Molecular Phylogenetics of the Hermit Crab Genera PAGURISTES Dana, 1851, AREOPAGURISTES Rahayu, 2005, and PSEUDOPAGURISTES McLaughlin, 2002 (Crustacea: Decapoda: Anomura) With Descriptions of Two New Species

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Catherine W. Craig

APPROVED:

Darryl L. Felder, Chair Professor of Biology	Caryl Chlan Professor of Biology
Scott France Professor of Biology	Suzanne Fredericq Professor of Biology
Rafael Lemaitre Adjunct Professor of Biology Smithsonian Institution	Mary Farmer-Kaiser Dean of the Graduate School

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List of Abbreviations

AU	Approximately Unbiased
Alb	Alboran Sea
Bs	Bootstrap Value
CCDB	Crustacean Collection of the Department of Biology, University of São Paulo, Ribeirão Preto, São Paulo, Brazil
eInd	eastern Indian Ocean
KH	Kishino-Hasegawa
ML	Maximum Likelihood
MNHN	Muséum National d’Histoire Naturelle, Paris, France
NCBI	National Center for Biotechnology Information
neCarib	northeastern Caribbean Sea
neGMx	northeastern Gulf of Mexico
nePac	northeastern Pacific Ocean
NIWA	National Institute of Water and Atmospheric Research Invertebrate Collection, Greta Point, Wellington, New Zealand
NTOU	National Taiwan Ocean University, Keelung City, Taiwan
nwAtlantic	northwestern Atlantic Ocean
nwCarib	northwestern Caribbean Sea
nwGMx	northwestern Gulf of Mexico
nwPac	northwestern Pacific Ocean
PCR	Polymerase Chain Reaction
seCarib	southeastern Caribbean Sea
seGMx	southeastern Gulf of Mexico

sePac	southeastern Pacific Ocean
SH	Shimodaira-Hasegawa
Sl	Carapace shield length
swCarib	southwestern Caribbean Sea
swGMx	southwestern Gulf of Mexico
swPac	southwestern Pacific Ocean
Tas	Tasman Sea
UF	Florida Museum of Natural History Invertebrate Zoology Collection, University of Florida, Gainesville, Florida, USA
ULLZ	University of Louisiana at Lafayette Zoological Collection, University of Louisiana at Lafayette, Lafayette, Louisiana, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., USA
wInd	western Indian Ocean
wPac	western Pacific Ocean
ZRC	Zoological Reference Collection, Department of Zoology, National University of Singapore, Kent Ridge, Singapore, Republic of Singapore

Introduction

Paguroids (hermit and king crabs) are a speciose and important group within Decapoda. Members of Anomura, the morphologically unique infraorder sister to Brachyura ("true crabs"), the superfamily Paguroidea Latreille, 1802 today includes more than 1000 species (McLaughlin *et al*. 2010; Lemaitre & McLaughlin 2020). Although the superfamily is largely made up of asymmetrical animals with membranous abdomens that require a gastropod shell for protection, other forms exist that are symmetrical and make their homes in non-gastropod enclosures such as driftwood or sponges. Some are commonly found with anemone symbionts and many are found at abyssal depths. Hermit crabs are nearly ubiquitous in coastal marine environments from barrier islands to coral reefs and extensively populate deep banks of the continental shelf.

Historically, there has been significant controversy about relationships within and among paguroid families. Often the lines between families and significant genera have been blurry, with nomenclature shifting over time to settle into our present system of classification of hermit crabs. (Forest *et al*. 2000). Based on its distinctive soft-bodied asymmetry, the seminal paguroid genus, *Pagurus* Fabricius, 1775, was formed from a subdivision of the otherwise crab-like genus *Cancer* Linnaeus, 1758. Originally exemplified by *Cancer bernhardus* Latreille, 1810 (later *Pagurus bernhardus*, *Eupagurus bernhardus*, and briefly *Bernhardus typicus*), the newly designated *Pagurus* included taxa considered today to be members of the crab families Diogenidae Ortmann, 1892 and Paguridae Latreille, 1802. Through many permutations and further divisions of the tribe Paguridea, the name *Pagurus* came to be so broadly applied that it was no longer exemplified by the originally designated type species. These historical nomenclatorial nuances are well summarized by McLaughlin (1974) and Forest *et al*. (2000), but a brief overview is presented herein.

Several currently recognized hermit crab genera, including *Pagurus*, *Calcinus* Dana, 1851, and *Dardanus* Paul'son, 1875, have direct origins in the pagurid subdivision Ordinaires, one of three proposed by H. Milne Edwards (1836). Ordinaires was further subdivided into Dextres, Senestres, and Aequimanes (H. Milne Edwards 1848), with the right--handed taxa of Dextres grouped with *Pagurus bernhardus* and classified as the subgenus *Eupagurus* by later authors (Brandt 1851). In his taxonomic treatments, Dana (1851, 1852) bypassed the subcategories of Ordinaires, instead establishing two new genera: *Calcinus,* for left-handed species with calcareous claw tips, and *Bernhardus*, typified by *Pagurus bernhardus* (designated as *Bernhardus typicus* Dana, 1851). This latter classification scheme left the generic name *Pagurus* available for assignation to a subdivision of Paguridea that included primarily left-handed taxa with corneous claw tips, the type of which was *Pagurus punctulatus* Miers, 1879 (Dana 1852). Eventual elevation of *Eupagurus* to generic status and subsequent recognition of its seniority to *Bernhardus* (Stimpson 1856, 1858) allowed the reversion of the generic name *Pagurus* to right-handed hermit crabs of the type *Pagurus bernhardus* (Benedict 1896). This accomplished, *Pagurus* sensu Dana was designated *Dardanus*, the type of which then became *Dardanus megistos* Herbst, 1804 (Rathbun 1903). The generic name *Pagurus* was firmly affiliated with the type *Pagurus bernhardus* by rulings of the International Commission of Zoological Nomenclature in the 1950's (Forest & Holthuis 1955; Hemming 1957; Forest *et al*. 2000).

A simple taxonomic hierarchy is presented by Borradaile (1907) in which the tribe Paguridea included four families (Pylochelidae Spence Bate, 1888; Paguridae; Coenobitidae

Dana, 1851; Lithodidae Samouelle, 1819). The family Paguridae was further divided into subfamilies Pagurinae (including hermits with closely spaced third maxilliped bases, both those with equally sized chelipeds as well as left-handed hermits) and the Eupagurinae (including only right-handed hermit crabs with widely spaced third maxilliped bases). In the mid 20th century, this classification framework was used as a starting point for a suggested revision based on assessment of larval characteristics within Paguridea (MacDonald *et al*. 1957). In that work, support was found for two distinct lineages within Paguroidea, one of which included the symmetrical, carcinized king crabs (family Lithodidae). Additional findings indicated a close relationship between semiterrestrial land hermit crabs (Coenobitidae) and one family of asymmetrical hermit crabs (Diogenidae), whereas another family of hermit crabs (Paguridae) was most closely related to the symmetrical, crab-like king crabs (Lithodidae). The ultimate result was a suggestion that the superfamily Paguroidea be reorganized into two superfamilies, Paguroidea (Paguridae + Lithodidae) and Coenobitoidea (Coenobitidae + Diogenidae), each representing a distinct pathway to an asymmetrical body plan, and in the case of the new Paguroidea, a return to the symmetrical, crablike form by lithodids. Challenges have been made to the hypothesis surrounding the origin of the crab-like king crabs from within asymmetrical hermit crabs (McLaughlin 1983), but molecular studies, including the analyses presented Chapters 1 and 3 of this volume, continue to support the hypothesis (Cunningham *et al*. 1992; Zaklan & Cunningham 1992; Tsang *et al*. 2011; Bracken-Grissom *et al*. 2013; Wolfe *et al.* 2019).

Aside from Ordinaires, the remaining pagurid divisions of H. Milne Edwards (1836), Appendicules and Armes, emcompassed many species that would later become constituents of the genera *Paguristes* Dana, 1851, and *Diogenes* Dana, 1851, respectively (Forest *et al*.

2000). *Diogenes* is a moderately speciose genus in its own right, underpinning the family Diogenidae, and as such it is of considerable interest to many hermit crab systematists. However, *Paguristes*, along with closely allied genera *Areopaguristes* Rahayu & McLaughlin, 2010, and *Pseudopaguristes* McLaughlin, 2002, were chosen as the focus of the present work due, in part, to the sheer number of species included among them (more than 200), but also because emerging genetic evidence challenged the monophyly of *Paguristes* and *Areopaguristes,* signaling potential convergence of characters currently applied for generic diagnosis (Bracken-Grissom *et al*. 2013).

Certain elements of taxonomic uncertainty surrounding *Paguristes*, *Areopaguristes*, and *Pseudopaguristes,* have served as guiding themes across the entire body of the present work, although more detailed taxonomic context and objectives are included with each individual study as applicable. As it stands presently, there is some controversy surrounding the foundations of the genus *Paguristes*, which has at its heart the recent reassignment of the generic type species *Paguristes hirtus* Dana, 1851 to the genus *Tetralobistes* Ayon-Parente & Hendrickx, 2010 (Ayon-Parente & Hendrickx 2013). This reassignment leaves the taxonomic foundation of *Paguristes* and allied genera shaky, and an impetus to resolve this generic-level instability has provided an overarching goal of the studies combined herein. In addition to informing future revisions and confirming new species, this volume seeks to establish a framework for further comparative analyses of morphological change and evolution among paguroid subgroups. Beginning with the phylogenetic analyses of a geographically localized subset of limited taxonomic scope, the present body of work sought to develop a genetic data set capable of evaluating species level biodiversity and generic monophyly in accordance with these broad aims.

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Chapter 1: Molecular Phylogenetic Analysis of the *Paguristes tortugae* Schmitt, 1933 Complex and Selected Other Paguroidea (Crustacea: Decapoda: Anomura)

Abstract

Morphological characters, as presently applied to describe members of the *Paguristes tortugae* Schmitt, 1933 species complex, appear to be of limited value in defining phylogenetic relationships within the genus, and may have similarly misinformed understanding of relationships between members of this complex and those presently assigned to the related genera *Areopaguristes* Rahayu & McLaughlin, 2010 and *Pseudopaguristes* McLaughlin, 2002. Previously undocumented observations of similarities and differences in color patterns among populations additionally suggest genetic divergences within some species, or alternatively seem to support phylogenetic groupings of some species. In the present study, a Maximum Likelihood (ML) phylogenetic analysis was undertaken based on the H3, 12S mtDNA, and 16S mtDNA sequences of 148 individuals, primarily representatives of paguroid species from the western Atlantic. Some hypotheses regarding the evolutionary relationships among three genera of diogenid hermit crabs were refuted by the Kishino-Hasegawa (KH), Shimodaira-Hasegawa (SH), and Approximately Unbiased (AU) tree topology tests, among them the hypothesis that *Areopaguristes* Rahayu & McLaughlin, 2010 is monophyletic. A lack of support for the monophyly of *Areopaguristes* calls into question the phylogenetic validity of gill number for the differentiation of *Paguristes, Areopaguristes*, and *Pseudopaguristes*. The study was inconclusive with regard to the relationships among these three genera, but previously unknown diversity within both *Paguristes* and *Areopaguristes* was demonstrated. Existence of an undescribed species confounded under the name *Paguristes tortugae* Schmitt, 1933 was supported by genetics, morphology, and coloration. A second undescribed species with remarkable similarity to *Areopaguristes hummi* Wass, 1955 was discovered based on genetics and coloration, and both are to be described in a separate paper.

Key Words: Diogenidae, *Paguristes*, systematics, hermit crab, mtDNA, 16S, 12S, Histone 3.

Introduction

Within the infraorder Anomura, the superfamily Paguroidea (sensu McLaughlin *et al*. 2010) includes nearly 1200 species by current estimates (Lemaitre & McLaughlin 2020; WoRMS 2020). These hermit crabs are nearly ubiquitous in coastal marine environments from the intertidal to abyssal depths. A large body of morphological and genetic research on paguroid systematics has focused on the relationships between controversial, large-scale groupings (family level and above), as well as the phenomenon of carcinization (MacDonald *et al*. 1957; McLaughlin 1983; Forest 1987; Cunningham *et al*. 1992; Scholtz & Richter 1995; Morrison *et al*. 2002; Dixon *et al*. 2003; Ahyong *et al*. 2004; McLaughlin *et al*. 2007; Reimann *et al*. 2011; Tsang *et al*. 2011; Bracken-Grissom *et al*. 2013; Keiler *et al*. 2017; Palero *et al*. 2019). Emerging evidence from molecular phylogenetics, CO1 barcoding studies, and phylogenomic analyses demonstrates that evolutionary relationships within Anomura and among paguroid groups are not always clear cut, suggesting that the taxonomic scope of some families and many of the genera they encompass will require revisions in order to reconcile current classifications with phylogenetic relationships (Landschoff & Gouws 2018; Noever & Glenner 2018; Tan *et al*. 2018; Wolfe *et al*. 2019).

The most species-rich genus of diogenid hermit crabs with diverse morphology and coloration as well as global distribution, is *Paguristes* Dana, 1851, which includes an estimated 118 species (WoRMS 2020; Lemaitre & McLaughlin 2020). *Paguristes* is typified by the eastern Pacific species *Paguristes hirtus* Dana, 1851, a taxon formally placed into synonymy with *P. weddellii* H. Milne Edwards, 1848 by Haig (1955), though this synonymy was recently called into question in the reassignment of *P. weddellii* to *Tetralobistes* Ayon-Parente & Hendrickx, 2010 (Ayon-Parente & Hendrickx 2013). *Paguristes,* as currently considered, is generally diagnosed by the presence of distinctive paired first and second pleopods modified as male gonopods, 13 pairs of gills, and non-cheliform fourth pereopods (Dana 1851; Forest *et al*. 2000; Schweitzer & Fledmann 2001; Rahayu 2005).

Two additional diogenid genera, *Pseudopaguristes* McLaughlin, 2002 and *Areopaguristes* Rahayu, 2005, must be considered along with any discussion of *Paguristes*. *Pseudopaguristes* was established with *P. janetkae* McLaughlin, 2002 from Guam as the type species. Paired gonopods were noted to occur in *P. janetkae* that implied a relationship to *Paguristes*. However, a lesser number of gill pairs, 8 rather than 13, was considered by McLaughlin (2002) to necessitate the establishment of a separate genus. Even though the original generic diagnosis has been somewhat amended (Asakura 2004; Asakura & Kosuge 2004), the genus continues to be expanded upon and at present includes around 13 species from the western Pacific and two species from the western Atlantic (Rahayu 2005; Rahayu 2008; McLaughlin *et al*. 2010; Lemaitre & McLaughlin 2020). The discovery by Rahayu (2005) of 12 gill pairs in some western Pacific species previously assigned to *Paguristes* resulted in a reassignment of those taxa to the genus *Stratiotes* Thomson, 1899, which was later found to be a preoccupied name and thus replaced by *Areopaguristes* Rahayu & McLaughlin, 2010. Membership in *Areopaguristes* has been expanded since Rahayu's (2005) finding to now include several western Atlantic species with similar characteristics, most of which were also formerly placed in *Paguristes*. Like *Paguristes* and *Pseudopaguristes*, *Areopaguristes* has so far been presumed monophyletic. Although barcoding efforts have begun to address the issue (Landschoff & Gouws 2018) neither the monophyly of the three genera, nor the association among them have yet been specifically evaluated by a multi-gene molecular phylogenetic analysis.

In the western Atlantic, a prominent subset of the genus *Paguristes* is comprised of species closely resembling *Paguristes tortugae* Schmitt, 1933 (McLaughlin & Provenzano 1974). This informal morphological grouping or complex, includes a number of species that are distributed through the western Atlantic, including within the Gulf of Mexico. The species of this complex, originally defined by McLaughlin & Provenzano (1974) to include *P. tortugae*, *P. hewatti* Wass, 1963, *P. angustithecus* McLaughlin & Provenzano, 1974, *P. perplexus* McLaughlin & Provenzano, 1974, *P. hernancortezi* McLaughlin & Provenzano, 1974, *P. anomalus* Bouvier, 1918, and *P. invisisacculus* McLaughlin & Provenzano, 1974, are characterized primarily by the presence of dense plumose setation on the carapace and thoracic appendages. Since the taxonomic treatment of the complex by McLaughlin & Provenzano (1974), the proposed constituency of the complex has expanded to now include *P. maclaughlinae* Martinez-Iglesias & Gomez, 1989, from Cuba; *P. werdingi* Campos & Sanchez, 1995, and *P. zebra* Campos & Sanchez, 1995 from Colombia; and *P. scarabinoi* Lima & Santana, 2017 from Uruguay. The species of this complex have been regarded as closely related to one another, but no phylogenetic analysis has investigated their relationships on the basis of morphology or genetics. However, *P. hewatti* has been transferred to the genus *Areopaguristes* on the basis of its 12 gill pairs (Rahayu 2005) and *P. invisisacculus* was transferred to the genus *Pseudopaguristes* on the basis of its 8 gill pairs

(Rahayu 2005). Herein we question both of these reassignments based solely on gill numbers.

Within the *Paguristes tortugae* complex, some characters are diagnostic at the species level, but there is little consensus as to which morphological features might reliably link species or groups of species within the complex. Many morphological characters that have been applied in comparative studies of the complex are known to vary with specimen size (Provenzano & Rice 1966; McLaughlin & Provenzano 1974), while others show high intraspecific variation independent of size (McLaughlin & Provenzano 1974). Such variability, along with convergent morphological evolution, can obscure true genetic divergence and lead to misinterpretation of evolutionary relationships (Knowlton 1986; Bickford *et al*. 2007; da Silva *et al*. 2011). However, modern DNA-based molecular phylogenetic methods provide excellent alternative tools for investigation of cryptic diversity as well as phylogenetic relationships in difficult groups such as the *P. tortugae* complex (Knowlton 2000; Plaisance *et al*. 2009; Virjenhoek 2009; Puillandre *et al*. 2011; Pante *et al.* 2015).

