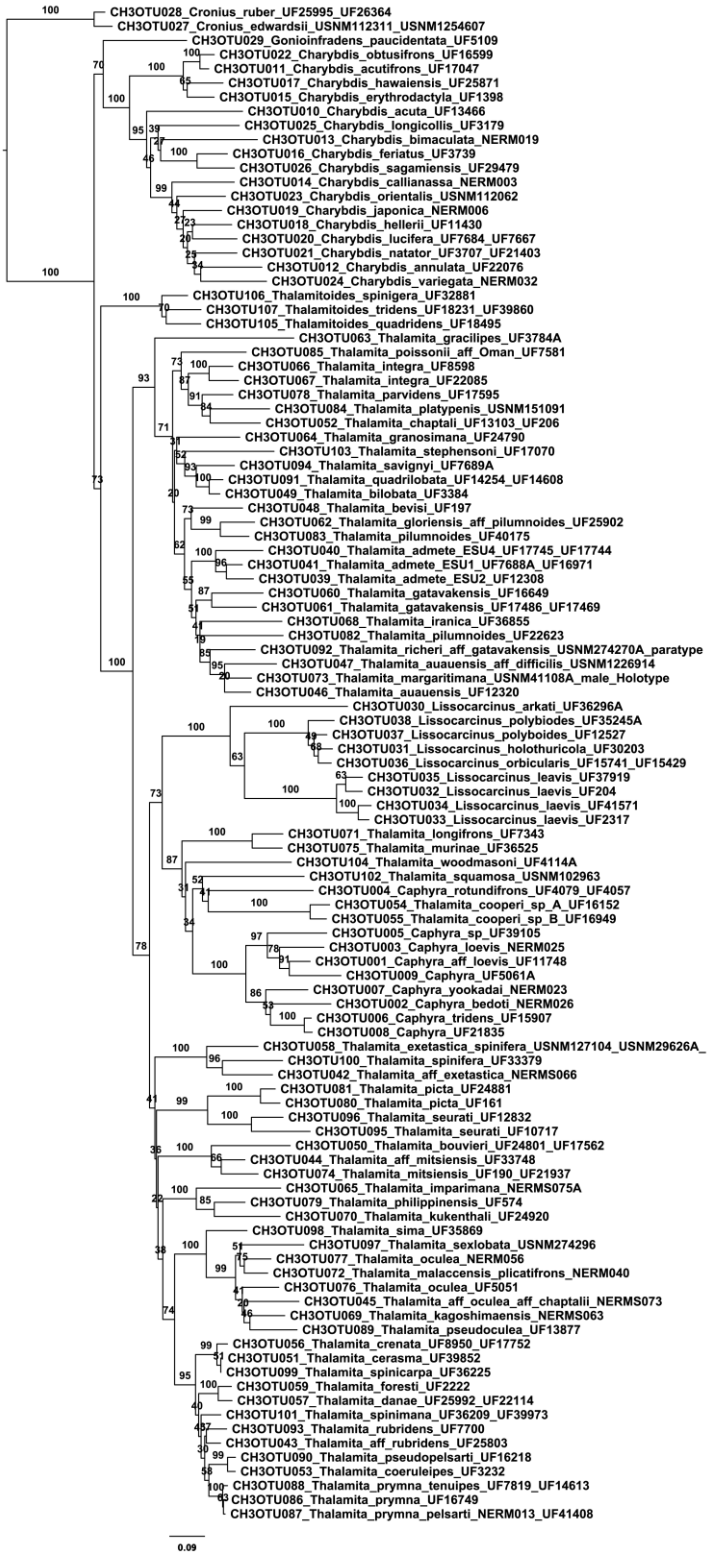

Figure 4-2. ML phylogram of Thalamitinae based on analyses of 107 OTUs and a 2444 bp alignment of partial CO1, 16S rRNA, 18S rRNA, and H3 sequence data. Support values (based on 500 replicate searches) appear above each node.