Biodiversity studies of decapod crustaceans (Knowlton 1986; Felder *et al*. 2009b) have increasingly drawn attention to the role of color in detecting cryptic species diversity. Color and its patterning have been shown to support separations at the species level for carideans (Knowlton & Mills 1992; Grippa & d'Acoz 1996; Matthews *et al*. 2002; Rhyne & Lin 2006; Anker *et al*. 2008; Bracken & Felder 2014; Hultgren *et al*. 2014; Soledade *et al.* 2019), astacideans (Patoka *et al*. 2015), achelatans (Burton & Davie 2007; Tourinho *et al.* 2012), brachyurans (Castro 1982; Williams & Felder 1986; Ng & Huang 1997; Davie *et al*. 2010; Mendoza 2013; Mantelatto *et al.* 2014; Chenari *et al.* 2017), and varied anomurans

(Macphearson & Machordom 2001; Hiller *et al*. 2006; Hiller & Werding 2019), including paguroid anomurans (Haig & McLaughlin 1983; Poupin & McLaughlin 1998; Komai 2001; Malay & Paulay 2010; Malay *et al*. 2012; Negri *et al*. 2012, 2014; Perez-Barros *et al*. 2015; Jung *et al*. 2018; Lemaitre *et al*. 2018; Landschoff & Gouws 2018; Malay *et al.* 2018; Felder *et al*. 2019). In the *Paguristes tortugae* complex, some constituent species show well-defined and markedly different color schemes with little intraspecific variation or sexual dimorphism (McLaughlin & Provenzano 1974). Key literature (Provenzano 1959; McLaughlin & Provenzano 1974, Strasser & Price 1999), and extensive photographic evidence compiled by us document variation in color among individuals otherwise assignable by current definition as *P*. *tortugae.* Although these differences have long been observed, they have historically been regarded as ecomorphic variations of the phenotype closely tied to habitat substrate color (McLaughlin & Provenzano 1974), which could indeed apply to some paguroid taxa (Mandai *et al*. 2018).

The present study applies DNA-based molecular phylogenetic methods to illuminate evolutionary relationships among western Atlantic diogenid hermit crabs presently assignable to the *Paguristes tortugae* complex, including suspected constituents of the complex that might have instead been assigned to the genera *Areopaguristes* or *Pseudopaguristes*. On the basis of these analyses, this study also explores the utility of color patterns in defining previously known or undescribed cryptic species, as well as the potential use of color in characterization of generic-level clades within the genera *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*.

Materials and Methods

Taxon sampling was biased to western Atlantic representatives of the genus *Paguristes* with a specific focus on specimens assignable to the *P. tortugae* complex. Species identifications for specimens included in the analysis were determined from literature accounts related to the complex reports of the Gulf of Mexico fauna (Provenzano 1959, 1965; Felder 1973; McLaughlin & Provenzano 1974; Abele & Kim 1986; Strasser & Price 1999; Felder *et al.* 2009a). A color photograph database assembled by one of us (DLF) was consulted to identify color variants, and ethanol-preserved voucher specimens used for these photographs were integrated into the analyses as possible. Many specimens were accessed from the University of Louisiana Lafayette Zoological Collection (ULLZ), now deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), where they remain cross-listed under ULLZ catalog numbers. Other materials for DNA sequencing were accessed from the Florida Museum of Natural History, University of Florida, Gainesville, FL (UF). Specimens selected for DNA sequencing were limited primarily to sequence-quality material collected after 1999. Occasional attempts to sequence older material were also made with varied success. Every effort was made to include at least two representatives of each putative taxon or variant population. Specimens used in this study were either directly preserved in 80% ethyl alcohol (EtOH), or first frozen in either seawater or glycerol at −80°C before later being transferred to 80% EtOH.

One-hundred-forty-eight individuals representing approximately 60 nominal species of 35 decapod genera were included in the phylogenetic analysis. Histone 3, 12S, and 16S sequences for 102 individuals were generated for this project, while sequences for the remaining 46 were obtained from GenBank (Table 1.1). Many high-level anomuran and paguroid relationships are unclear (Ahyong & O'Meally 2004; Ahyong *et al.* 2010; Bracken-Grissom *et al*. 2013; Wolfe *et al.* 2019), but a general consensus that Brachyura is the sister-group (Forest 1987; Scholtz & Richter 1995; Dixon 2003; Ahyong & O'Meally 2004; McLaughlin *et al*. 2007; De Grave *et al*. 2009; Bracken-Grissom *et al*. 2013) continues to be supported by emerging literature (Tan *et al*. 2015, 2018; Wolfe *et al*. 2019). Therefore, in addition to eight anomuran species from outside of Paguroidea, four brachyuran representatives were included in the analysis as an outgroup, though none represent lineages suggested as outgroups by existing studies that focused on the higher relationships of Paguroidea (McLaughlin & Lemaitre 1997; McLaughlin *et al.* 2007; Noever & Glenner 2017; Wolfe *et al*. 2019).

Genomic DNA was extracted from gill, abdominal tissue, eggs (when available), or whole appendages when necessary, using the Qiagen DNeasy DNA extraction kit (Qiagen, Cat. No. 69504). The DNA purity and concentration was evaluated using the NanoDrop Lite Spectrophotometer (ThermoFisher Scientific, Cat. No. ND-LITE-PR). Two mitochondrial markers and one nuclear marker were selectively amplified using polymerase chain reaction (PCR). A fragment of the mitochondrial large subunit rDNA (16S) of approximately 550 base-pairs (bp) in length was amplified using the primers 16S 1472 and a combination of 16SL2 and 16Sar, or primer pair 16S-CWC-01f and 16S-CWC-01r. A fragment of the mitochondrial small subunit rDNA (12S) approximately 310 bp in length was amplified using primers 12Sf and 12S1r. A fragment of the nuclear marker, Histone 3 (H3) of approximately 350 bp in length was amplified using primer pair H3f and H3r. Full primer information is presented in Table 1.2. Reactions were performed in 25 µL volumes using one of four basic mixtures: 1) 30–50 ng DNA template, 0.8 µM each primer, 200 µM dNTPs, 2.5

μL DreamTaq Green Buffer, 1.5 units DreamTaq Green (ThermoFischer Scientific Inc., Cat. No. EP0712); 2) 30–50 ng DNA template, 0.5 μM each primer, 200 μM dNTPs, 2.5 μL DreamTaq Green Buffer, 1 unit DreamTaq Green; 3) 30–50 ng DNA template, 0.8 μM each primer, 200 μM dNTPs, 2.5 μL DreamTaq Green Buffer, 1.5 units DreamTaq Green, 1 μL 1% Bovine Serum Albumin; 4) 30–50 ng DNA template, 0.4 μM each primer, 200 μM dNTPs, 2.5 μL DreamTaq Green Buffer, 1 unit DreamTaq Green, 1 μL 1% BSA. PCR cycling protocols were as follows: initial denaturation for 3 min at 96°C; 35–40 cycles with denaturation for 30 s at 96°C, annealing for 30 s–1 min at 50–54°C (H3af/H3r, 12Sf/12Sr, 16S 1472/16SL2/16Sar) or for 45 s at 56°C (16S-CWC-01f/16S-CWC-01r), elongation for 1 min at 72ºC; final extension of 10 min at 72°C (Table 1.2).

PCR products were purified using SureClean Plus (Bioline USA Inc, SKU 37047). Purified PCR product was cycle-sequenced using the ABI Big-Dye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems Inc, Foster City, CA, USA). For some sequencing reactions, the manufacturer's protocol for Big-Dye mediated sequencing was modified to accommodate the use of BDX64 Big-Dye Enhancing Buffer (Molecular Cloning Labs, Cat. No. BDX-100), an additive enabling cycle-sequencing with reduced quantities of Big-Dye chain terminators. Cycle sequencing products were purified by filtration though Sephadex G-50 Medium (GE Healthcare Bio-Sciences, Cat. No. 17-0043-01) in Applied Biosystems Centri-Sep Spin Columns (ThermoFisher Scientific, Cat. No. 401762). The samples were then analyzed on an ABI PRISM 3130 Genetic Analyzer (Applied Biosystems Inc., Foster City, CA USA).

Sequence contigs were assembled in Sequencher 4.1.2 (GeneCodes Corporation, Ann Arbor, MI). A Multiple Sequence Alignment was generated for each marker individually in

MAFFT (Katoh *et al*. 2002) under G-INS-i criteria for H3, and E-INS-i criteria for 12S and 16S (Katoh *et al*. 2017). Ambiguously aligned regions were trimmed from each alignment by GBlocks (Castresana 2000). Default parameters were used in GBlocks for the H3 marker, but for the 12S and 16S alignments the following parameter modifications were made: 1) minimum length of block = 8; 2) allowed gap positions = half. The resulting single-gene alignments were concatenated into a single aligned matrix in SequenceMatrix (Vaidya *et al.* 2011). Model partitions were assigned to alignment regions corresponding to the three individual markers, with the H3 marker further partitioned by codon. A Maximum Likelihood (ML) phylogeny, along with 1000 bootstrap replicates, was inferred in RAxML (Stamatakis 2006) under a GTR+Gamma model of nucleotide substitution (Rodriguez *et al.* 1990).

To enable hypothesis testing, an ultrametric constraint tree was generated in Mesquite (Maddison & Maddison 2017) by manual restructuring of a generic star phylogeny to reflect a monophyletic *Areopaguristes* without restricting the placement of *Areopaguristes* within the overall tree topology. The best ML tree reflecting the constrained topology was inferred using the RAxML (Stamatakis 2006) Black-Box tool available on the CIPRES Science Gateway (Miller *et al.* 2010) under GTR+Gamma. Additional trees were similarly generated to reflect alternative hypotheses about the relationships among *Paguristes*, *Areopaguristes*, and the three subclades of Diogenidae. These included: *Paguristes* and *Areopaguristes* as monophyletic sister clades; Diogenidae Clades 1, 2, and 3 united as a single monophyletic clade; Diogenidae Clade 2 + Coenobitidae + Diogenidae Clade 3 monophyletic and sister to Paguridae Clade 1 + Lithodidae + Paguridae Clade 2; Diogenidae Clade 2 + Coenobitidae + Diogenidae Clade 3 monophyletic and sister to Diogenidae Clade 1 (Table 1.3). Topology testing in the form of the Approximately Unbiased (AU, Shimodaira 2002), Kishino-Hasegawa (KH, Kishino & Hasegawa 1989), and Shimodaira-Hasegawa (Shimodaira & Hasegawa 1999) tests of tree topology was performed in IQtree v1.6.3 (Nguyen *et al*. 2015; Chernomor *et al*. 2016). Under all three criteria, topologies with p-values less than 0.05 were considered refuted hypotheses that were unlikely to represent an accurate phylogenetic reconstruction (Shimodaira 1999, 2002).

Results

The unrefined alignments for the H3, 12S, and 16S each incorporated 450, 981, and 821 positions respectively. Removal of ambiguously aligned regions and large gaps resulted in single marker alignments of approximately 214, 329, and 442 positions. After concatenation, the final alignment length was 987 base pairs for 148 individuals. One thousand nonparametric bootstrap replicates were generated in the course of our phylogenetic analysis and were interpreted as measures of confidence for clades inferred in our most likely ML tree topology (Felsenstein 1985). Bootstrap values are not universally regarded as an infallible measure of clade probability (Sanderson 1995; Alfaro *et al*. 2003; Anisimova & Gascuel 2006; Susko 2010), but theory and empirical evidence supports their utility in establishing confidence intervals for ML tree topologies generated using data sets similar to ours (Hedges 1992; Hillis & Bull 1993; Efron *et al.* 1996; Sanderson 1995; Mort *et al*. 2000; Soltis & Soltis 2003; Galtier 2004; Regier *et al*. 2013; Lemoine *et al*. 2018). In our study, nodes with bootstrap support values of 50 or greater were treated as stable inferences of the phylogenetic relationships among the species or groups of species united at that node.

The multigene ML analysis revealed deep divisions within the family Diogenidae, which was partitioned into three distinct clades in the best ML tree topology (Fig. 1.1).

Diogenidae Clade 1 (bootstrap 96), was composed of the three genera *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*, all of which were confined to Clade 1. Subdivisions of Diogenidae Clade 1 included four monophyletic subclades as follow: 1) *Paguristes tortugae*, *P*. "nr. *tortugae* **n. sp.**", *A. hewatti*, *P. hernancortezi*, *P. anomalus*, *Pseudopaguristes invisisacculus*, *A. tudgei*, and individuals of yet unknown identity (Subclade 1a, bootstrap <50); 2) *Paguristes triangulatus, P. grayi, P. spinipes, P. moorei, P. puncticeps,* and some species of unknown identities (Subclade 1b, bootstrap <50); 3) *Areopaguristes oxyophthalmus, A. "*nr. *oxyophthalmus* **n. sp.**", and numerous morphologically similar individuals of unknown identity from the eastern Pacific (Subclade 1c, bootstrap 98), 4) *Areopaguristes hummi*, *A. "*nr. *hummi* **n. sp.**", and morphologically similar individuals of unknown identity from the eastern Pacific (Subclade 1d, bootstrap 100). The second major diogenid clade, Diogenidae Clade 2, counted among its constituent genera *Clibanarius* Dana, 1852 and *Calcinus* Dana, 1851 and showed significant support for a sister relationship to our representatives of Coenobitidae, *Coenobita clypeatus* and *Birgus latro* Linnaeus, 1767 (bootstrap 77). However, Diogenidae Clade 2 was not supported as an independent clade. Comprised of the genera *Bathynarius* Forest, 1989 and *Dardanus* Paul'son, 1875, Diogenidae Clade 3 showed significant bootstrap support individually (bootstrap 52) and a significantly supported sister relationship to a clade combining Diogenidae Clade 2 and Coenobitidae (bootstrap 100). When Diogenidae Clade 2, Coenobitidae, and Diogenidae Clade 3 were considered together as a monophyletic clade, that grouping was sister to a monophyletic clade composed of Paguridae Clade 1, Lithodidae, and Paguridae Clade 2, although bootstrap support for the relationship was not significant (Fig. 1.1). The multigene ML analysis did not recover a clade supporting a monophyletic

Areopaguristes, and hypothetical trees that included such a clade were refuted by quantitative comparisons (Table 1.3).

For the evaluation of hypothetical relationships among major paguroid clades by the AU, KH, and SH tests, a p-value between 0 and 1 was generated for each tree inferred under topological constraints defined by us *a priori*. Constraints were chosen that specified genetic relatedness congruent with current paguroid taxonomy or speculated relationships among paguroid groups of various taxonomic levels. The AU, SH, and KH tests yielded low p-values for our constraint trees (Table 1.3) and showed that none were likely to be the "true" tree (Shimodaira 1999, 2002). This underscored the outcome of our unconstrained ML analysis that indicated a lack of monophyly for several accepted paguroid groups corresponding to clades incorporated into our constraint trees (Fig. 1.1).

Discussion

Diogenidae has been considered by many authors to be a monophyletic family encompassing 22 genera and closely allied with or sister to Coenobitidae (MacDonald *et al*. 1957; McLaughlin 1983, 2002; Cunningham *et al*. 1992; McLaughlin & Lemaitre 1997; Forest & McLaughlin 2000; Ahyong & O'Meally 2004; McLaughlin *et al*. 2007, 2010; De Grave *et al*. 2009; Schnabel *et al*. 2009), but evidence from phylogenetic studies ranging across Decapoda suggests that the family Diogenidae may not be monophyletic (Tudge 1997; Tsang *et al*. 2008, 2011; Bybee *et al*. 2011; Schnabel *et al*. 2011; Bracken-Grissom *et al*. 2013; Gong *et al*. 2018; Landschoff & Gouws 2018; Tan *et al*. 2018; Wolfe *et al*. 2019). Our analysis concurs with the latter findings on the topic of diogenid monophyly by recovering a clade that integrates the diogenid genera *Bathynarius*, *Calcinus*, *Clibanarius*, and *Dardanus*, with the coenobitid genera *Birgus* and *Coenobita* (bootstrap 100) while relegating all species of *Areopaguristes*, *Paguristes*, and *Pseudopaguristes* to Diogenidae Clade 1 (Fig. 1.1). Although the phylogenetic validity of these two major clades in our study and others is irrefutable, the present study included representatives of only four of the 22 diogenid genera, putting the determination of appropriate revisions at the family level beyond the scope of the present study. Therefore, the clade nomenclature here employed maintains *Coenobita clypeatus* and *Birgus latro* as members of Coenobitidae, while designating the diogenid clades most closely associated with Coenobitidae as two independent subgroups of diogenid genera: Diogenidae Clade 2 (*Calcinus*, *Clibanarius*) and Diogenidae Clade 3 (*Bathynarius*, *Dardanus*).

With regard to the phylogenetic validity of Diogenidae Clade 1, Clade 2, and Clade 3, our outcomes mirror those from a molecular ML analysis of Anomura by Bracken-Grissom *et al*. (2013) that included 66 paguroids and recovered an assemblage of diogenid hermit crabs with a generic constituency consistent with our Diogenidae Clade 1. Although not addressed in detail by that study, an additional finding by Bracken-Grissom *et al*. (2013) was a significantly supported (bootstrap 100) assemblage of 16 species corresponding to an assemblage from our analysis in which Diogenidae Clade 2, Coenobitidae, and Diogenidae Clade 3 are united (bootstrap 100). Additional support for our three diogenid clades can be found in a recent CO1 barcoding study (Landschoff & Gouws 2018) and a study of mitochondrial gene rearrangements (Gong *et al*. 2018). Both studies recovered a polyphyletic Diogenidae having three groupings with constituencies congruent with those of our three diogenid clades. The convergence of our phylogenetic analysis with these previous studies provides ample justification for our evaluation of the phylogenetic status of Diogenidae, refuting the hypothesis of a monophyletic Diogenidae by three metrics (Table 1.3).

Nonetheless, it is important to acknowledge that the taxonomic sampling of Paguroidea in our study, as well as those cited, was limited and that taxonomic under-sampling can cause errors in the accuracy of phylogenetic inference (Zwickl & Hillis 2002; Hillis *et al*. 2003; Weins 2003). Thus, further work with more robust taxonomic coverage is necessary to clarify foundational relationships among paguroid genera and families.

Phylogenetic results presented herein reveal potential trends in morphology and generic constituency across the four subclades within Diogenidae Clade 1 (Fig. 1.1). Among these subclades, Subclade 1a includes the *Paguristes tortugae* complex, a group established herein as having constituent species that are by varied authors assigned to *Paguristes*, *Pseudopaguristes*, or *Areopaguristes*, whereas a second subclade, Subclade 1b, encompasses only *Paguristes* species. Two other assemblages, Subclade 1c and Subclade 1d, count only *Areopaguristes* species as constituents. Correlations between morphological groupings based on telson armature frequently applied to the genus *Paguristes* (McLaughlin & Provenzano 1975) and some Diogenidae Clade 1 genetic subclades are recognizable in the present study, with most species included in the monophyletic Subclade 1b belonging to the group of *Paguristes* spp. with unarmed telsons. However, there is no corresponding monophyletic clade of taxa with with armed telsons. The correspondence of telson morphology to at least part of our molecular phylogenetic findings suggests that, beyond its utility in species diagnosis within *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*, telson armature could prove to be of value in future generic level revisions in this group (McLaughlin & Provenzano 1975; Komai Miyake 1978; Komai 2001; McLaughlin & Rahayu 2005; Rahayu 2006; Rahayu & McLaughlin 2006; McLaughlin 2008; Lemaitre & Felder 2012; Komai *et al*. 2015).

In contrast to a recent finding that would place a monophyletic *Paguristes* as sister to *Areopaguristes* and *Pseudopaguristes* (Landschoff & Gouws 2018), our unconstrained ML phylogeny reveals that species presently assigned to the genus *Areopaguristes* on the basis of gill formula are not monophyletic across the *P. tortugae* complex, nor within other subclades of Diogenidae Clade 1 (Fig. 1.1). The results of the KH, SH, and AU tests provide substantial quantitative support for the distribution of *Areopaguristes, Pseudopaguristes,* and *Paguristes* species, as currently recognized, throughout multiple genetic subclades within Diogenidae Clade 1. The p-values refute the general monophyly of *Areopaguristes,* as well as the hypothesis that *Paguristes* and *Areopaguristes* are monophyletic sister clades (Table 1.3). This lack of support for generic monophyly has important implications for the taxonomic status of all three genera, as it demonstrates that gill formula likely represents little more than convergent evolution among subgroups presently assigned to *Paguristes, Areopaguristes*, and *Pseudopaguristes*. Thus, among the extensively represented western Atlantic members in our phylogenetic analyses that are presently treated under these genera there is no more justification for assignment of some to the otherwise western Pacific genera *Areopaguristes* or *Pseudopaguristes* than there is for them to remain, for now, in *Paguristes*. Indeed, the single western Pacific "*Pseudopaguristes* sp." in our analysis, likely an undescribed species, is well separated from any western Atlantic species that might be currently treated under that genus on the basis of its gill formula.

Establishing the limits of a *Paguristes* s.s. is clearly required in the course of eventual generic revisions to the diogenids, which is beyond the scope of the present study. With the eastern Pacific *Paguristes hirtus* Dana, 1851, as the type of the genus, we find no compelling reason to reject the conclusion by Haig (1955) that it was a junior synonym of *P. weddellii* H.

Milne Edwards, 1848. This synonymy was called into question by Ayon-Parente & Hendrickx (2013), who moved *P. weddellii* to *Tetralobistes* Ayon-Parente & Hendrickx, 2010, but in our opinion, this unnecessarily leaves *Paguristes* orphaned for lack of a type species. We at present lack adequate sequence-quality materials of *P. weddellii* to fully address its relationships in our molecular phylogenetic tree, but strongly suspect it to be most closely affiliated with Subclade 1d, otherwise comprised of *Areopaguristes* spp. from the western Atlantic and eastern Pacific. This is suggested on the basis of readily evident morphological similarities between *A. hummi*, morphologically similar genetic relatives of *A. hummi*, and *P. weddellii*, as well as incomplete sequence comparisons, both of which will be addressed in a coming paper (Craig *et al*., in preparation).

The internal structure of the genetic clade encompassing species assignable to the *Paguristes tortugae* complex shows significant support for a previously unrecognized cryptic species close to *P. tortugae* (Fig. 1.1). Well prior to present genetic evidence for this new species, freshly collected specimens could be designated as one of two distinct color forms that were otherwise both assignable to *P. tortugae* by diagnostic morphology (Provenzano 1959, 1965; Williams 1965; McLaughlin & Provenzano 1974; Strasser & Price 1999). In the description of *P. tortugae* little mention was made of color (Schmitt 1933), and subsequent descriptions of preserved *P. tortugae* specimens described them as “colorless” (Holthuis 1959), “whitish” (Provenzano 1959, Williams 1965), or “straw colored” (McLaughlin & Provenzano 1974). Some accounts detailed prominent red spines on the mesial margin of the manus and carpus of the cheliped (Provenzano 1959; Holthuis 1959; Williams 1965). Others described “pinkish legs” (Holthuis 1959) or purple to reddish legs (Provenzano 1965). Most accounts agreed that the eyestalks and antennular peduncles of *P. tortugae* bore dark bands near mid-length, visible in life and in preservation (Wass 1955; Holthuis 1959; Provenzano 1959, 1965; Williams 1965; McLaughlin & Provenzano 1974; Strasser & Price 1999). It was accepted that color varied in live examples of the species (Provenzano 1965; McLaughlin & Provenzano 1974; Williams 1965), with lighter colored variants of *P. tortugae* reportedly comparable to *A. hewatti* (Wass 1963; McLaughlin & Provenzano 1974). From comparison among photographic accounts of voucher specimens of *A. hewatti*, *P*. *tortugae*, and our cryptic undescribed species labelled *P*. “nr. *tortugae* ”, one set of specimens morphologically attributable to *P*. *tortugae* shows some similarity in color to *A. hewatti*. This set of specimens, with background color generally pale rose to buff, is regarded by us to represent *P*. *tortugae* s.s.A second set of specimens bears more similarity to a previously noted (Strasser & Price 1999) but undescribed species close to *P*. *tortugae*, and is perhaps representative of the “darker” forms of *P*. *tortugae* noted by McLaughlin & Provenzano (1974). This second color-form, with a tan to olive background color marked by vibrant red spines on the carpi of the chelipeds and pereopods, is regarded by us to be the cryptic new species herein labelled as *P*. “nr. *tortugae* ”. Three individuals of this putative new species are included in our analysis, and together they form a monophyletic clade with high bootstrap support (bootstrap 100). Equally high bootstrap support links our cryptic species to *P. tortugae* s.s., confirming the two as genetically distinct sister lineages (bootstrap 100). While recorded variation in color within *P*. *tortugae* s.l. was previously suggested to be an ecomorphic variant correlated with substrate color (McLaughlin & Provenzano 1974), the molecular evidence presented here demonstrates a clear correspondence between color variation and genetic divergence in the case of these species. Minor differences in morphology also support the separation, but full comparative treatment of this and color characters is deferred to a companion paper formally describing *P*. “nr. *tortugae* **n. sp.**” as a new species (Craig & Felder, in preparation).

Areopaguristes hummi and several eastern Pacific allies form a well-supported clade (bootstrap 100), but the close affinity of that group with the rest of Diogenidae Clade 1 does not show significant bootstrap support. In our ML phylogeny, a *A. hummi* complex includes specimens of unclear assignment, many of which are from the eastern Pacific coast of Panama. With these unidentified Pacific specimens included, the *A. hummi* complex is strongly monophyletic (bootstrap 100). Multiple individuals of *A. hummi* from the Gulf of Mexico cluster together with high support (bootstrap 100), and *A.* “nr. *hummi* **n. sp.**”, our new species from Atlantic coast of Central America, is sister to our assemblage of *A. hummi* representatives (bootstrap 97).

Definitive morphological characters for *Areopaguristes* “nr. *hummi* **n. sp.**” are not readily apparent, but support for its separation is found in the coloration of fresh specimens. As described by Wass (1955), *A. hummi* is characterized by a vibrant blue patch on the distal portion of the chelar merus mesial face, bounded anteriorly by a well-defined, curved, black marking (the “meral rainbow”). *Areopaguristes* “nr. *hummi* **n. sp.**” lacks this blue patch, and the black patterning seen on the mesial face of the merus is restricted to a well-defined, crescent shaped marking at the distal margin (the “meral crescent”). Other differences are apparent in the coloration of the head appendages, predominantly the ocular peduncles, which exhibit a golden color in *A.* “nr. *hummi* **n. sp.**”, in contrast to the blue hue of *A. hummi*. Adding support for the establishment of *A.* “nr. *hummi* **n. sp.**”, the geographic distribution of the two species does not overlap. *Areopaguristes hummi* is found broadly across the Gulf of Mexico (Wass 1955; Strasser & Price 1999; Felder *et al.* 2009a), while our new species, *A*. “nr. *hummi* **n. sp.**”, is currently known only from the Atlantic coast of Central America. As with *A*. “nr. *hummi* **n. sp.**”, full comparative treatment of morphology and color characters is deferred to a companion paper formally describing *A*. “nr. *hummi* **n. sp.**” as a new species (Craig & Felder, in preparation).

The phylogenetic inference presented here demonstrates the potential for color and pattern to predict broader clade composition for species of the *Paguristes tortugae* complex. This becomes evident when trends in head appendage color and pattern are superimposed on our phylogenetic analysis. In the phylogenetic analysis, the core of the *P*. *tortugae* complex is divided into two primary clades. One of these, consisting of *P*. *tortugae*, *P*. “nr. *tortugae* **n. sp.**”, *A*. *hewatti,* and *P*. *hernancortezi*, encompasses only species with banded or spotted eyestalks. In the other subclade, composed of *Areopaguristes tudgei*, *Pseudopaguristes invisisacculus*, and *Paguristes anomalus* all species have blue head appendages and distally blue eyestalks. In this case, three species currently treated in three different genera on the basis of supposedly fundamental differences in gill formula, are instead grouped by eyestalk color in conformation with their molecular genetic clade grouping.

Paguristes tortugae complex constituents not included in our molecular analysis can be speculatively placed according to this trend, with *P*. *zebra* as a potential constituent of the banded eyestalk clade, while *P*. *scarabinoi* falls among the species with blue head appendages. The qualitative nature of these observations limits definitive conclusions that can be drawn, but evidence of this phenomenon all the more compels hermit crab systematists to include color of fresh specimens as a character of potential value in both species distinctions and determination of phylogenetic groupings of species.

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Table 1.1. Voucher specimens used for ML phylogenetic inferences, showing catalog number, collection locality, and NCBI GenBank accession numbers for partial sequences of H3, 12S mtDNA, and 16S mtDNA. (Museum abbreviations: MNHN = Muséum National d'Histoire Naturelle, Paris, France); NTOU = National Taiwan Ocean University, Keelung City, Taiwan; UF = Florida Museum of Natural History Invertebrate Zoology Collection, University of Florida, Gainesville, Florida, USA; ULLZ = University of Louisiana at Lafayette Zoological Collection, Lafayette, Louisiana, USA; USNM = National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Taxon Name	Catalog No.	Country: Locality	Accession Number H3 / 12S / 16S
Albuneidae			
Albunea gibbesii	ULLZ 7376/USNM 1541769	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	KF182698 / KF182373 / KF182558
Lepidopa dexterae	ULLZ 4867/USNM 1540594	Belize: Stann Creek, northwestern Caribbean	KF182704 / KF182375 / KF182561
Calappidae			
Calappa gallus	KC3083	Japan: Shirihama, northwestern Pacific	EU921049 / EU920886 / EU920916
Diogenidae			
Areopaguristes hewatti	ULLZ 6861/USNM 1543164	USA: Texas, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes hewatti	ULLZ 6876/USNM 1542683	USA: Texas, northwestern Gulf of Mexico	KF182733 / KF182377 / KF182535
Areopaguristes hewatti	ULLZ 7710/USNM 1543169	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Areopaguristes hewatti	ULLZ 7133/USNM 1542127	USA: Texas, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes hewatti	ULLZ 7134/USNM 1542128	USA: Texas, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes hummi	ULLZ 6880/USNM 1542630	USA: Texas, northwestern Gulf of Mexico	KF182730 / KF182379 / KF182541
Areopaguristes hummi	ULLZ 6926/USNM 1541590	USA: Florida, Fort Pierce, western Atlantic	KF182731 / KF182380 / KF182542
Areopaguristes hummi	ULLZ 13232/USNM 1546831	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes hummi	ULLZ 14571/USNM 1547704	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes nr. *hummi*	ULLZ 15009/USNM 1548225	Panama: Bocas del Toro, southwestern Caribbean	pending / pending / pending
Areopaguristes oxyophthalmus	ULLZ 10859/USNM 1545362	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes oxyophthalmus	ULLZ 13746/USNM 1547232	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes nr. *oxyophthalmus*	ULLZ 14926/USNM 1548050	Panama: near Isla Cañas, northeastern Pacific	pending / pending / pending
Areopaguristes nr. *oxyophthalmus*	ULLZ 9676/USNM 1544504	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending

Areopaguristes nr. *oxyophthalmus*	ULLZ 9692/USNM 1544519	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes tudgei	ULLZ 12576/USNM 1547127	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Areopaguristes sp.	ULLZ 9380/USNM 1544293	Costa Rica: Gulf of Papagayo, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9674/USNM 1544502	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9675/USNM 1544503	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9678/USNM 1544506	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9680/USNM 1544508	Panama: east of Isla Los Venaditos, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9688/USNM 1544516	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9691/USNM 1544518	Panama: east of Isla Los Venaditos, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9693/USNM 1544520	Panama: east of Isla Los Venaditos, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 14921/USNM 1548565	Panama: Panama Bay, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 14922/USNM 1548044	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 14923/USNM 1548046	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 14925/USNM 1548049	Panama: near Isla Cañas, northeastern Pacific	pending / pending / pending
Bathynarius anomalus	USNM 1297334	Curaçao: southeastern Caribbean	pending / pending / pending
Birgus latro	KC 6694	unavailable	KF182696 / KF182421 / KF182532
Calcinus laevimanus	NTOU A01100	Taiwan: western Pacific	KJ133080 / KJ132385 / KJ132524
Calcinus obscurus	ULLZ 14924/USNM 1548047	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Calcinus tibicen	ULLZ 8528/USNM 1543755	USA: Florida, Fort Pierce, western Atlantic	pending / pending / pending
Calcinus tibicen	ULLZ 9973/USNM 1544616	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Calcinus tibicen	ULLZ 12528/USNM 1546374	Belize: Southwater Cay, northwestern Caribbean	pending / pending / pending
Calcinus tibicen	ULLZ 14920/USNM 1548043	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Calcinus sp.	UF 020715	Juan de Nova Island: Mozambique Channel, Indian Ocean	pending / pending / pending
Clibanarius antillensis	ULLZ 9433/USNM 1544313	USA: Florida, Fort Pierce, western Atlantic	KF182693 / KF182424 / KF182529

Clibanarius corallinus	ULLZ 10121/USNM 1544831	French Polynesia: Tuamotu Archipelago, southern Pacific	KF182694 / KF182423 / KF182528
Clibanarius vittatus	ULLZ 4781/USNM 1540545	USA: Florida, northeastern Gulf of Mexico	KF182692 / KF182422 / KF182527
Coenobita clypeatus	ULLZ 9968/USNM 1544612	Belize: Carrie Bow Cay, northwestern Caribbean	KF182695 / KF182420 / KF182531
Coenobita perlatus	MNHN Pg-8024	New Caledonia: Chesterfield Island, western Pacific	HQ241557 / HQ241501 / HQ241512
Dardanus insignis	USNM 1297351	Curaçao: southeastern Caribbean	pending / pending / pending
Dardanus venosus	ULLZ 6711/USNM 1541655	USA: Florida, northeastern Gulf of Mexico	KF182697 / KF182428 / KF182533
Dardanus venosus	USNM 1297351	Curaçao: southeastern Caribbean	pending / pending / pending
Dardanus sp.	ULLZ 9694/USNM 1544521	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Dardanus sp.	ULLZ 9486/USNM 1535468	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Paguristes acanthomerus	UF 029439	Taiwan: Yilan County, northwestern Pacific	pending / pending / pending
Paguristes anomalus	ULLZ 7536/USNM 1543121	Mexico: Yucatan Peninsula: southwestern Gulf of Mexico	pending / pending / pending
Paguristes anomalus	ULLZ 14495/USNM 1547686	Dutch Antilles: Saba Bank, northeastern Caribbean	pending / pending / pending
Paguristes grayi	ULLZ 9963/USNM 1544609	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Paguristes grayi	ULLZ 11744/USNM 1545936	Panama: Zapatillas Island, southwestern Caribbean	KF182728 / KF182382 / KF182537
Paguristes grayi	ULLZ 12533/USNM 1546377	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Paguristes hernancortezi	ULLZ 16085/USNM 1618808	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Paguristes inconstans	USNM 1297248	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes jalur	UF 005421	Mascarene Islands: Reunion Island, southern Indian Ocean	pending / pending / pending
Paguristes moorei	ULLZ 10860/USNM 1545363	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Paguristes moorei	ULLZ 14050/USNM 1547438	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Paguristes moorei	USNM 1297281	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes moorei	USNM 1297282	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes moorei	ULLZ 8172/USNM 1543433	USA: northeastern Gulf of Mexico	pending / pending / pending
Paguristes planatus	USNM 1297344	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes puncticeps	ULLZ 6801/USNM 1541861	southwestern Gulf of Mexico	KF182727 / KF182383 / KF182538