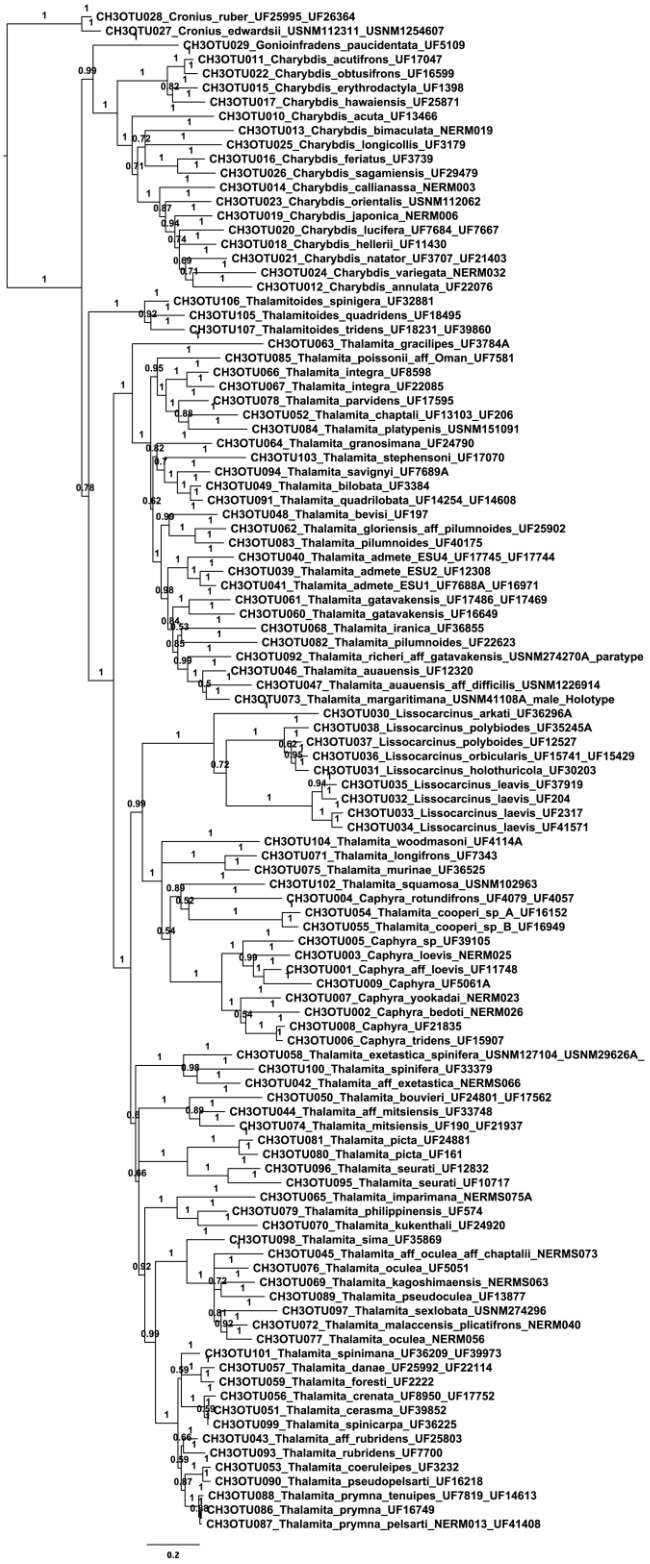

Figure 4-3. BI majority rule consensus tree of Thalamitinae based on analyses of 107 OTUs and a 2444 bp alignment of partial CO1, 16S rRNA, 18S rRNA, and H3 sequence data. BI posterior probability values appear above each node.

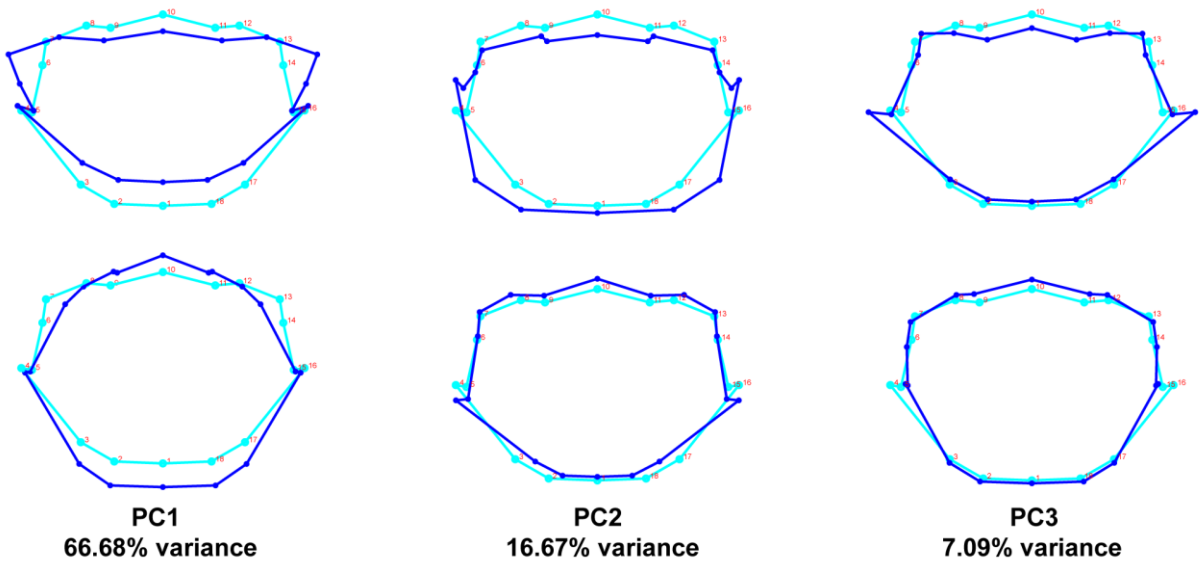

Figure 4-4. Average and most divergent carapace shape difference described by Principal Components 1, 2 and 3. Light blue wire frames depict the mean shape for each PC. Dark blue wire frames depict the most divergent shape described, with the upper row depicting the shapes described by the maximum PC axis values while the bottom row depicts those for the minimum PC axis values.

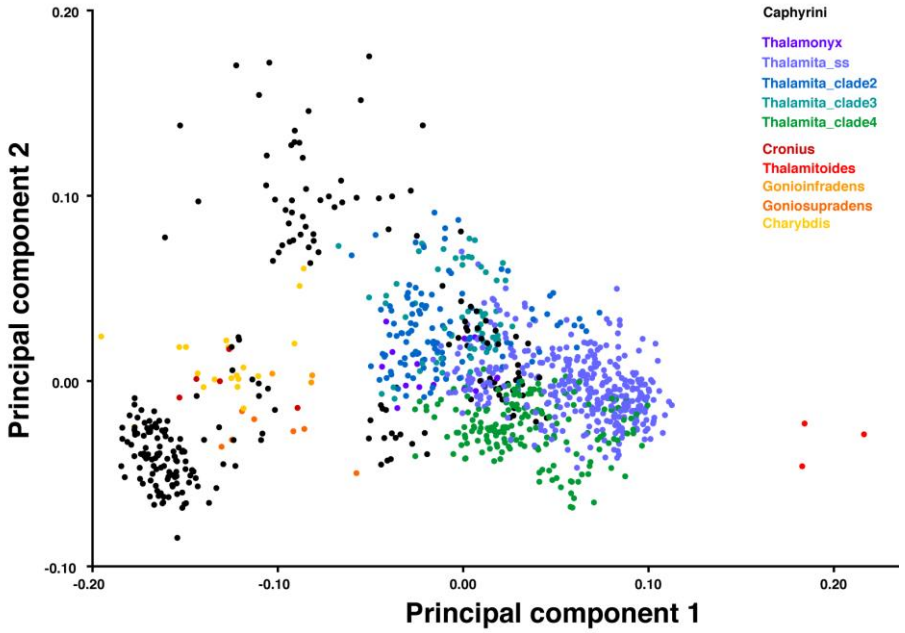

Figure 4-5. A two-dimensional theoretical morphospace of Thalamitinae carpace shape based on PC1 and PC2 for 103 taxa and 995 Thalamitinae specimens. Clade distinctions in Table 4-1.

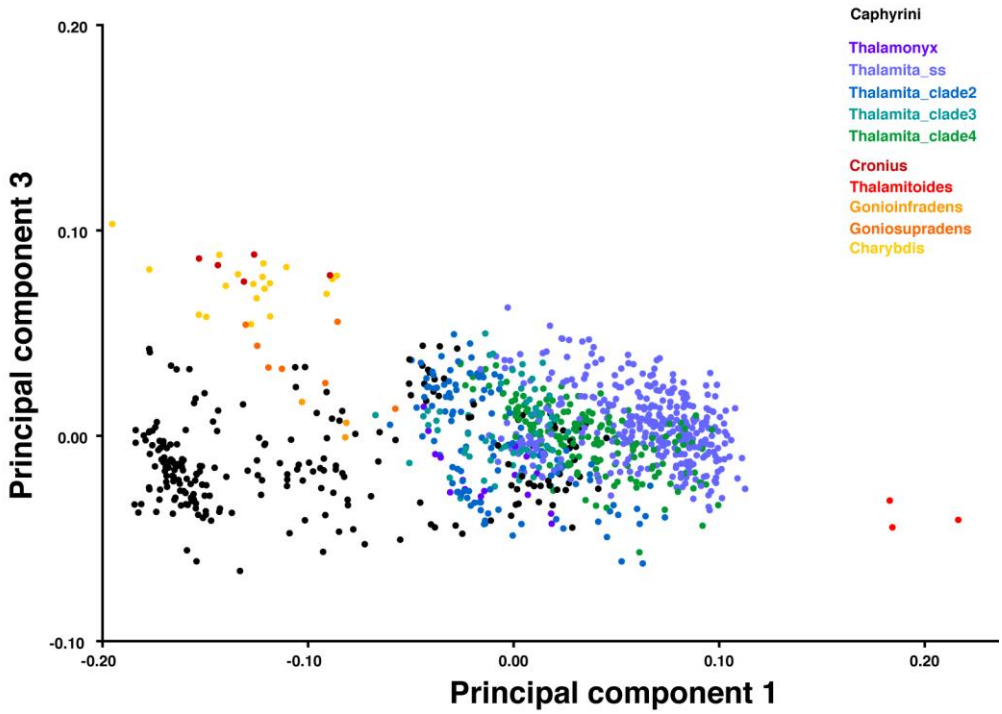

Figure 4-6. A two-dimensional theoretical morphospace of Thalamitinae carpace shape based on PC1 and PC3 for 103 taxa and 995 Thalamitinae specimens.