Paguristes puncticeps	ULLZ 8271/USNM 1543851	USA: Sackett Bank, northeastern Gulf of Mexico	pending / pending / pending
Paguristes puncticeps	ULLZ 11742/USNM 1545934	Panama: Zapatillas Island, southwestern Caribbean	pending / pending / pending
Paguristes puncticeps	ULLZ 13331/USNM 1546875	Panama: Bocas del Toro, southwestern Caribbean	pending / pending / pending
Paguristes puncticeps	ULLZ 14301/USNM 1547659	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Paguristes sericeus	ULLZ 6525/USNM 1541664	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Paguristes sericeus	ULLZ 7118/USNM 1541753	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	pending / pending / pending
Paguristes sericeus	ULLZ 7966/USNM 1543167	USA: northeastern Gulf of Mexico	pending / pending / pending
Paguristes spinipes	ULLZ 14487/USNM 1547681	Dutch Antilles: Saba Bank, northeastern Caribbean	pending / pending / pending
Paguristes spinipes	USNM 1297376	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes spinipes	USNM 1297338	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes tortugae	ULLZ 4783/USNM 1540547	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Paguristes tortugae	ULLZ 6800/USNM 1541858	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	KF182732 / KF182676 / KF182534
Paguristes tortugae	ULLZ 11148/USNM 1545610	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Paguristes tortugae	UF 032577	French Antilles: northeastern Caribbean	pending / pending / pending
Paguristes nr. *tortugae*	ULLZ 4782/USNM 1540546	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Paguristes nr. *tortugae*	ULLZ 13665/USNM 1547026	Panama: Bocas del Toro, southwestern Caribbean	pending / pending / pending
Paguristes nr. *tortugae*	UF 015380	USA: Florida, Tampa Bay, northeastern Gulf of Mexico	pending / pending / pending
Paguristes triangulatus	ULLZ 6892/USNM 1541875	Mexico: Yucatan Peninsula: southwestern Gulf of Mexico	pending / pending / pending
Paguristes triangulatus	ULLZ 7719/USNM 1543174	USA: northeastern Gulf of Mexico	pending / pending / pending
Paguristes triangulatus	ULLZ 8250/USNM 1543418	USA: northeastern Gulf of Mexico	pending / pending / pending
Paguristes wassi	ULLZ 7326/USNM 1541761	Mexico: Yucatan Peninsula,: southwestern Gulf of Mexico	pending / pending / pending
Paguristes wassi	ULLZ 9371/USNM 1544277	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	pending / pending / pending
Paguristes wassi	UF 031881	French Antilles: northeastern Caribbean	pending / pending / pending
Paguristes sp.	ULLZ 14919/USNM 1548041	Panama: Perlas Island, northeastern Pacific	pending / pending / pending

Paguristes sp.	ULLZ 15256/USNM 1548292	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Paguristes sp.	ULLZ 15920/USNM 1618807	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1297247	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1297274	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622332	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622333	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622334	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622335	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622336	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622337	Curaçao: southeastern Caribbean	pending / pending / pending
Pseudopaguristes invisisacculus	ULLZ 11115/USNM 1545589	Belize: Twin Cays, northwestern Caribbean	pending / pending / pending
Pseudopaguristes sp.	UF 016878	Australia: Queensland, southwestern Pacific	pending / pending / pending
Epialtidae			
Chorilia longipes	KC3089	Japan: Okinoshima, northwestern Pacific	EU921052 / EU920889 / EU920919
Galatheidae			
Galathea rostrata	ULLZ 7681/USNM 1532702	USA: Florida, northeastern Gulf of Mexico	KF182684 / KF182388 / KF182523
Hippidae			
Emerita talpoida	ULLZ 9434/USNM 1544314	USA: Florida, Fort Pierce, western Atlantic	KF182702 / KF182419 / KF182557
Leucosiidae			
Praebebalia longidactyla	KC3086	unavailable	EU921071 / EU920904 / EU920931
Lithodidae			
Cryptolithodes sp.	ULLZ 11844/USNM 1545963	USA: Alaska, Sitka Sound, northeastern Pacific	KF182669 / KF182402 / KF182574
Lithodes santolla	ULLZ 11875/USNM 1546000	Patagonia	KF182671 / KF182400 / KF182572
Paralomis sp.	KC3506	unavailable	KF182666 / KF182399 / KF182571
Munidae			
Munida iris	ULLZ 8366/USNM 1532757	USA: Florida, southeastern Gulf of Mexico	KF182685 / KF182389 / KF182521
Munida pusilla	ULLZ 8322/USNM 1543605	USA: northwestern Gulf of Mexico	KF182686 / KF182390 / KF182522
Paguridae			
Agaricochirus sp.	USNM 1297342	Curaçao: southeastern Caribbean	MK830040 / MK848215 / MK848231

Catapagurus sp.	USNM 1297635	Curaçao: southeastern Caribbean	pending / pending / pending
Iridopagurus reticulatus	ULLZ 10032/USNM 1544746	Belize: Southwater Cay, northwestern Caribbean	KF182688 / KF182413 / KF182581
Pagurus brevidactylus	ULLZ 7065/USNM 1541856	Yucatan Peninsula: southwestern Gulf of Mexico	KF182679 / KF182407 / KF182563
Pagurus bullisi	ULLZ 11056/USNM 1545566	USA: Louisiana, northwestern Gulf of Mexico	KF182668 / KF182410 / KF182568
Pagurus maclaughlinae	ULLZ 11975/USNM 1546071	USA: Florida, northeastern Gulf of Mexico	KF182680 / KF182408 / KF182566
Pagurus marshi	ULLZ 11110/USNM 1545586	Belize: Twin Cays, northwestern Caribbean	KF182682 / KF182409 / KF182564
Pagurus pollicaris	ULLZ 11954/USNM 1546054	USA: Louisiana, northwestern Gulf of Mexico	KF182737 / KF182403 / JN800550
Pagurus “provenzanoi”	ULLZ 9685/USNM 1544513	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Pagurus “provenzanoi”	ULLZ 9687/USNM 1544515	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Pagurus “provenzanoi”	ULLZ 9690/USNM 1544517	Panama: near Isla Cavada, northeastern Pacific	pending / pending / pending
Pagurus stimpsoni	ULLZ 16546/USNM 1618809	Belize: Twin Cays, northwestern Caribbean	pending / pending / pending
Phimochirus formani	ULLZ 7685/USNM 1543129	USA: Florida, northeastern Gulf of Mexico	MK830050 / - / MK848221
Phimochirus formani	ULLZ 14352/USNM 1547566	USA: Florida, northeastern Gulf of Mexico	MK830053 / MK848204 / MK848222
Phimochirus formani	ULLZ 14572/USNM 1547705	USA: Louisiana, northwestern Gulf of Mexico	MK830048 / MK848205 / MK848223
Phimochirus tunnelli	ULLZ 5789/USNM 1541146	USA: Louisiana, northwestern Gulf of Mexico	MK830051/ MK848206 / MK848224
Phimochirus tunnelli	ULLZ 7825/USNM 1543233	USA: northwestern Gulf of Mexico	MK830052 / MK848208 / MK848225
Phimochirus tunnelli	ULLZ 7973/USNM 1543319	USA: northeastern Gulf of Mexico	KF182678 / KF182415 / KF182578
Phimochirus tunnelli	ULLZ 13837/USNM 1547302	USA: Louisiana, northwestern Gulf of Mexico	- / MK848209/ MK848226
Phimochirus operculatus	ULLZ 9917/USNM 1534602	Belize: Carrie Bow Cay, northwestern Caribbean	MK830046 / MK848212 / MK848229
Phimochirus randalli	ULLZ 7071/USNM 1541890	Yucatan Peninsula: southwestern Gulf of Mexico	KF182676 / KF182417 / KF182576
Phimochirus randalli	ULLZ 7345/USNM 1541699	Yucatan Peninsula: southwestern Gulf of Mexico	KF182677 / KF182418 / KF182577
Phimochirus venustus	ULLZ 9677/USNM 1544505	Panama: near Isla Cavada, northeastern Pacific	MK830045 / MK848214 / MK848230
Protoniopagurus bioperculatus	USNM 1297246	Curaçao: southeastern Caribbean	pending / pending / pending
Pylopagurus macgeorgei	ULLZ 7675/USNM 1543124	USA: northwestern Gulf of Mexico	pending / pending / pending

Tomopagurus merimaculosus	ULLZ 9441/USNM 1544315	Costa Rica: eastern Pacific Ocean	KF182673 / KF182411 / KF182567
Tomopagurus sp.	ULLZ 16203/USNM 1549571	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Xylopagurus cancellarius	ULLZ 9443/USNM 1544319	Costa Rica: northeastern Pacific	KF182683 / KF182406 / KF182584
Xylopagurus cancellarius	ULLZ 9689/USNM 1544522	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Parapaguridae			
Paragiopagurus pilimanus	USNM 1253320	Curaçao: southeastern Caribbean	pending / pending / pending
Sympagurus acinops	ULLZ 11020/USNM 1545560	USA: northwestern Gulf of Mexico	KF182701 / KF182371 / KF182526
Porcellanidae			
Allopetrolisthes spinifrons	ULLZ 5979/USNM 1541241	Chile: Pozo Toyo, southeastern Pacific	KF182714 / KF182398 / KF182550
Pachycheles rugimanus	ULLZ 6903/USNM 1541675	USA: Florida, northeastern Gulf of Mexico	KF182705 / KF182392 / KF182543
Petrolisthes armatus	ULLZ 10098/USNM 1544814	USA: Florida, southeastern Gulf of Mexico	KF182708 / KF182396 / KF182549
Raninidae			
Cosmonotus grayi	KC3092	Japan: Okinoshima, northwestern Pacific	EU921051 / EU920888 / EU920918

Table 1.2. Histone 3 (H3), 12S mtDNA, and 16S mtDNA primers used in this study.

Gene	Primer	Primer Sequence	Annealing Temperatures	Reference
H3 forward	H3af	5' - ATGGCTCTGACCAAGCAGACVGC - 3'		Colgan *et al.* 1998
H3 reverse	H3r	5' - ATATCCTTRGGCATRGTGAC - 3'	50–54°C for 30–60 s	Colgan *et al.* 1998
12S forward	12Sf	5' - GAAACCAGGATTAGATACCC - 3'		Buhay *et al.* 2007
12S reverse	12S1r	5' - AGCGACGGGCGATATGTATAG - 3'	50–54°C for 30–60 s	Buhay *et al.* 2007
16S forward	16S 1472	5' - AGATAGAAACCAACCTGG - 3'		Crandall & Fitzpatrick 1996
16S reverse	16SL2	5' - TGCCTGTTTATCAAAAACAT - 3'		Schubart *et al.* 2002
16S reverse	16Sar	5' - CGCCTGTTTATCAAAAACAT - 3'	50–54°C for 30–60 s	Palumbi *et al.* 1991
16S reverse	16S-CWC-01r	5' - CCGGTTTGAACTCAAATCATGT - 3'		new
16S forward	16S-CWC-01f	5' - TAAAGTCTAGCCTGCCCACT - 3'	52–58°C for 30–60 s	new

Table 1.3. Results of KH, SH and AU testing in IQtree v1.6.3. Trees are ranked by AU p-values. Under the KH, SH and AU metrics, trees with p-values <0.05 can be excluded from the 95% confidence set of tree topologies.

Constraint	−lnL	KH	SH	AU
Unconstrained ML tree	30826.652			
Diogenidae Clade 2 + Diogenidae Clade 3 + Coenobitidae sister to Paguridae + Lithodidae	31034.330	0	$1.8e^{-03}$	$5.60e^{-04}$
Diogenidae Clade 2 + Diogenidae Clade 3 + Coenobitidae sister to Diogenidae Clade 1	31271.991	0	0	$6.96e^{-06}$
Monophyletic Diogenidae	31005.604	0	$1.33e^{-02}$	$2.02e^{-09}$
Monophyletic *Areopaguristes*	31238.640	0	0	$5.12e^{-44}$
Areopaguristes and *Paguristes* as monophyletic sister clades	31666.816	0	0	$2.15e^{-47}$

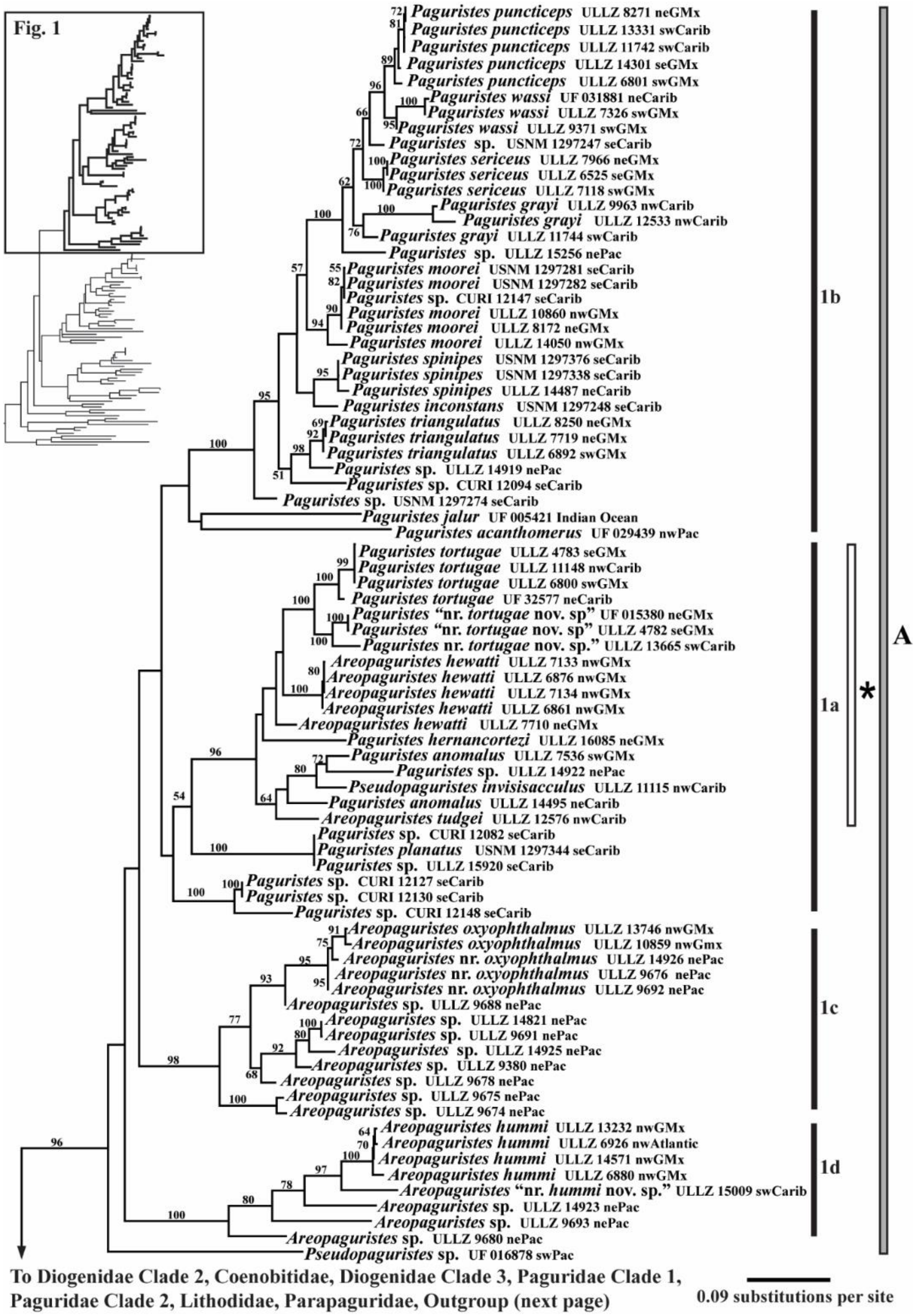

Figure 1.1. Maximum Likelihood phylogeny (−lnL: 26590.631) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions per site. A) denotes Diogenidae Clade 1, with subdivisions 1a, 1b, 1c, and 1d. An asterisk (*) denotes the *Paguristes tortugae* complex. B) denotes Paguridae Clade 1. C) denotes Lithodidae. D) denotes Paguridae Clade 2. E) denotes Diogenidae Clade 2. F) denotes Coenobitidae. G) denotes Diogenidae Clade 3. H) denotes the family Parapaguridae. For branch labels, taxon name is followed by voucher catalog number and abbreviated collection locality (Table 1.1).

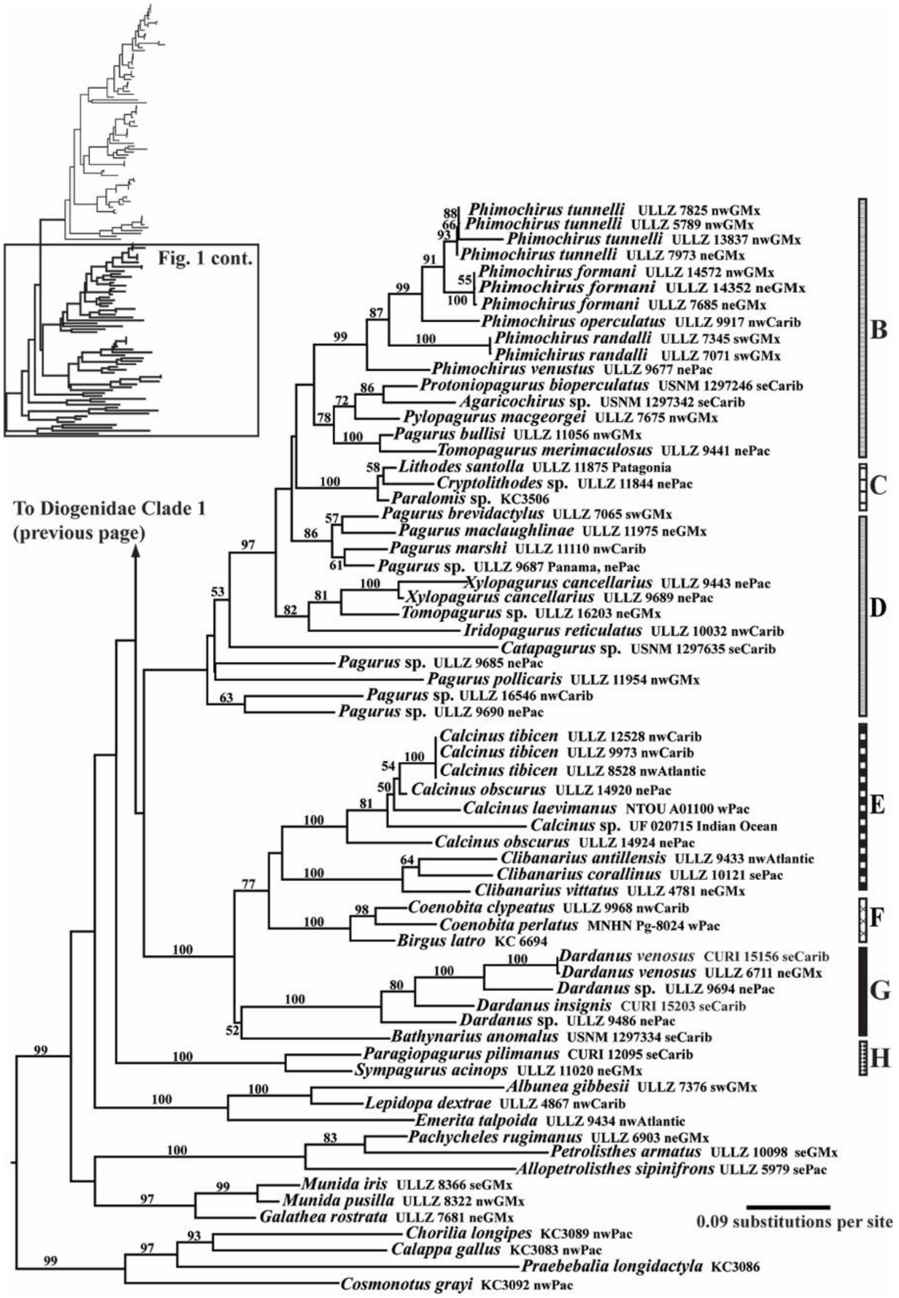

Figure 1.1, continued from previous page. Maximum Likelihood phylogeny (−lnL: 26590.631) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions per site. A) denotes Diogenidae Clade 1, with subdivisions 1a, 1b, 1c, and 1d. An asterisk (*) denotes the *Paguristes tortugae* complex. B) denotes Paguridae Clade 1. C) denotes Lithodidae. D) denotes Paguridae Clade 2. E) denotes Diogenidae Clade 2. F) denotes Coenobitidae. G) denotes Diogenidae Clade 3. H) denotes the family Parapaguridae. For branch labels, taxon name is followed by voucher catalog number and abbreviated collection locality (Table 1.1).

[Prepared as a co-authored manuscript for submission to *Zootaxa*]

Chapter 2: Two new Species of Marine Hermit Crabs Allied with the *Paguristes tortugae* Complex (Crustacea: Decapoda: Anomura) From the Western Atlantic

Abstract

Although a recent molecular phylogenetic analysis focusing on a subset of western Atlantic *Paguristes* Dana, 1851, *Areopaguristes* Rahayu & McLaughlin 2010, and *Pseudopaguristes* McLaughlin, 2002 was somewhat inconclusive with regard to the relationships among those three genera, it revealed formerly undescribed diversity in the form of two new cryptic species genetically related to the *Paguristes tortugae* complex. The ability of our molecular phylogenetic analysis to aid in confirming two new species previously overlooked by systematists underscores the reality that undetected diversity persists within the *P. tortugae* species complex. One of the new species is a sister taxon to *A. hummi* (Wass, 1955) that, despite otherwise high levels of morphological similarity between the two, is readily separated from Wass' taxon by significant differences in coloration. A second new species is a genetic sister taxon to *P. tortugae* Schmitt, 1933, even though it was regarded in earlier literature as no more than an ecomorphic variant expressing protective coloration related to habitat substrate color. Both new species are described based on morphological characters, including coloration, and genetics.

Introduction

Ortmann, 1892 has historically been treated as a monophyletic family by many (MacDonald *et al*. 1957; McLaughlin 1983, 2002; Cunningham *et al*. 1992; McLaughlin & Lemaitre 1997; Forest & McLaughlin 2000; Ahyong & O'Meally 2004; McLaughlin *et al*. 2007, 2010; Ahyong *et al*. 2009; De Grave *et al.* 2009) whereas other studies argued against this hypothesis (Tudge 1995, 1997; Tsang *et al*. 2008, 2011; Bybee *et al*. 2011; Schnabel *et al*. 2011; Bracken-Grissom *et al*. 2013; Gong *et al*. 2018; Landschoff & Gouws 2018; Tan *et al*. 2018; Wolfe *et al*. 2019). The argument against diogenid monophyly was supported, in part, by molecular phylogenetic evidence presented in our previous paper (Craig & Felder, in review), the results of which revealed a polyphyletic Diogenidae composed of three genetic clades. One of these monophyletic subgroups, Diogenidae Clade 1, included all *Paguristes* Dana 1851, *Areopaguristes* Rahayu & McLaughlin, 2010, and *Pseudopaguristes* McLaughlin, 2002 species for which genetic data was analyzed, thus suggesting that Diogenidae Clade 1 represented a multi-generic complex of over 200 species (McLaughlin & Lemaitre 2020; WoRMS 2020). The three constituent genera of Diogenidae Clade 1 were once thought to be readily differentiated from each other by gill-pair number (McLaughlin 2002; Forest *et al*. 2000; Rahayu 2005, McLaughlin & Rahayu 2010), but additional findings of previous molecular phylogenetic analyses indicated that gill-pair number was not evolutionarily conserved within any of the three genera (Bracken-Grissom *et al.* 2013; Craig & Felder, in preparation). Molecular findings have continued to support that the three genera are closely allied, but the evolutionary relationships so far inferred at the generic level have remained poorly defined (Bracken-Grissom *et al*. 2013; Landschoff & Gouws 2018; Craig & Felder, in preparation).

Despite substantial uncertainty surrounding diogenid relationships at the levels of family and genus, some historically recognized species-level morphogroups could be roughly correlated to monophyletic genetic clades within Diogenidae Clade 1 in recent molecular phylogenetic analyses (Bracken-Grissom *et al*. 2013; Craig & Felder, in review). One of these morphogroups has long been recognized as a complex of species known as the

Paguristes tortugae complex, which included many western Atlantic species of *Paguristes*, although several of which have been tranferred to *Areopaguristes* or *Pseudopaguristes*. In past morphological accounts, the composition of the group included seven species, all having a characteristic fringe of setae along the margins of the thoracic appendages (McLaughlin & Provenzano 1974). Included were the namesake of the complex, *Paguristes tortugae* Schmitt, 1933, along with *Areopaguristes hewatti* Wass, 1963, *P. hernancortezi* McLaughlin & Provenzano, 1974, *P. angustithecus* McLaughlin & Provenzano, 1974, *P. perplexus* McLaughlin & Provenzano, 1974, *P. anomalus* Bouvier, 1918, and *Pseudopaguristes invisisacculus* McLaughlin & Provenzano, 1974.

The complex has since been expanded to include several more species from the western Atlantic. Four of these, *Paguristes maclaughlinae* Martinez-Iglesias & Sanchez, 1989, *P. werdingi* Campos & Sanchez, 1995, *P. zebra* Campos & Sanchez, 1995, and *P. scarabinoi* Lima & Santana, 2017, were assigned to the complex at the time of their descriptions, based primarily on the characteristic pattern of setation. Phylogenetic analysis of available genetic data had, in some cases, suggested the inclusion of *Areopaguristes tudgei* Lemaitre & Felder, 2012 (Bracken-Grissom *et al*. 2013; Craig & Felder, in preparation) and *A. hummi* Wass, 1933 (Bracken-Grissom *et al.* 2013), although morphological arguments for these assignments were not conclusive (Lemaitre & Felder 2012). With these additions, the *P. tortugae* complex now spans a broad geographic distribution throughout the western Atlantic (Felder *et al.* 2009; Lemaitre & Tavares 2015), with constituent species found across multiple ecoregions (Spalding *et al.* 2007) from the Carolinean province on the eastern coast of North America, southwards beyond Rio de Janerio, Brazil (Table 2.1).

As indicated by morphology, coloration, and the integration of insights from DNA-based phylogenetic analyses, two previously undescribed western Atlantic species associated with the *Paguristes tortugae* complex are herein formally described in accord with typically applied morphological characters (Forest & McLaughlin 2000). From the Gulf of Mexico, a species sister to *P. tortugae* Schmitt, 1933 is formally described as *P.* "nr. *tortugae* **n. sp.**", as long predicted by morphology and comparative evaluation of color photography (Strasser & Price 1999). A second new species, found along the Caribbean coast of Central America, is the genetic sister taxon to a well-known Gulf of Mexico species, *A. hummi.* Structural morphological characters for distinction of *A. "*nr. *hummi* **n. sp**." remain elusive, but the new species is easily differentiated from *A. hummi* by striking differences in head appendage color as well as distinctive markings of the cheliped merus.

Material and Methods

Specimens examined for this study were accessed from the University of Florida Natural History Museum (UF), Gainesville, Florida, USA, as well as the University of Louisiana at Lafayette Zoological Collection (ULLZ), Lafayette, Louisiana, USA, now housed at the National Museum of Natural History, Smithsonian Institution (USNM), Washington D.C., USA.

Shield lengths (sl) were measured in millimeters (mm) from the tip of the rostrum to the posterior margin of the shield. All measurements were determined +/− 0.1 mm with a calibrated ocular micrometer or digital caliper. Illustrations were made on a Wild M5 or Leica MZ8 dissecting microscope with a camera lucida. The resulting drawings were digitally refined in Adobe Photoshop.

To characterize the color patterns of each genetic subgroup, visual comparisons were made among digital photographs corresponding to genetic voucher specimens from ULLZ.

Color photographs originate from the photographic database assembled by one of us (DLF), and were made on a 35 mm digital Fuji FinePix camera with a 60 mm Nikon macro lens, using either clove-oil narcotized freshly collected animals or defrosted specimens that had been frozen shortly after collection.

Results

Taxonomy

Family Diogenidae Ortmann, 1892

Areopaguristes “nr. *hummi* n. sp.”

(Figs 2.1D, C; 2.2A–G, I; 2.3; 2.4)

Type material. *Panama*. holotype male (ULLZ 15099 / USNM 1548225), sl 2.5 mm, Bocas del Toro, 03 August, 2004, coll. D.L. Felder *et al.*, by SCUBA, depth 3 m. Deposited in ULLZ, University of Louisiana, Lafayette.

Paratypes: *Panama*. 1 male sl 2.5 mm, 1 male sl 2.3 mm (ULLZ 18007), Bocas Del Toro, Almirante pilings, 11 August 2004, by snorkelers. Deposited in ULLZ, University of Louisiana at Lafayette.

Diagnosis. Twelve pairs biserial gills. Antennal flagellum short with dense setae approximately 6–8 articles in length originating on ventral surfaces. Antennular peduncles extending beyond the cornea distal margins by at least 0.5 the length of the ultimate peduncular segment. Ocular acicles subtriangular, flushly abutted along mesial margins with numerous spines along lateral border. Rostrum obsolete. Maxillule proximal and distal endite mesial borders bearing brushes of short, finger-like setae, exopod external lobe with dorsal projection well developed. Second and third pereopod dactyli unarmed. Second pereopod propodi, carpi, and meri dorsal margins each bearing row of acute spines, many with corneous tips. Telson weakly asymmetrical, posterior lobe terminal margins well armed. Male first pleopod inferior lamella distal margin bearing single row of curved spines. In life, eyestalks uniformly golden or straw colored, cheliped merus mesial surface lacking blue markings, with distinct black crescent at distal extremity.

Description. Twelve pairs of biserial gills. Shield (Fig. 2.2B) subtriangular, length slightly exceeding width. Dorsal surface central region convex, bearing widely spaced tufts of setae, most abutting spines or tubercles; lateral surface bearing widely-spaced low tubercles and small spinules; anterior margins between rostrum and lateral projections weakly concave; anterolateral angle obtuse, bearing irregularly spaced spines and spinules. Rostrum obsolete, unarmed, not extending distally beyond lateral projections. Lateral projections each bearing prominent spine and tuft of setae. Branchiostegite lateral surface with granular texture, moderately setose, with dorsal and anterior margins each bearing row of small spines. Posterior carapace poorly calcified, lateral surfaces bearing scattered setae.

Ocular peduncles (Fig. 2.2B) subcylindrical, narrowing slightly at mid-length, diameter at base approximately equal to that at cornea, lacking any banding, spotting, or other patterning, corneas black. Ocular acicles subtriangular; mesial margins unarmed and flushly abutted at the midline; lateral margins somewhat oblique, bearing numerous small spines.

Antennular peduncles (Fig. 2.2B) extending anteriorly beyond cornea distal margin by approximately 0.7 times the length of ultimate segment; ultimate segment dorsal surface with row of minute setae; basal segment lateral surface bearing minute spine, distolateral angle bearing spine; flagellum secondary (ventral) ramus well developed.

Antennal peduncles (Fig. 2.2B) extending anteriorly slightly beyond cornea distal margin. Fifth segment without remarkable characteristics. Fourth segment dorsodistal angle bearing small spine, easily obscured by antennal acicle from dorsal view. Third segment ventromesial distal angle bearing acute spine; ventral margin sparsely setose. Second segment dorsolateral distal angle bearing acute spine; dorsomesial distal angle likewise. First segment unarmed. Antennal acicles extending anteriorly slightly beyond 0.5 distal length of ocular peduncles; lateral margin unarmed and sparsely setose; mesial margin oblique, bearing numerous spines and short setae. Antennal flagellum short, not extending beyond chelae fingertips, densely setose, setae approximately 6–8 articles in length and originating on ventral surface of articles.

Mandible (Fig. 2,2F) with incisor edge calcareous; ultimate segment of palp relatively narrow, length not equal to the combined length of penultimate and basal segments. Maxillule (Fig. 2.2D, E) with proximal and distal endite mesial margins bearing robust, finger-like setae interspersed with fine, hair-like setae; endopod internal lobe distal angle with dorsal projection well developed (Fig. 2.2D), external lobe sharply recurved, length approximately 0.7 times that of internal lobe, margins of both lobes bearing scattered setae. Maxilla (Fig. 2.2I) proximal and distal endite mesial margins densely setose; endopod tapered distally, not overeaching distal apex of scaphognathite; scaphognathite recurved, margins densely setose. First maxilliped (Fig. 2.2A) endopod length approximately 0.7 times that of exopod; exopod tapering distally; epipod well developed. Second maxilliped (Fig. 2.2G) endopod basis bearing sparse small spinules. Third maxilliped (Fig. 2.2C) endopod merus internal surface with distomesial angle bearing acute spine, external surface bearing small spine at midline; ischium with crista dentata well developed, lacking accessory tooth.

Chelipeds (Fig. 2.3A–D) subequal in size, similarly armed, fingers opening transversely, tips slightly crossed; dorsal surfaces of chelae and carpi densely covered with tufts of plumose setae partially obscuring armature beneath, longer setae forming dense fringe along dorsolateral and dorsomesial margins of chelae, and carpus; fixed and moveable finger each terminating in tapered corneous tip. Dactyl length approximately 3 times maximum height; cutting edge bearing calcareous teeth and widely spaced tufts of stiff bristles; dorsal surface bearing irregularly spaced spines, most abutting tuft of setae; dorsomesial margin bearing irregular row of corneous-tipped spines decreasing in size distally, most abutting tuft of setae; mesial surface bearing irregular row of conical spines continuing distally as unevenly spaced small tubercles, most abutting tufts of setae. Fixed finger not extending beyond cheliped dactyl; cutting edge bearing calcareous teeth bordered with row of stiff bristles ventrally. Palm dorsal surface somewhat convex; dorsolateral surface bearing 2 irregular longitudinal rows of strong spines, each spine abutting tuft of setae; dorsolateral margin bearing longitudinal row of spines continuing onto fixed finger lateral margin; ventral surface bearing widely spaced tubercles, spines, and tufts of setae; lateral surface bearing irregular, longitudinal row of spines interspersed with tufts of short setae; mesial surface slightly convex, bearing shallow rugae and small tubercles. Carpus length approximately 0.3 times that of chela; dorsal surface bearing scattered conical spines and spinules interspersed with setae; dorsolateral and dorsomesial margins well defined and slightly elevated, each bearing row of corneous-tipped spines; dorsolateral surface bearing evenly spaced spines; mesial surface bearing scattered small tubercles and spines. Merus length approximately 2.5 times that of carpus, subtriangular in cross section; dorsal margin bearing small tubercles proximally, as well as dense cluster of conical spines and spinules distally, some with corneous tips, ultimate distal margin bearing widely spaced spines;

ventromesial margin bearing unevenly spaced, irregular spines; lateral surface bearing irregularly spaced spines ventrally; ventrolateral margin with row of conical spines increasing in size distally. Ischium ventromesial margin bearing row of blunt spinules and scattered setae. Coxa ventrodistal angle with dense tuft of setae visible in mesial view.