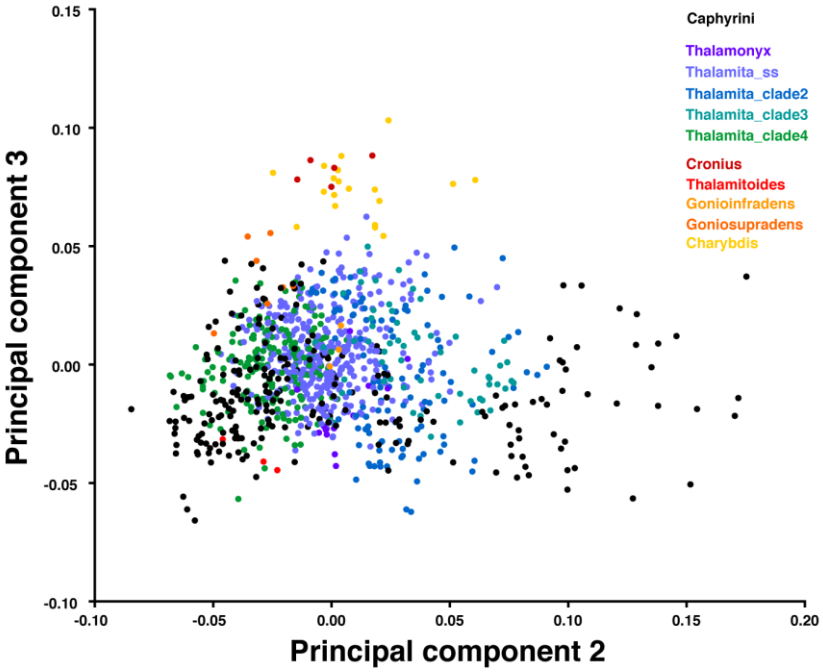

Figure 4-7. A two-dimensional theoretical morphospace of Thalamitinae carpace shape based on PC2 and PC3 for 103 taxa and 995 Thalamitinae specimens.

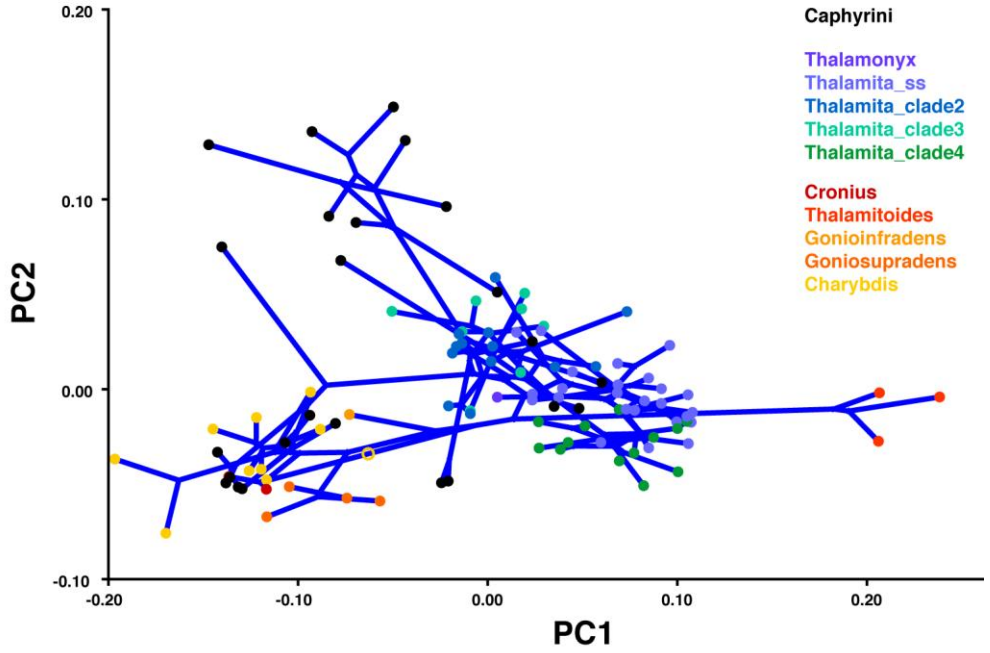

Figure 4-8. Two-dimensional theoretical phylomorphospace of Thalamitinae carapace shape for 103 taxa based on PC1 and PC2 of taxon averaged shape coordinates.

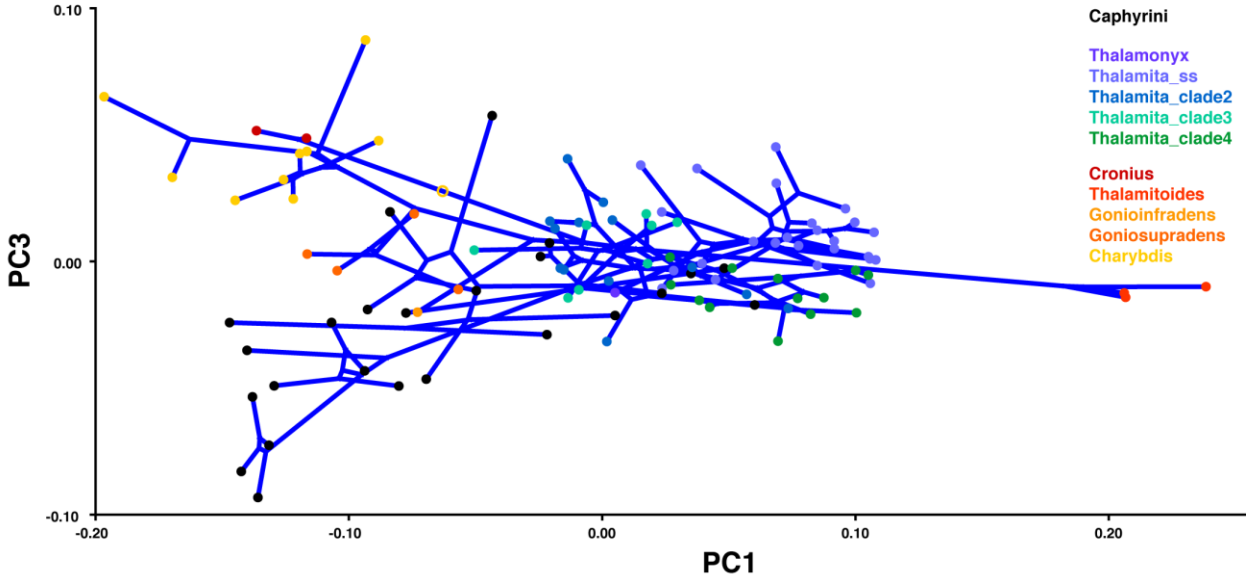

Figure 4-9. Two-dimensional theoretical phylomorphospace of Thalamitinae carapace shape for 103 taxa based on PC1 and PC3 of taxon averaged shape coordinates.

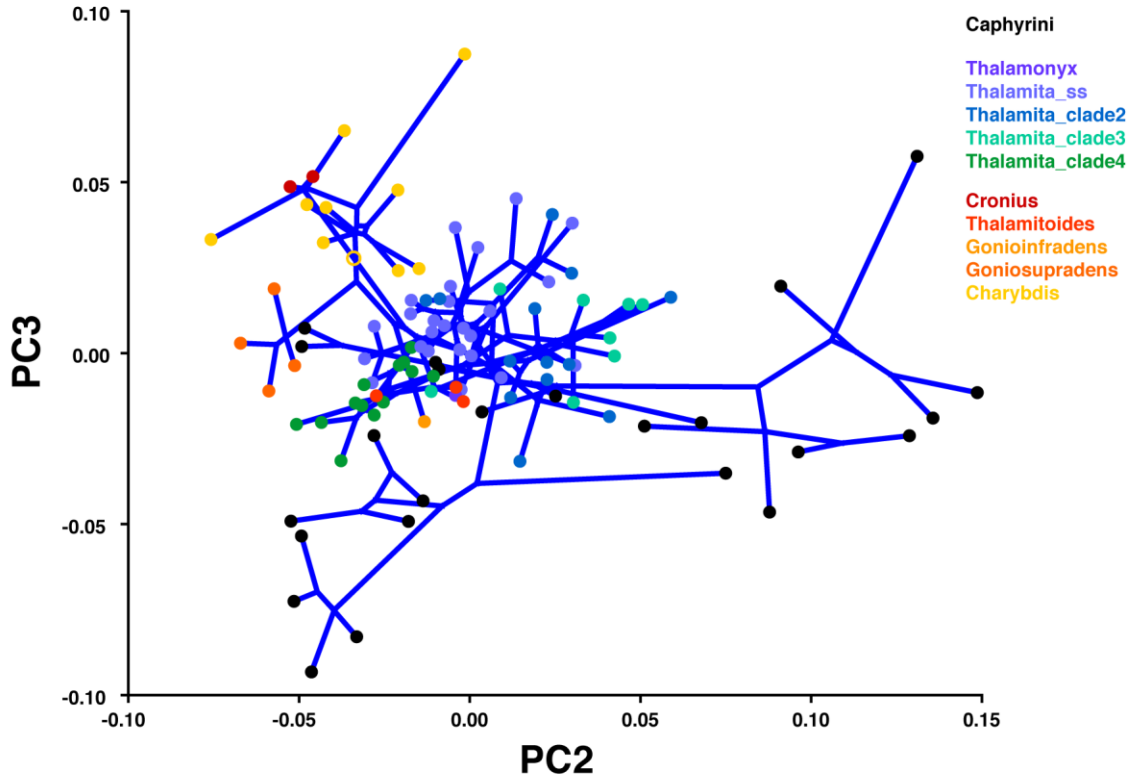

Figure 4-10. Two-dimensional theoretical phylomorphospace of Thalamitinae carapace shape for 103 taxa based on PC2 and PC3 of taxon averaged shape coordinates.