Second pereopod (Fig. 2.3E, F) slender, extending beyond cheliped by approximately 0.5 the length of the second pereopod dactyl; dorsal and ventral margins of dactyl, propodus, carpus and merus bearing dense fringe of setae. Dactyl subcylindrical, length as much as 10 times maximum height, curved ventrally from lateral view and terminating in curved corneous claw; dorsal and ventral margins unarmed, bearing widely spaced tufts of setae; mesial and lateral surfaces likewise. Propodus length approximately 0.7 times that of dactyl; dorsal margin armed with slender spines decreasing in size distally (in mesial view); ventral margin unarmed; dorsolateral surface bearing widely spaced low tubercles, some abutting tufts of setae; mesial surface bearing scattered small tubercles and widely spaced tufts of setae. Carpus length approximately 0.5 times that of propodus; dorsal margin bearing row of irregularly spaced spines (in mesial view); ventral margin unarmed; lateral surface (Fig. 2.3E) moderately convex, dorsolateral surface with slight longitudinal ridge bearing low tubercles abutting tufts of setae; dorsomesial surface bearing sparse small tubercles and tufts of setae. Merus length approximately 2 times that of carpus, somewhat laterally compressed; dorsal margin bearing irregular tubercles and spines abutting tufts of setae; lateral surface bearing prominent tubercle abutting dense tuft of setae distally; dorsolateral surface bearing irregularly spaced, small tubercles and scattered tufts of setae. Ischium laterally compressed, mesial and lateral surfaces subtriangular, dorsodistal angle bearing prominent spines. Coxa without distinguishing characters.

Third pereopod (Fig. 2.4A, B) similar in proportions and armature to second pereopod except as noted. Propodus length approximately 8 times that of dactyl; dorsal margins lacking distinct spines or spinules. Carpus dorsal margin unarmed except for small spine at dorsodistal angle; lateral surface longitudinal ridge less prominent than that of second pereopod. Merus length approximately 1.5 that of carpus; dorsal margin lacking distinct spines or spinules. Ischium length approximately 0.5 times that of merus; mesial and lateral surfaces subrectangular; dorsolateral surface bearing irregularly spaced minute tubercles. Sternite of third pereopod with anterior lobe subrectangular, bearing rounded tubercles with dense tufts of setae.

Fourth pereopod (Fig. 2.4D) not extending beyond distal margin of third pereopod merus, segments somewhat laterally compressed; propodus, carpus, and merus dorsal margins bearing dense fringe of long setae. Dactyl (Fig. 2.4E) terminating in elongate corneous claw abutting dense tuft of bristles dorsally; distoventral margin bearing 2 (in holotype) acute spines abutting preungual process. Preungual process well-developed, slender, length slightly less than that of corneous claw. Propodus length approximately 2 times that of dactyl; ventrolateral surface bearing narrow propodal rasp extending approximately 0.3 the length of the segment. Carpus, merus, and ischium/basis similar in length, dorsal and ventral margins of each bearing dense fringe of setae. Coxa distal margin with fringe of stiff setae; ventromesial surface with row of minute spines interspersed with setae.

Fifth pereopod (Fig. 2.4C) chelate; fixed finger subequal in length to dactyl; appendage segments generally subcylindrical. Propodus elongate, length approximately 3 times maximum height; lateral surface bearing rasp continuous across dactyl, fixed finger and approximately 0.3 the distal length of the segment; ventromesial surface concave, bearing dense patch of setae distally.

Abdomen curled, poorly sclerotized. Male first (Fig. 2.4F, G) and second (Fig. 2.4H) pleopods each paired and modified as gonopods; pleopods 3–5 unpaired, uniramous. Male first pleopod inferior lamella lateral margin fringed with setae, distal margin with single row of curved spines; internal lamella narrow and somewhat reduced, distal margin bearing tuft of long setae; external lamella extending slightly beyond the inferior lamella distal margins; second pleopod (Fig. 2.4H) ultimate segment terminal lobe somewhat deflected laterally and densely setose.

Uropods (Fig. 2.4I) strongly asymmetrical, left robust and elongate. Telson (Fig. 2.4I) weakly asymmetrical (in holotype); left lobe somewhat longer than right, deep lateral incisions dividing anterior and posterior portions; anterior lobes subovate; posterior lobes subtriangular to subquadrate, left and right separated by well-defined cleft, left lobe terminal margin bearing prominent conical spines with corneous tips, curving outward somewhat, right lobe bearing smaller, irregular spines, some with corneous tips.

Size. Largest male examined, sl 2.5 mm

Color. (Fig. 2.1C, D). Pale buff or peach background color marked with irregular orange to rust patches over cheliped and carapace shield. Walking legs bearing irregular orange to rust banding on propodus, carpus, and merus. Second and third pereopod dactyls each bearing two distinct orange to rust bands alternating with white. Cheliped merus mesial surface bearing black, crescent shaped marking at distal extremity and lacking any blue markings. Eyestalks solid golden yellow, lacking any bands, stripes, or spotting.

Distribution and habitat. So far known only by the type serries, *A*. “nr. *hummi* **n.**

sp.” is found near Bocas del Toro, Panama, in the southwestern Caribbean and has been collected in shallow water approximately 3 m deep.

Morphological variations. In general, smaller paratypes show reductions in the number and prominence of spines on the thoracic appendages and telson terminal margins. This is especially evident on the dorsal surfaces of the chelae and carpus. Accompanying this variation, the number of spines abutting the preungular process of the fourth pereopod is reduced from 2 to 1 when our smallest male (sl 2.1 mm) is compared to our largest, the holotype male (sl 2.5 mm). For the ocular acicles, the mesial margins are always unarmed and flushly abutted at the midline, although the lateral margin shape can range from straight and oblique as in the holotype male (Fig. 2.2B), to fan-shaped in the smaller paratypes, resembling more closely *Paguristes weddellii* (Fig. 2.2H) or *Areopaguristes lemaitrei* (Fig. 2.2J). However, the most notable variation among paratypes is in the shape of the telson, which shows higher degrees of asymmetry in the smaller individuals.

Remarks. Evidence for separation of *Areopaguristes* “nr. *hummi* **n. sp.**” from its sister species, *A. hummi*, is derived from multiple sources. So far, the known occurrence of our new species along the Caribbean coast does not overlap with that of *A. hummi*, a species that has been recorded from many localities spread across the Gulf of Mexico (Table 2.1). Further differences between this new species and *A. hummi* are present in markings and in-life coloration of the cheliped merus and head appendages. The latter species (Fig. 2.1A, B) is readily recognized by the prominent blue spot upon the cheliped merus mesial surface that is bordered along the distal edge by a black semicircular band (Fig. 1A), whereas this new species (Fig. 2.1C, D) lacks the blue meral spot, and the semicircular black band at the distal margin of the merus mesial surface is reduced to a black crescent-shaped marking (Fig.

2.1C). As confirmed via photographic records, the eyestalks, antennular peduncles, and antennal flagella of *A. hummi* are predominantly solid blue in hue (Fig. 1B). This coloration of the head appendages definitively sets *A. hummi* apart from *A.* “nr. *hummi* **n. sp.**”, with light orange to straw-colored eyestalks likewise confirmed through photographic documentation of in-life color (Fig. 2.1D).

In addition to its striking morphological similarity to *Areopaguristes hummi*, our new species shares several general characteristics with species of *Areopaguristes* and the *P.tortugae* complex (Table 2.2). However, as suggested by genetic evidence (Craig & Felder, in review), the treatment of *A. hummi* and its closest genetic allies as closely related to the *P. tortugae* complex may not be warranted, and morphological characters offer conflicting support. Favoring their inclusion in the *P. tortugae* complex, *A. hummi*, *A.* “nr. *hummi* **n. sp.**”, and their nearest genetic associates exhibit the characteristic fringe of setae on the thoracic appendages, an armed telson, and spines upon the male gonopod external lobe inferior lamella. As with all other complex constituents, both *A. hummi* and *A.* “nr. *hummi* **n. sp.**” bear an epipod on the first maxilliped. This epipod is likewise present in the generic type species *A. setosus* (Rahayu 2005) but recent emendments to the generic diagnosis based on evaluations of *A. oxyophthalmus* and *A. preadator* assert that the presence of the first maxilliped epipod is not required for assignment to the genus (Ayon-Parente *et al*. 2015). The full significance of variability in this character across *Areopaguristes* remains unexplored, but the presence or absence of the first maxilliped epipod is so far diagnostic at the species level and shows potential utility in the designation of *Areopaguristes* subgroups, or perhaps even future generic diagnoses.

Casting doubt on the affinity of *Areopaguristes hummi* and *A.* “nr. *hummi* **n. sp.**”

with other *P*. *tortugae* complex constituents, the pereopods of *A*. *hummi* and its genetic allies are slender and generally subcylindrical with the proportions of the pereopod segments, especially the elongate nature of the dactyl, drastically different from those of *P*. *tortugae* and its genetic allies such as *A*. *hewatti*. Additionally, the ocular acicles of *A*. *hummi* and *A*. "nr. *hummi* **n. sp.**" are greatly dissimilar in shape and orientation from those of other species currently considered members of the *P. tortugae* complex. Being flushly abutted at the midline and accompanied by a greatly reduced rostrum, the configuration most closely resembles that of a handful of eastern Pacific species including *A*. *lemaitrei* Ayon-Parente & Hendrickx, 2012 (Fig. 2.2J), *A*. *waldoschmitti* Ayon-Parente & Hendrickx, 2012, and the generic type of *Paguristes, P*. *weddellii* H. Milne Edwards, 1848 (Fig. 2.2H). Further, for *A*. *hummi* and *A*. "nr. *hummi* **n. sp.**", the gonopod (Fig. 2.4G, H) in males is shorter and stouter than that of most other species of *Paguristes* and *Areopaguristes* from the western Atlantic, aside from *A*. *tudgei*.

Paguristes **"nr. *tortugae* n. sp."**

(Figs 2.5B; 2.6–2.8)

Type material. *Florida*. Holotype male, sl 5.6mm (ULLZ 4782 / USNM 1540546, DNA voucher, photo voucher), Florida Keys, Pigeon Key, 09 June 2001.

Paratypes: *Belize*. 2 males sl 6.1 mm (photo voucher), 3.4 mm (ULLZ 12171 / USNM 1546239), Big Pine Key, Boogie Canal, scallop dredge, 2–3 m, 07 July, 1979; 1 female sl 2.0 mm, 1 female sl 3.0 mm (DNA voucher, photo voucher), (ULLZ 11116 / USNM 1545590), Twin Cays, rubble, 20 Feb 2009; 1 male sl 4.2 mm (ULLZ 3563 / USNM 1540063, photo voucher), Carrie Bow Cay, 1 m, 20 Apr 1983; *Florida.* 1 male sl 6.3 mm (ULLZ 15244 / USNM 1548287, photo voucher) Content Keys, dredge, 2–4 m 27 Jun 1984; 1 male sl 5.6

mm (photo voucher), 1 male sl 4.3 mm (ULLZ 15245 / USNM 1548289), Big Pine Key, Newfoundland Harbor, dredge, 2–4 m; 1 female sl 3.2mm (ULLZ 5647 / USNM 1542520, photo voucher), Florida, 09 Sep 2003; 1 male sl 6.9 mm (UF 015380, DNA voucher), Tampa Bay, 4 km West of Sunshine Skyway, spoil heap with sponges, 6–7 m, 07 Feb 2009; *Gulf of Mexico*: 1 male, sl 3.9 mm and 1 male, sl 4.9 mm (ULLZ 8578 / USNM 1543769, DNA voucher, photo voucher, illustrated), NSF-III-055, 04 Jul 2006, D.L. Felder et al.; *Panama*: 1 female ovig. Sl 3.4 mm (ULLZ 13664 / USNM 1547025, DNA voucher), Bocas del Toro, 09°21.060' N; 82°15.540' W, grass beds and *Porites*, 2m, 08 Aug 2011; 1 male sl 4.7 mm (ULLZ 13663 / USNM 1547024, DNA voucher), Bocas del Toro, 09°21.060' N; 82°15.540' W, grass beds and *Porites*, 2m, 08 Aug 2011; 1 male sl 4.2 mm (ULLZ 13665 / USNM 1547026, DNA voucher), Bocas del Toro, 09°21.060' N; 82°15.540' W, grass beds and *Porites*, 2m, 08 Aug 2011; 1 male sl 3.60 mm, (ULLZ 16969, DNA voucher, photo voucher), Bocas del Toro, 03 Aug 2004; 1 male sl 3.80 mm, (ULLZ 16975, DNA voucher, photo voucher), Bocas del Toro, 05 Aug 2004; 1 male sl 2.60 mm (ULLZ 13330 / USNM 1546874, DNA voucher, photo voucher), Bocas del Toro, 07 Aug 2011; 1 male sl 3.6 mm (ULLZ 11743 / USNM 1545935, DNA voucher, photo voucher), Cayo Adriana, 09 Aug 2004; 1 male sl 3.75 mm, (ULLZ 16976, photo voucher), Bocas del Toro, Bastimentos, 06 Aug 2004.

Non-paratype material: *Panama*. 1 male sl 4.0 mm (ULLZ 13707 / USNM 1547066), Bocas del Toro, grass beds and *Porites*, 2 m, 08 Aug 2011; 1 male sl 3.7 mm (ULLZ 13708 / USNM 1547067), Bocas del Toro, 08 Aug 2011, grass beds and *Porites*, 2 m; *Mexico*. 1 juvenile sl 1.5 mm, 3 female ovig. Sl 4.1 mm, 3.6 mm, 5.1 mm, 1 female sl 3.4, 4 males sl 2.7 mm, 2.6 mm, 4.3 mm, 5.4 mm, (ULLZ 239 / USNM 1538562), Campeche, Isla Aguada, Laguna de Terminos, TFE I-B *Thalassia* beds, dip net, 05 Jan 1978; 1 male sl 11.5 mm

(ULLZ 88 / USNM 1542715), Campeche, northeast of Champoton, TFE II-B, grass beds, 07 Jan 1978; 1 male sl 3.68 mm, 1male sl 4.55 mm, 1 male sl 4.00 mm, 1 male sl 3.25 mm, 1 female, sl 4.05 mm (ULLZ 11745/ USNM 1545937), Barra del Tordo, 19 Aug 1979; 1 female sl 4.4 mm, 1 male sl 4.1 mm (ULLZ 230 / USNM 1542740), Yucatan, 5 miles North of Sabaplaya, USL TFE-I, 06 January, 1977; 1 female ovig. Sl 3.9 mm, 1 male sl 5.6 mm (ULLZ 93 / USNM 1542718), Campeche 5 miles N of Sabaplaya, intertidal rocks, corals, and sponges, TFE I-B, 06 Jan 1977; *Florida*. 1 female sl 3.0 mm (ULLZ 469 / USNM 1542655, photo voucher), 2 km south of Saint Lucie Inlet, 0.7–10 m, 26 June, 1979; 1 female ovig. Sl 4.0 mm (UF 031583) Big Bend area, northwest of Saint Petersberg, hard bottom, sponge reef, 29–30 m, 23 May 2012; 1 male, sl 3.3 mm (ULLZ 17737), Rabbit Key, 09 Dec 1998; 1 female ovig. Sl 3.8 mm, 1 female ovig. Sl 3.9 mm, 1 male sl 4.5 mm, 1 male sl 3.5 mm (ULLZ 11544 / USNM 1545758), Rabbit Key, *Thalassia* beds, 1.5 m, 22 Jul 1999; 1 male sl 4.1 mm (ULLZ 14019 / USNM 1547351), Big Pine Key, coral heads, 0.6–6 m, 03 Jul 1979; *Caribbean*. 1 male sl 2.5 mm (UF 032561), French Antilles, Saint Martin, Caye Verte, reef with sand and seagrass, 1–3 m, 25 Apr 2012; *Belize*: 1 female ovig. Sl 5.2 mm (ULLZ 9859 / USNM 1544679), Looe Key area XI, 24°32.910’ N; 81°24.355’ W; gorgonian reef, rubble and sponges, SCUBA, 6–7 m, 22 Jun 1984.

Diagnosis. Antennal flagellum slender with sparse setae 1–3 articles in length near joints of articles. Antennular peduncles not exceeding corneas, or exceeding corneas by less than 0.5 distal length of ultimate segment. Ocular peduncles subcylindrical, slightly narrower near midlength, always marked with distinct dark bands near midlength bordered by white distally and proximally, (often persisting in ethanol preserved specimens). Ocular acicles well separated by rostrum, with narrow anterior projection bifid or multifid, bearing a variable number of accessory spines laterally. Rostrum tapering evenly to an acute point. Cheliped manus dorsomesial margin bearing 3 strong, corneous-tipped spines. Cheliped carpus dorsomesial margins with 4 or 5 strong, corneous tipped, conical spines, color bright carmine red in life. Second pereopod carpus dorsal margin with row of acute spines and third pereopod carpus dorsal margin with 1 or more acute spines distally, bright carmine red in life. First maxilliped with epipod well developed. In life, carapace shield with patches of olive green to light brown, pereopods two and three with light brown to olive green background color, branchiostegites laterally translucent purple with some white spotting.

Description. Thirteen pairs of biserial gills. Shield (Fig. 2.6A) sub-triangular, length approximately 1.4 times width. Dorsal surface central region convex; lateral surfaces bearing irregularly spaced small tubercles, spinules, and spines interspersed with sparse setae; anterior margins between rostrum and lateral projections distinctly concave, paralleled by well-defined marginal ridge; anterolateral angle obtuse and rounded bearing numerous irregularly spaced spines and spinules. Rostrum triangular, extending anteriorly beyond lateral projections, lateral margins sloping evenly to an acute point and bearing fringe of setae. Lateral projections acute. Branchiostegite lateral surface with granular texture nearly obscured by tufts of long setae. Posterior carapace poorly calcified, lateral surfaces bearing scattered setae.

Ocular peduncles (Fig. 2.6A) subcylindrical, slightly narrower at midlength, diameter at base approximately equal to that of cornea, left longer than right; dorsomesial surface bearing tufts of long setae proximally.Ocular acicles (Fig. 2.6A) subtriangular, mesial borders unarmed and separated by rostrum; anterior projection bifid or multifid, lateral margin bearing 1 or more acute spines.