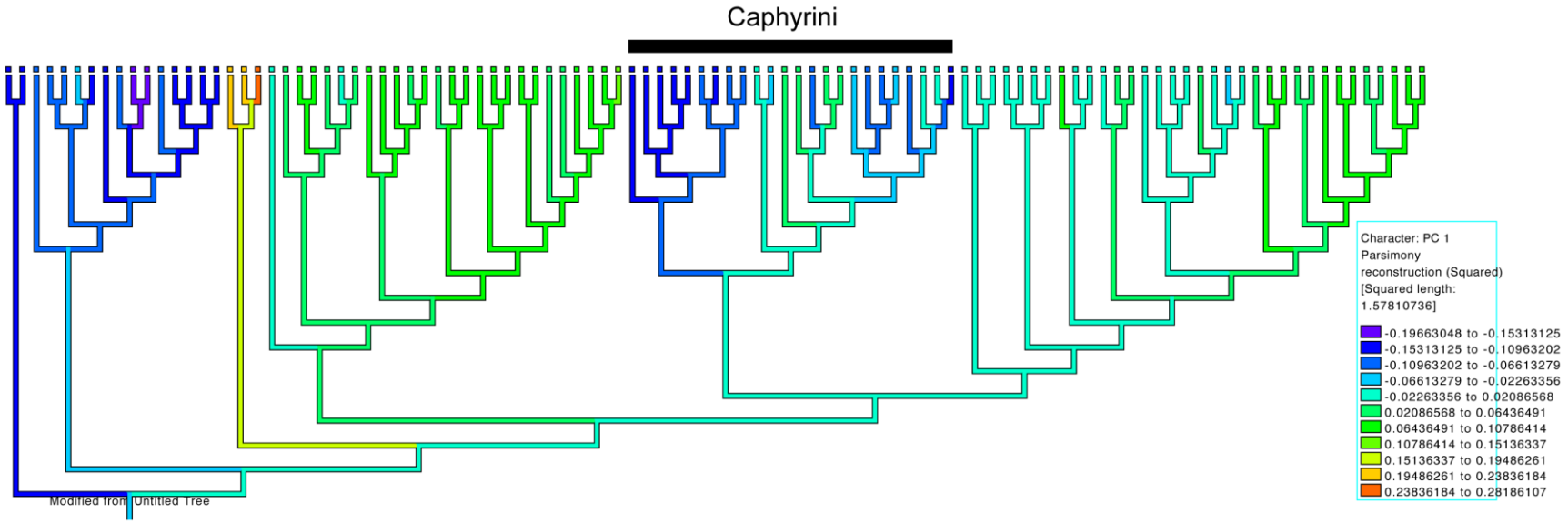

Figure 4-11. Principal Component axes 1 of Thalamitinae carapace shape for 103 taxa mapped on to the ML topology using unweighted squared change parsimony.

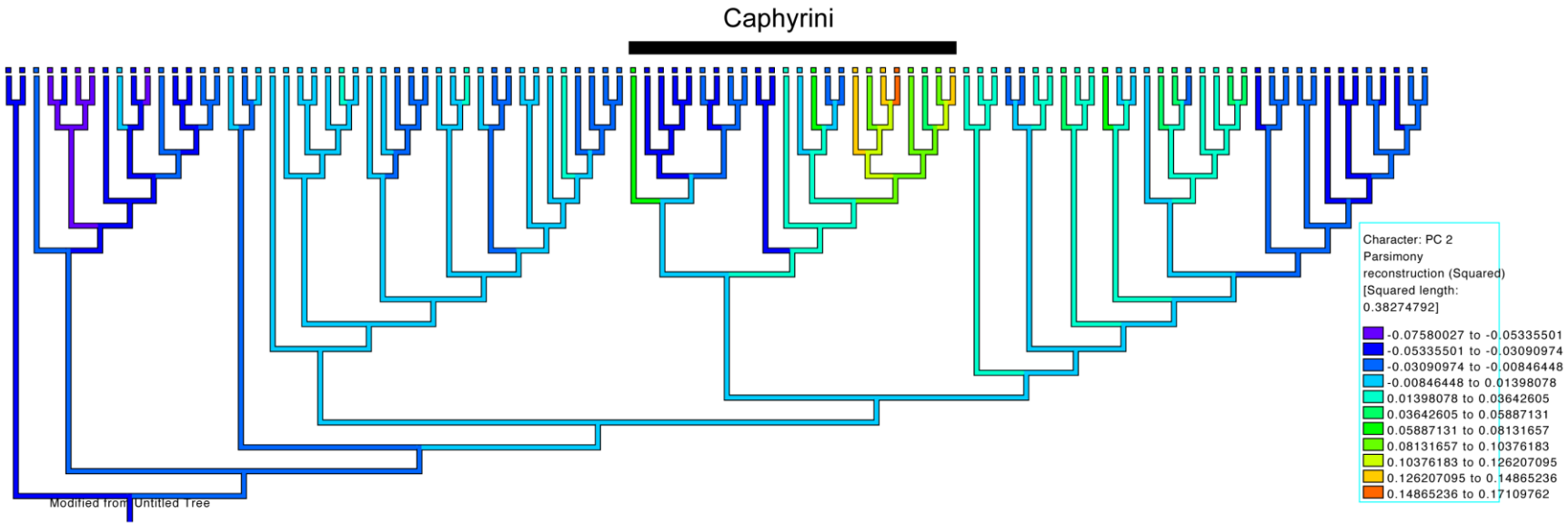

Figure 4-12. Principal Component axes 2 of Thalamitinae carapace shape for 103 taxa mapped on to the ML topology using unweighted squared change parsimony.

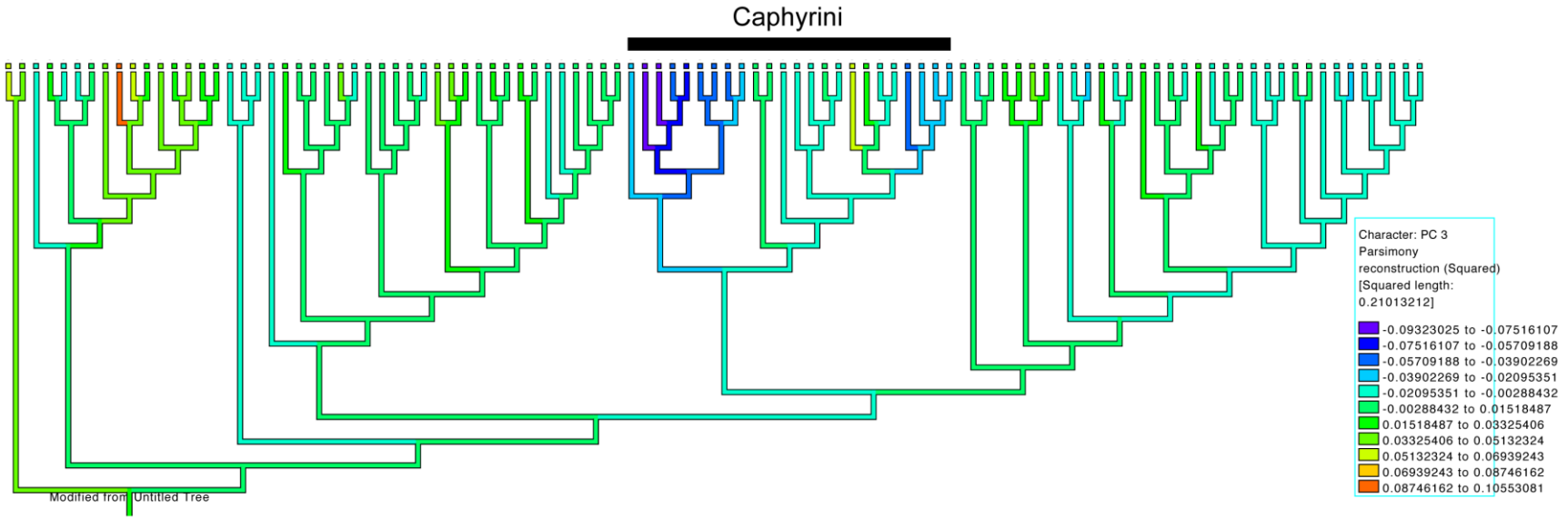

Figure 4-13. Principal Component axes 3 of Thalamitinae carapace shape for 103 taxa mapped on to the ML topology using unweighted squared change parsimony.

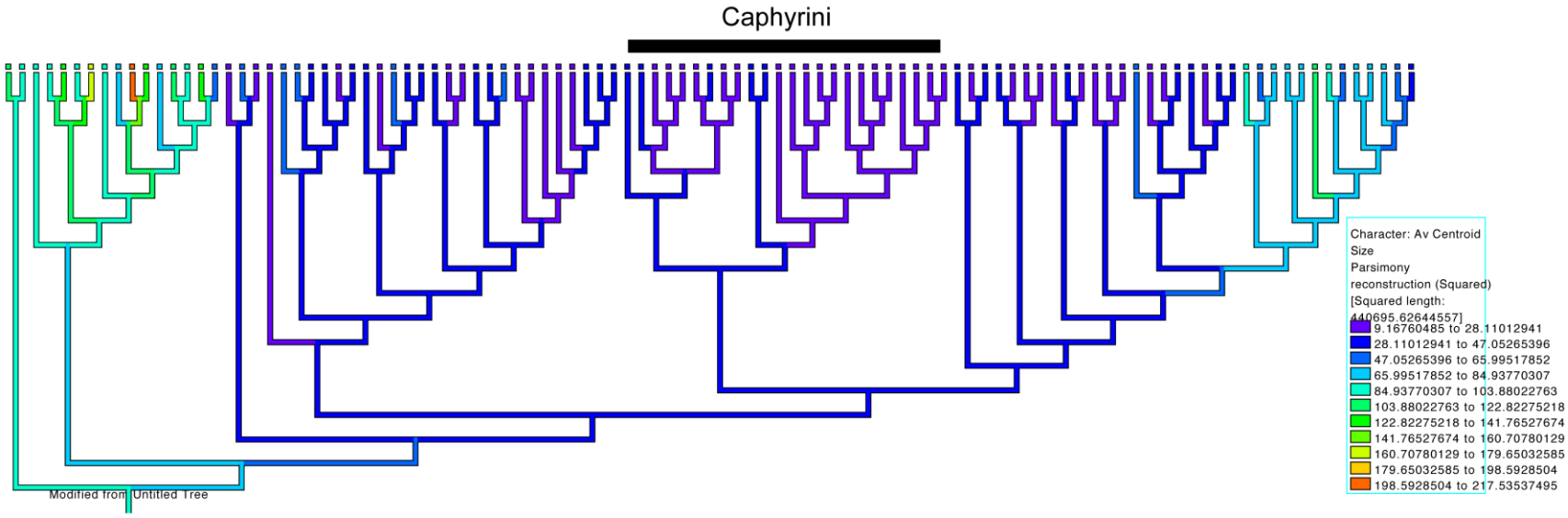

Figure 4-14. Average centroid sizes of carapace shape for 103 Thalamitinae taxa mapped on to the ML topology using unweighted squared change parsimony.

CHAPTER 5
SUMMARY AND FUTURE DIRECTIONS

Summary

The objective of this dissertation was to investigate the systematics, molecular phylogenetics and morphological evolution of symbiotic lineages in the brachyuran superfamily Portunoidea.