Antennular peduncles (Fig. 2.6A) not extending anteriorly beyond cornea distal margin in holotype (exceeding cornea distal margin by approximately 0.5 the length of the ultimate segment in some paratypes); basal segment lateral surface bearing small spine.

Antennal peduncles (Fig.2.6A) not extending anteriorly beyond cornea distal margin. Fifth segment without remarkable characteristics. Fourth segment dorsodistal angle bearing anteriorly angled spine. Third segment ventromesial distal angle bearing strong spine, somewhat obscured from dorsal view by dense fringe of setae. Second segment dorsolateral distal angle forming anterior projection terminating in single spine, lateral margin somewhat oblique, bearing 3 spines, dorsomesial distal angle bearing single spine. First segment dorsolateral distal angle bearing minute spine. Antennal acicles extending slightly beyond 0.5 mid-length of ocular peduncle, terminating in single spine; lateral margin bearing 2 or more spines (number variable among paratypes) interspersed with tufts of long setae; mesial border with 1 or more (number variable among paratypes) widely spaced spines partially obscured by dense fringe of setae. Antennal flagellum not extending beyond fingertips, sparse setae approximately 1–3 articles in length at joints of flagellar articles.

Mandible (Fig. 2.6F) with incisor edge calcareous; ultimate segment of palp broad, setose, length equal to the combined length of penultimate and basal segments. Maxillule (Fig. 2.6E) proximal and distal endite mesial margins densely setose; endopod internal lobe distal angle bearing sparse tuft of bristles, external lobe recurved, length approximately 0.7 times that of internal lobe, terminal angle bearing sparse setae. Maxilla (Fig. 2.6C) proximal and distal endite mesial margins densely setose; endopod tapered distally, not overreaching distal apex of scaphognathite; scaphognathite recurved, margins densely setose. First maxilliped (Fig. 2.6D) proximal and distal endite mesial margins densely setose; endopod length approximately 0.7 times that of exopod; exopod tapering distally, lateral margin densely setose, flagellum elongate and densely setose; epipod well developed, margins densely setose. Second maxilliped (Fig. 2.6H) basis mesial margin bearing small blunt spine. Third maxilliped (Fig. 2.6G, I) endopod merus external surface bearing 2 or more strong, curved spines on mesial margin; ischium external surface distomesial angle bearing 1 spine; crista dentata well developed, lacking accessory tooth.

Chelipeds (Figs 2.7A–D) subequal in size, similarly armed, opening transversely; dorsal surfaces of chelae and carpi densely covered with tufts of plumose setae partially obscuring armature beneath, longer setae forming dense fringe along dorsolateral and dorsomesial margins of chelae and carpus; both fixed and moveable finger with distal extremity terminating in hoof-like corneous claw. Dactyl length approximately 2.5 times maximum height; cutting edge bearing calcareous teeth decreasing in size distally and widely spaced tufts of stiff bristles; dorsal surface bearing irregularly spaced low tubercles and conical spines, many abutting tufts of setae or stiff bristles; dorsomesial surface bearing scattered low tubercles, each abutting tuft of setae; ventral surface cutting edge paralleled by longitudinal groove bearing widely spaced tufts of stiff bristles. Fixed finger not extending beyond moveable finger; cutting edge bearing numerous blunt calcareous teeth and scattered tufts of setae. Palm dorsal surface somewhat convex, bearing densely distributed conical tubercles and spines, some with corneous tips, most abutting tuft of setae (setae largely obscuring armature for most paratypes); dorsomesial margin well defined, bearing 3 conical spines with corneous tips; dorsolateral margin bearing row of numerous irregularly spaced conical spines, some with corneous tips; ventral and lateral surfaces bearing scattered low tubercles (blunt spines or conical tubercles in some larger paratypes) many abutting tufts of short setae. Carpus length approximately 0.5 times that of chela; dorsal surface midline bearing irregularly distributed conical spines interspersed tufts of setae; dorsomesial border well defined, armed with 4 (5 in some paratypes) conical spines with corneous tips, bright carmine red color in life; dorsolateral margin bearing continuous row of conical spines, some with corneous tips; dorsodistal margin with slight anterior projection near midline bearing small conical spines (number variable among paratypes) somewhat obscured by dense setae; lateral and mesial surfaces relatively smooth, setation sparse; ventrodistal angle forming hook-like projection bearing 1 or more small spines at distomesial extremity. Merus length approximately 2 times that of carpus, subtriangular in cross section; dorsal margin bearing irregularly spaced small spines proximally, transected subdistally by low ridge bearing conical spines, some with corneous tips; dorsodistal margin bearing conical spines near midline, some with corneous tips; mesial surface relatively smooth; ventromesial margin bearing row of conical spines distally; ventrolateral margin surface bearing row of irregularly spaced spines interspersed with long setae. Ischium mesial surface subtriangular; ventromesial margin bearing minute spines or spinules; ventrodistal margin bearing sparse tufts of setae. Coxa distal margin bearing dense fringe of setae; ventral surface densely setose.

Second pereopod (Figs 2.7E, F) extending beyond cheliped by approximate length of second pereopod dactyl when both fully extended, terminating in single corneous claw, segments somewhat laterally compressed; dorsal margins of dactyl, propodus, carpus, and merus bearing dense fringes of setae obscuring underlying armature for many paratypes; ventral margins likewise. Dactyl length approximately 5.5 times maximum height, curved ventrally from lateral view, terminating in curved corneous claw with enlarged spine and tuft of stiff bristles proximally; dorsal and ventral margins each bearing row of corneous-tipped spines (minute in smaller paratypes), increasing somewhat in size distally, observable at high magnification from mesial view; mesial surface bearing scattered small corneous spines (more prominent and often broadly distributed in larger paratypes). Propodus length approximately 0.7–1.0 times that of dactyl (ratio slightly variable in paratypes); dorsal margin bearing row of spines somewhat obscured by dense fringe of setae (in mesial view); mesial and lateral surfaces armed with series of low transverse ridges each bearing small spinules (visible in holotype and larger paratypes); and abutting row of setae. Carpus length approximately 0.7 times that of propodus; dorsal margin armed with numerous (number varies among paratypes) conical spines with corneous tips, color deep carmine red in life; dorsolateral surface with pronounced longitudinal ridge bearing dense tufts of long setae; dorsomesial surface bearing tufts of setae arranged in transverse rows. Merus length approximately 2 times that of carpus; dorsal margin bearing dense fringe of setae arranged in a series of transverse rows; ventral margin bearing row of widely spaced conical spines (in mesial view); ventrolateral surface bearing scattered tufts of short setae; distolateral margin bearing conical spines distally (number and prominence varies among paratypes). Ischium mesial and lateral surfaces subtriangular. Coxa without distinguishing characters.

Third pereopod (Figs 2.8A, B) not extending beyond claw of second pereopod, similar in proportion and armature to second pereopod except as noted here. Dactyl mesial surface bearing numerous corneous spines, more prominent and broadly distributed than those of second pereopod. Propodus mesial surface more tubercular and setose than that of second pereopod for most paratypes. Carpus dorsal margin with conical, corneous tipped spines restricted to distal 0.5; dorsodistal angle bearing somewhat enlarged conical spine.

Merus lateral surface slightly convex; dorsolateral surface bearing series of transverse rugae; mesial surface bearing elongate oblique rugae. Ischium length approximately 0.5 times that of merus; mesial and lateral surfaces subrectangular. Sternite of third pereopod subrectangular, left and right each bearing rounded tubercle with dense tuft of setae.

Fourth pereopod (Fig. 2.8D) laterally compressed, not extending beyond distal margin of third pereopod merus. Dactyl (Fig. 2.8E) robust, terminating in curved corneous claw dense tuft of setae dorsally; dorsal margin bearing tufts of stiff bristles; ventrolateral surface bearing 1–3 stout teeth interspersed with bristles, most distal tooth somewhat enlarged and abutting base of preungal process. Preungal process well-developed, length slightly less than that of corneous claw. Propodus length approximately 2 times that of dactyl; dorsal margin bearing long setae distally; ventrolateral surface bearing oblong rasp extending approximately 0.7 the distal length of segment. Carpus, merus, and ischium similar in length, dorsal and ventral margins of each bearing dense fringe of setae.

Fifth pereopod (Fig.2.8F) chelate, with length of fixed finger subequal to that of dactyl; segments generally subcylindrical. Propodal rasp continuous across dactyl, fixed finger, and approximately 0.3 distal length segment; ventromesial surface bearing dense patch of setae. Carpus somewhat recurved; dorsal margin bearing sparse setae. Merus lateral surface bearing irregular longitudinal row of setae near midline. Coxa lateral surface bearing dense tuft of setae and male sexual pore proximally.

Abdomen curled, poorly sclerotized. Male first (Figs 2.8G, H) and second pleopods paired and modified as gonopods, pleopods 3–5 unpaired; first pleopod inferior lamella (Fig. 2.8G) lateral margin bearing fringe of setae, distal margin with numerous irregular rows of curved teeth extending onto external surface, internal lamella distal margin bearing fringe of long setae, external lamella extending slightly beyond inferior lamella of distal margin; basal segment of second pleopod bearing sparse tuft of long setae at superior mesial angle. Female first pleopods paired, pleopods 2–5 unpaired, pleopod 5 uniramous; paired gonopores on coxa of third pereopod; brood pouch large, subovate to subquadrate; eggs approximately 0.5–0.7 mm in diameter.

Uropods (Fig. 2.8I) strongly asymmetrical, left robust and elongate. Telson (Fig. 2.8I) weakly asymmetrical, left lobe somewhat larger than right, deep lateral incisions dividing anterior and posterior portions; anterior lobes subovate to subtriangular, distolateral angles each bearing 1 or more (number variable in paratypes) conical spines; posterior lobes subtriangular, left and right separated by well defined cleft, terminal margins each bearing scattered bristles and numerous conical spines, some with corneous tips (number, prominence, and precise orientation of spines variable in paratypes).

Color. Carapace shield with patches of olive green to light brown, pereopods two and three with light brown to olive green background color, branchiostegites laterally translucent purple with some white spotting, ocular peduncles with distinct dark brown to almost black bands near midlength (bands often persisting in preservation as dark pink to orange) bordered with white both proximally and distally (Fig. 2.5B). Spines on cheliped carpus dorsomesial margins bright carmine red with corneous tips. Spines on third pereopod carpus dorsal margin bright carmine red.

Size. Largest examined: male, sl 11.5 mm.

Distribution and habitat. Broadly distributed across the Gulf of Mexico, eastern coast of South America, southeastern and southwestern Caribbean, and along the eastern coast of Florida; bathymetric distribution ranging between the intertidal zone and approximately 30 m in depth. Collected in arange of habitats including hard-bottom substrates, rubble, sandy bottoms with seagrass (*Thalassia*), reef communities, sponges, and coral (*Porites*).

Morphological variations. *Paguristes* “nr. *tortugae* **n. sp.**” shows a moderate range of intraspecific variation related to specimen size. Zones of spination are characteristic of the species, but within those zones, larger specimens exhibit fewer, more robust spines, especially on the ambulatory appendages. There are exceptions however, as in the case of the third pereopod dactyl mesial surface, where larger individuals show a broad distribution of corneous spines with moderate prominence, compared to the scattering of minute spines seen in most smaller individuals. In addition to variability of spination related to size, eyestalk shape shows some variance, with the eyestalks of smaller specimens tending to have a broader proximal base relative to the cornea, accompanied by a greater taper at mid-length when compared to the eyestalks of larger individuals.

Two notable morphological variations seemingly unrelated to size can be found among paratypes. In both large and small individuals, the cheliped carpus dorsomesial margin is typically armed with 4 prominent red spines, but for some paratypes there is a moderately sized fifth accessory spine at the base of the fourth most distal spine. In addition, antennular peduncle length relative to that of the eyestalk varies, with the antennular peduncle exceeding the cornea distal margin for some paratypes.

Remarks. Although the occurrence of *P. tortugae* in the northern Gulf of Mexico was once considered tentative (McLaughlin & Provenzano 1974), numerous records with ULLZ collection data confirm its occurrence throughout the Gulf of Mexico and Caribbean over a range of depths (Table 2.1). Collection data for *P*. “nr. *tortugae* **n. sp.**” specimens considered herein indicate that the geographic and bathymetric distributions of *P*. “nr. *tortugae* **n. sp.**” is approximately congruent with that of its parent species, *P. tortugae*. This is evident even at a very local scales, with examples of *P. tortugae* and *P.* “nr. *tortugae* **n. sp.**” specimens housed at USNM (formerly ULLZ) collected from overlapping localities and similar habitats. Despite this sympatry, the consistent disparity of color form between the two species, along with corresponding morphological characters, provides support for their separation with molecular phylogenetic analysis confirming the two as distinct sister lineages (Craig & Felder, in review).

McLaughlin & Provenzano (1974) cited color and pattern as diagnostic of at least five of the original constituent species of the *P*. *tortugae* complex. Historically, accounts detailing the color of *P*. *tortugae* itself established two color forms, both of which possess eyestalks bearing dark bands bordered by white near midlength (Wass 1955; Holthuis 1959; Provenzano 1959, 1965; Williams 1965; McLaughlin & Provenzano 1974; Strasser & Price 1999). Photographic evidence compiled by one of us in the course of long-term decapod biodiversity surveys in the western Atlantic corroborates literary accounts of these two sympatric color forms, both of which are morphologically consistent with existing diagnosis of *P*. *tortugae sensu* McLaughlin & Provenzano (1974). In our photographic accounts, specimens with a whitish to light purple background color (Fig. 2.5A) are considered herein to correspond to Schmitt’s (1933) *P*. *tortugae*, a form earlier documented as having a relatively light coloration (Provenzano 1959, Williams 1965, McLaughlin & Provenzano 1974) with rosy or purple-ish walking legs (Holthuis 1959, Provenzano 1965). The second color form, described in the present work as *P*. “nr. *tortugae* **n. sp.**” (Fig. 2.5B), has an overall light brown to olive green carapace, as well as dramatic red spines on the carpi of the walking legs, particularly the mesial margin of the manus and carpus of the cheliped. This coloration had been previously observed by other authors (Provenzano 1959; Holthuis 1959; Williams 1965), and is considered herein to correspond to the "darker" forms of McLaughlin & Provenzano (1974).

Despite their overall similarity to one another, morphological differentiation of *Paguristes tortugae* and *P*. "nr. *tortugae* **n. sp.**" can be made by considering the precise shape of the rostrum. For both species, the rostrum is well developed, extending past the lateral projections of the shield and separating the ocular acicles. However, in *P. "*nr. *tortugae* **n. sp.**" the rostrum tapers evenly to an acute point (Fig. 2.6A), whereas that of *P. tortugae* exhibits slightly rounded shoulders to either side of the rostrum apex (Fig. 2.6B). In addition, oblique rugae are present on the merus of the second pereopod in our new species that are lacking in *P*. *tortugae*.

Discussion

The composition of the *Paguristes tortugae* complex originally included seven species, *Paguristes tortugae*, *A. hewatti*, *P*. *hernancortezi*, *P*. *angustithecus*, *P*. *perplexus*, *P*. *anomalus*, and *P. invisisacculus* (= *Pseudopaguristes invisisacculus*), all exhibiting a dense fringe of setae on the thoracic appendages. Subsequently, the complex grew to include newly discovered species. Campos & Sanchez (1995) included two from northern Colombia, *Paguristes zebra* and *P*. *werdingi.* More recent additions from the western Atlantic are *P*. *maclaughlinae* Martinez-Iglesias and Gomez, 1989 of Cuba, and the Brazilian species, *P*. *scarabinoi* Lima and Santana, 2017. Genetic data are not yet available to confirm the phylogenetic affinities of these additional species to the *P*. *tortugae* complex.

Areopaguristes "nr. *hummi* **n. sp.**" and its sister species *A. hummi* could be considered constituents of the *Paguristes tortugae* complex based on possessing a dense fringe of setae on the thoracic appendages, the currently used broad diagnostic criteria for the complex. However, genetic evidence does not support a definitive and close affinity between *A. hummi* s.s. or *A.* "nr. *hummi* **n. sp.**" and *P. tortugae* itself. Instead, *A. hummi* and *A.* "nr. *hummi* **n. sp.**" Are shown to be distant relatives of *P. tortugae* in our analyses (Craig & Felder, in review) of western Atlantic members of *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*. Such a finding is consistent with the morphological disparities discussed herein that are evident when *A. hummi* and *A.* "nr. *hummi* **n. sp.**" are compared to the *Paguristes tortugae* complex constituents, such as *A. hewatti*, that are most morphologically and genetically similar to *P. tortugae* (Table 2.2).

Besides the characteristic fringe-like distribution of setae on the thoracic appendages, unifying morphological characters for the *Paguristes tortugae* complex as historically used have remained elusive (Provenzano & Rice 1966; McLaughlin & Provenzano 1974). Some characters that are confirmed as diagnostic at the species level, such as the form of the brood pouch and the coloration of the head appendages (McLaughlin & Provenzano 1974; Provenzano 1959, 1965), may also prove useful in delimiting subgroups within the complex when combined with genetic findings. Aside from *Areopaguristes tudgei* Lemaitre & Felder, 2012 and *P. anomalus*, genetic allies of *P. tortugae* that lack brood pouches entirely, other presumed or genetically confirmed associates of *P. tortugae* can be grouped into three divisions based on brood pouch morphology: those with subovate to subquadrate pouches (*P. tortugae*, *A. hewatti*, *P. zebra*, *P. hernancortezi*), those with slender, blade shaped pouches (*P. angustithecus*, *P. scarabinoi*), and those with triangular pouches (*P. perplexus*, *Pseudopaguristes invisisacculus*). Findings of genetic phylogenetic analyses have so far mirrored some of these groupings by recovering a well-supported clade including *Paguristes tortugae*, *A. hewatti*, and *P. hernancortezi*, all species having subovate to subquadrate brood pouches. Species possessing blade-shaped brood pouches are found only outside of that genetic clade (Craig & Felder, in preparation). Additionally, coloration and patterning of the head appendages is somewhat predictive of these brood pouch group assignments, with subovate to subquadrate brood pouches correlated with banded or spotted eyestalks. These two trends can be extended and applied to species for which genetic data is not yet available such as *P. zebra*, a species with irregularly banded eyestalks and a subovate brood pouch that shares many additional morphological characters with genetically confirmed *P. tortugae* complex constituents (Table 2.2).