Chapter 2 investigated the molecular phylogenetics of 168 portunoid taxa with four molecular markers. I show that the eight valid families fall into four distinct lineages that I formally recognize as Brusinidae, Carcinidae, Geryonidae and Portunidae. However, while the later three constitute a Portunoidea sensu stricto clade, the placement of Brunsinidae in this superfamily remains uncertain. Results also revealed that the symbiotic Caphyrinae genera *Caphyra* and *Lissocarcinus* are highly derived within the Thalamitinae genus *Thalamita*. Conversely, molecular analyses strongly support the placement of the non-symbiotic caphyrine genus *Coelocarcinus* in Carcinidae. I recognize the subfamily Caphyrinae as a tribe, comprised of *Caphyra*, *Lissocarcinus* and two new genera, *Zygita* and *Trierarchus*. These new genera were named to accommodate *Thalamita* species falling within this symbiotic clade. I redefine Thalamitinae to accommodate the addition of Caphyrini and the genus *Cronius*. These results provide phylogenetic context for understanding morphological evolution in Portunoidea, especially, Thalamitinae. The inclusion of *Cronius* in Thalamitinae provides a clearer distinction between Portuninae *s.l.* and Thalamitinae. The new placement of Caphyrini clarifies the origin and nature of symbiosis in portunid crabs.

Chapter 3 provided a systematic review of the symbiotic caphyrine genus *Lissocarcinus*. I studied the morphology of 177 specimens from six of the nine valid

Lissocarcinus species. Genetic work was carried out on 85 of these specimens. Original descriptions and, where possible, type material were studied for all species. I showed that *L. elegans* belongs in *Caphyra*, while the holothurian symbiont *L. ornatus* is a junior synonym of *L. orbicularis.* Genetic and morphological results provided strong evidence that *L. laevis* is a species complex comprised of at least four species. Finally, CO1 data suggests that *L. polybioides* consists of at least three genetically distinct ESUs, but no morphological differences were evident among these ESUs (based on the limited material available). I thus demonstrate that *Lissocarcinus* is more diverse than previously thought, comprising at least 10 species.

In Chapter 4 I used a geometric morphometric (GMM) approach to investigate the evolutionary patterns of carapace shape changes associated with the emergence of symbiosis in Thalamitinae. Carapace shape is a functionally significant trait associated with swimming efficiency. Non-symbiotic portunoids, including most thalamitines, are efficient swimmers while symbiotic forms are not. I performed GMM analyses on 995 specimens from 103 species, and generated a molecular phylogeny of 107 species. I demonstrated a strong phylogenetic component to carapace shape, and showed that the greatest morphological disparity accumulated in the symbiotic Caphyrini clade. This chapter also provided a wealth of data amenable to additional analyses (see below).

Future Directions

Morphological diversity (i.e., disparity) is an important measure of biodiversity and understanding its evolutionary dynamics is a major aim of macroevolutionary research (Jablonski, 2000). However, morphology evolves within bounds set by intrinsic developmental processes and so typically remains highly constrained even when significant changes occur (Erwin, 2007; Gerber et al., 2008; Gould & Lewontin, 1979;

Jablonski, 2000; Klingenberg, 1998; Klingenberg, 2010; Olson-Manning et al., 2012). While it remains important to investigate the disparity dynamics responsible for adult forms, especially those generated during ecological diversification, some researchers have suggested that concurrent analyses of developmental disparity (e.g., changes in ontogenetic growth patterns) may significantly improve our understanding of how morphology evolves. In GMM studies, developmental disparity has been investigated by examining changes in allometric growth patterns (e.g., Adams & Nistri, 2010; Gerber et al., 2008; Klingenberg & Zimmermann, 1992; Sanger et al., 2013; Wilson & Sánchez-Villagra, 2010). In this context, allometry concerns how an organism's shape changes as it grows (Mitteroecker et al., 2005; Klingenberg 1998). Phylogenetic comparative analyses of allometry can help characterize the significance of disparity in adult forms. For example, it can reveal if a species' adult morphology is the result of attaining a larger or smaller size within a clade specific, conserved growth trajectory (constituting hypermorphic or progenic heterochronic change, respectively; see Klingenberg, 1998). Such results would suggest that morphological disparity accumulated under shared, clade specific, developmental constraint. Alternatively, these analyses could reveal that interspecific disparity of adult forms correlate with changes in allometric growth patterns between members of a single clade (signifying the clade experienced a variety of distinct heterochronic changes). This would suggest that disparate adult morphologies are the result of both novel morphological and developmental change.

Morphometric data presented in Chapter 4 includes numerous specimens of different sizes for most OTUs, making it suitable for additional analyses exploring phylogenetic patterns of allometric growth in carapace shape. Chapter 4 demonstrated

that the emergence of symbiosis in Caphyrini was marked by significant accumulation of morphologic disparity in carapace shape. Analyses of allometric patterns would allow one to evaluate whether this disparity accumulated under clade specific developmental constraints. Comparisons could include symbiotic versus non-symbiotic clades. In turn this may help reveal if significant ecological transitions correspond to the evolution of developmentally, as well as morphologically, novel diversity.

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BIOGRAPHICAL SKETCH

Nathaniel completed an Honors Bachelor of Science in biology at Oregon State University in 2005, a Master of Arts in ecology and evolutionary biology at the University of Kansas in 2009, and a Doctor of Philosophy in zoology from the University of Florida in 2016. He has conducted research on snakes, birds, parasitic cnidarians and here, crabs. He is currently very captivated by crabs and does not foresee pursuing any significant diversions from the group in the near future.