Some species typically considered as constituents of the *P. tortugae* complex are not accommodated by phylogenetically supported trends regarding brood pouch shape or head appendage coloration. *Paguristes angustithecus* has banded eyestalks, a feature which has historically prompted the proposal of an alliance with *P. tortugae* and *A. hewatti* (McLaughlin & Provenzano 1974). However, the banded eyestalks of *P. angustithecus* are not accompanied by a subovate or subquadrate brood pouch. Segregation of *P. angustithecus* from the patterned eyestalk clade is further prompted when the length of the setae on the antennal flagellum is compared among these potentially allied species (Table 2.2). The long setae of the antennal flagellum, along with a blade-shaped brood pouch, distinguish *P. angustithecus* from *P. tortugae* and its closest allies, but unite it with *P. scarabinoi.* When *P. angustithecus* is not considered a constituent of the patterned eyestalk clade, the species remaining are exemplified by *P. tortugae*, sharing many potentially diagnostic characters. This raises the speculation that *P. scarabinoi* and *P. angustithecus* together represent a unified phylogenetic subgroup independent of *P. tortugae* and its closest allies, rather than anomalies among them.

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Table 2.1: Type localities and geographic distributions of *Paguristes*, *Areopaguristes*, and *Pseudopaguristes* species commonly associated with the *Paguristes tortugae* complex. Following brief descriptors, numerically designated Ecoregions corresponding to those defined by Spalding *et al*. 2007 are designated by "( )". Numbered references are listed below the table.

Species	Type Locality	Ecoregion(s) (Spalding et al. 2007)	Depth	References
Areopaguristes Rahayu & Mclaughlin, 2010				
A. hewatti Wass, 1963	Texas, USA	northern Gulf of Mexico (43)	shallow–16 m	4, 10, 12, 19
A. hummi Wass, 1955	Florida, USA, Franklin County	Carolinian (42), northern Gulf of Mexico (43), southern Gulf of Mexico (69), Floridian (70), Greater Antilles (65), southern Caribbean (66), southwestern Caribbean (67)	shallow–22 m	1, 3, 9, 11, 12, 13, 14, 17, 18. 19
A. "nr. *hummi* **n. sp.**"	Panama, Bocas del Toro	southwestern Caribbean (67)	shallow–3 m	19
A. tudgei Lemaitre & Felder, 2012	Belize, Carrie Bow Cay	western Caribbean (68)	< 1 m	7, 19
Paguristes Dana, 1851				
P. angustithecus McLaughlin & Provenzano, 1974	Venezuela	southern Caribbean (66), southern Gulf of Mexico (69), Guianan (71), Amazonian (72); northeastern Brazil (75)	25–91 m	6, 10
P. anomalus Bouvier, 1918	Cuba, Fortaleza	Bermuda (62), eastern Caribbean (64), Greater Antilles (65), southern Caribbean (66), southern Gulf of Mexico (69)	< 1–63 m	1, 10, 11, 19
P. hernancortezi McLaughlin & Provenzano, 1974	Florida, Sanibel Island	Carolinean (42), northern Gulf of Mexico (43), southern Gulf of Mexico (69), Floridian (70)	55–73 m	1, 10, 13, 19
P. maclaughlinae Martinez-Iglesias & Gomez, 1989	Cuba, Isla de la Juventud	Greater Antilles (65)	603 m	5
P. perplexus McLaughlin & Provenzano, 1974	French Guiana	Greater Antilles (65), southern Caribbean (66), southwestern Caribbean (67), Guianan (71), Amazonian (72) northeastern Brazil (75)	< 1–91 m	6, 10

P. scarbinoi Lima & Santana, 2017	Caribbean, Uruguay	Uruguay-Buenos Aires Shelf (183)	66–68 m	8
P. tortugae Scmitt, 1933	Florida, Dry Tortugas	Carolinian (42), northern Gulf of Mexico (43), Bahamanian (63), Greater Antilles (65), southern Gulf of Mexico (69), Floridian (70), northeastern Brazil (75), eastern Brazil (76), southeastern Brazil (180)	< 1–91 m	1, 2, 5, 10, 11, 13, 14, 15, 16, 17, 18, 19
P. "nr. *tortugae* **n. sp.**"	Florida, Pigeon Key	northern Gulf of Mexico (43), southwestern Caribbean (67), southern Gulf of Mexico (69), western Caribbean (68), Floridian (70)	~1–41 m	10, 17, 19
P. werdingi Campos & Sanchez, 1995	Colombia, Santa Marta	southern Caribbean (66), southwestern Caribbean (67)	~20 m	3
P. zebra Campos & Sanchez, 1995	Columba, Cartegena	southern Caribbean (66), southwestern Caribbean (67)	~5 m	3
Pseudopaguristes McLaughlin, 2002				
P. invisisacculus McLaughlin & Provenzano, 1974	Florida, Ragged Key	northern Gulf of Mexico (43), Greater Antilles (65), western Caribbean (68), southern Gulf of Mexico (69)	< 1–20 m	1, 9, 10, 19

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1. Abele & Kim 1986
2. Boos *et al.* 2012
3. Campos & Sanchez 1995
4. Felder 1973
5. Martinez-Iglesias & Gomez 1989
6. Hernandez-Avila *et al.* 2007
7. Lemaitre & Felder 2012
8. Lima & Santana 2017
9. Manjon-Cabeza *et al.* 2002
10. McLaughlin & Provenzano 1974
11. Provenzano 1959
12. Rahayu 2005
13. Raz-Guzman *et al.* 1986
14. Rodriguez-Almaraz *et al.* 2005
16. Soto *et al.* 1999,
17. Strasser & Price 1999
18. Wass 1955
19. ULLZ/USNM holdings

Table 2.2: Summary of diagnostic morphological characters for species commonly regarded as the *Paguristes tortugae* complex.

Species	acicles	rostrum	setae of antennal flagellum	antennule length	eyestalk shape	eyestalk patterning	brood pouch	male gonopod inferior lamella	female first pleopods
Areopaguristes									
A. hewatti	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrower at midlength	banded near midlength	large; subovate	armed	present; paired
A. hummi	flushly abutted	obsolete	6–8 articles in length	exceeding corneas	subcylindrical; slightly narrower at midlength	solid blue	absent	armed	absent
A. "nr. *hummi* **n. sp.**"	flushly abutted	obsolete	6–8 articles in length	exceeding corneas	subcylindrical; slightly narrower at midlength	solid, straw colored	unconfirmed	armed	unconfirmed
A. tudgei	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	slightly exceeding cornea	subcylindrical; greatly swollen at base	distally solid blue	absent	unarmed	present; paired
Paguristes									
P. angustithecus	widely separated	exceeding lateral projections; acute tip	6–8 articles in length	Equal to, or exceeding corneas	subcylindrical; slightly narrower at midlength	banded near midlength	elongate; blade shaped	armed	present; paired
P. anomalus	widely separated	exceeding lateral projections; rounded	1–3 articles in length	not exceeding corneas	subcylindrical; bulbous base	distally solid blue	absent	armed	present; paired

P. hernancortezi	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrower at midlength	spotted; somewhat translucent	small; subquadrate	armed	present; paired
P. maclaughlinae	widely separated	not exceeding lateral projections; rounded tip	1–3 articles in length	greatly exceeding corneas	subcylindrical slightly swollen at base;	patterning absent in preservation	large; subquadrate	armed	unconfirmed
P. perplexus	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrower at midlength	dark bands at midlength	subtriangular	armed	present; paired
P. scarabinoi	widely separated	exceeding lateral projections; acute tip	6–8 articles in length	not exceeding corneas	subcylindrical; slightly narrower at midlength	patterning absent in preservation	elongate; blade shaped	armed	present; paired
P. tortugae	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrower at midlength	banded at midlength	large; subovate / subquadrate	armed	present; paired
P. “nr. *tortugae* **n. sp.**”	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas or exceeding corneas somewhat	subcylindrical; slightly narrower at midlength	banded at midlength	large; subovate / subquadrate	armed	present; paired
P. werdingi	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; bulbous base	distally solid blue	absent	armed	present; paired
P. zebra	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrower at midlength	irregular dark bands along length	large; subovate / subquadrate	armed	present; paired
Pseudopaguristes									

P. invisisacculus	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrower at midlength	distally solid blue	subtriangular	armed	present; paired

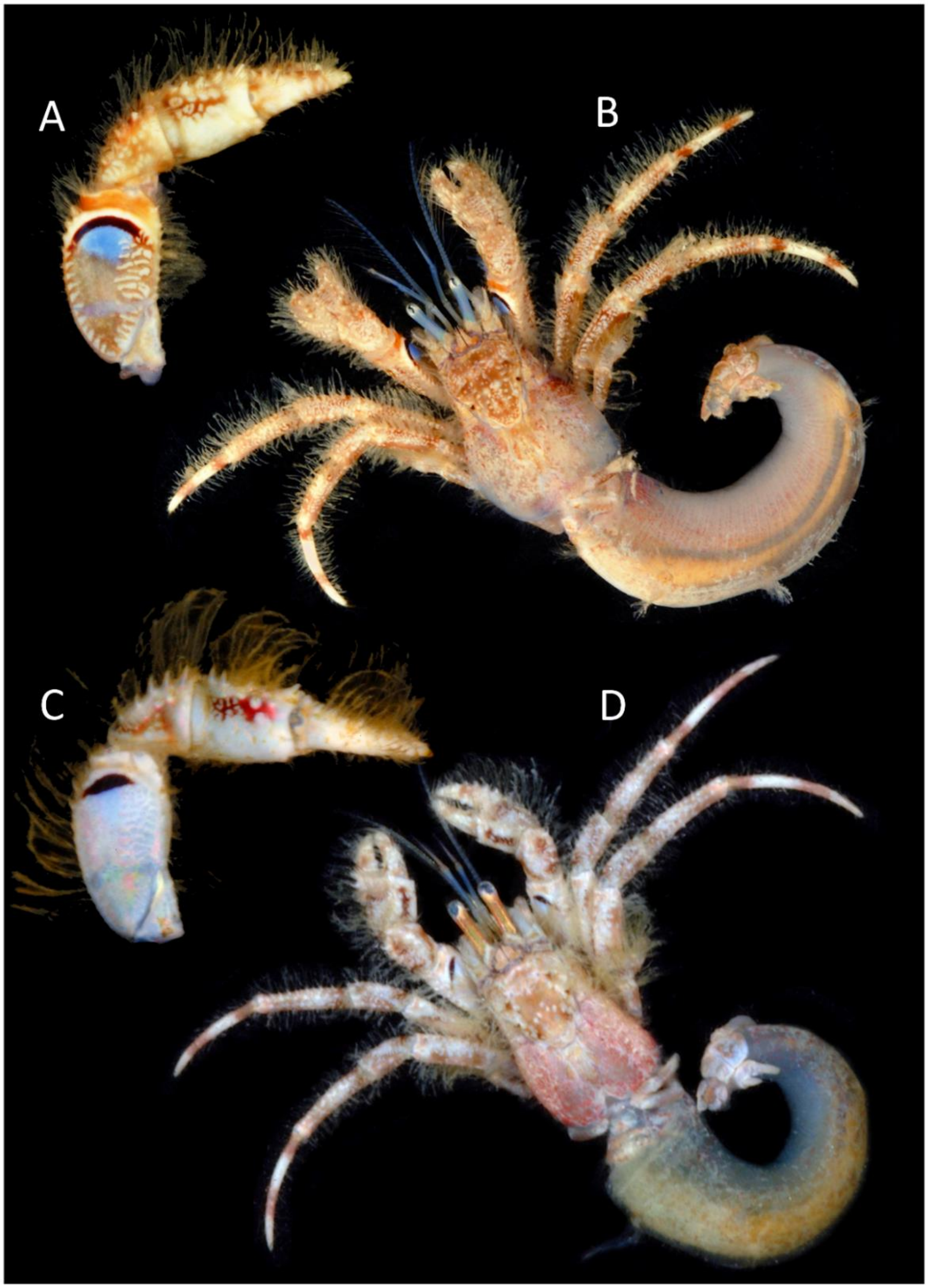

Figure 2.1. *Areopaguristes hummi* s.s., A, B, female, s.l. 3.2 mm, (ULLZ 13232 / USNM 1546831), northwestern Gulf of Mexico; A, left cheliped merus, mesial surface; B, carapace, dorsal view. *Areopaguristes* “nr. *hummi* **n. sp**.”, C, D, male, s.l. 4.2 mm (ULLZ 15009 / USNM 1548225), Panama, southwestern Caribbean; C, left cheliped, mesial surface; D, carapace, dorsal view.

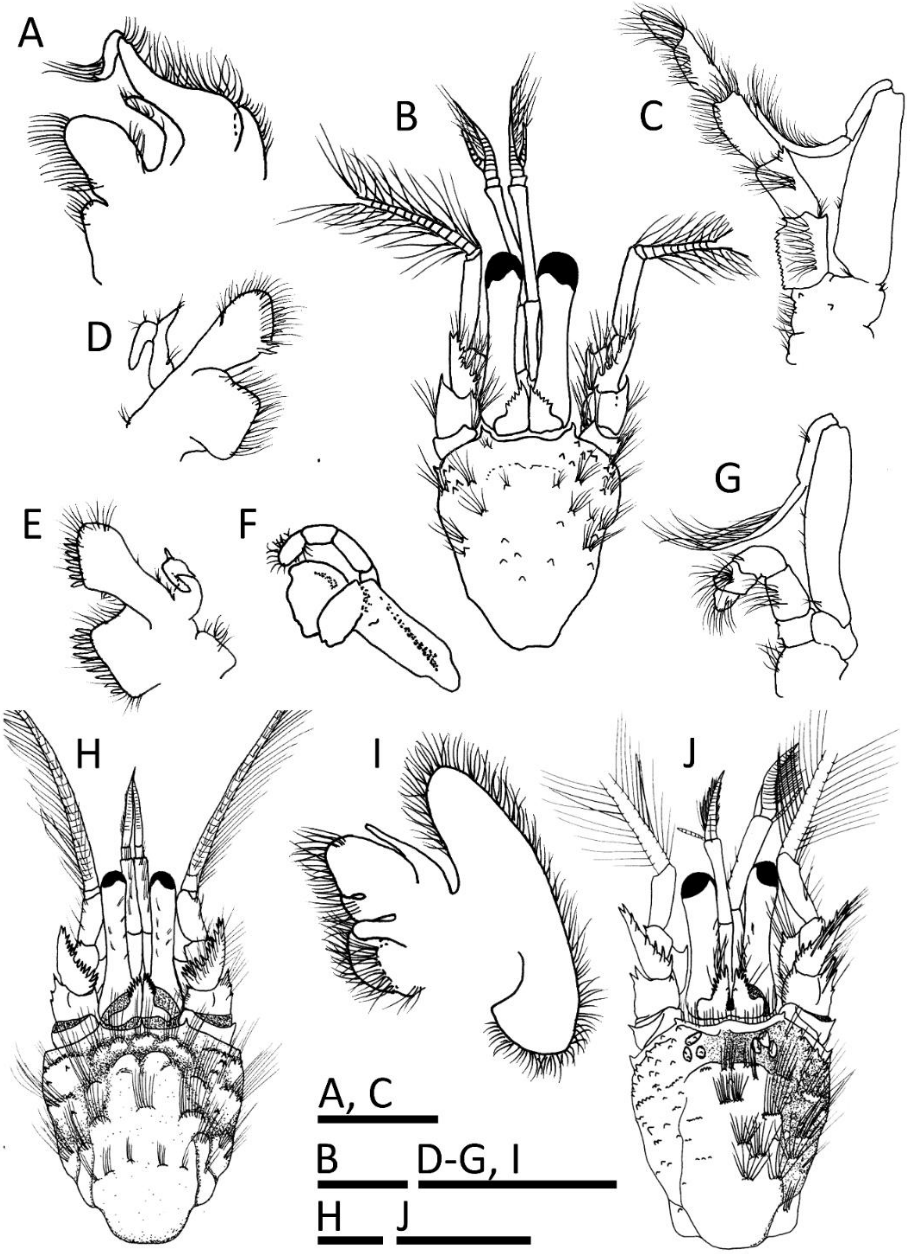

Figure 2.2. *Areopaguristes* "nr. *hummi* **n. sp.**" A–G, I, holotype male, s.l. 2.5 mm (ULLZ 15009 / USNM 1548225), Panama, southwestern Caribbean; H, *Tetralobistes weddellii* (H. Milne Edwards, 1848), female, s.l. 8.3 mm (CCDB/FFCLRP/USP # 809), from: Ayon-Parente & Hendrickx 2013, Fig. 1B; J, *Areopaguristes lemaitrei* Ayon-Parente & Hendrickx, 2012, holotype male, s.l. 3.40 mm (EMU-9520), from: Ayon-Parente & Hendrickx 2012, Fig. 1A; A, right first maxilliped, internal surface; B, carapace shield, dorsal surface; C. right third maxilliped, internal surface; D, right maxillule, external surface; E, right maxillule, internal surface; F, right mandible, internal surface; G, right second maxilliped, internal surface; H, carapace shield dorsal surface; I, right maxilla, internal surface; J, carapace shield, dorsal surface. Scale bars = 1.0 mm (A–J).

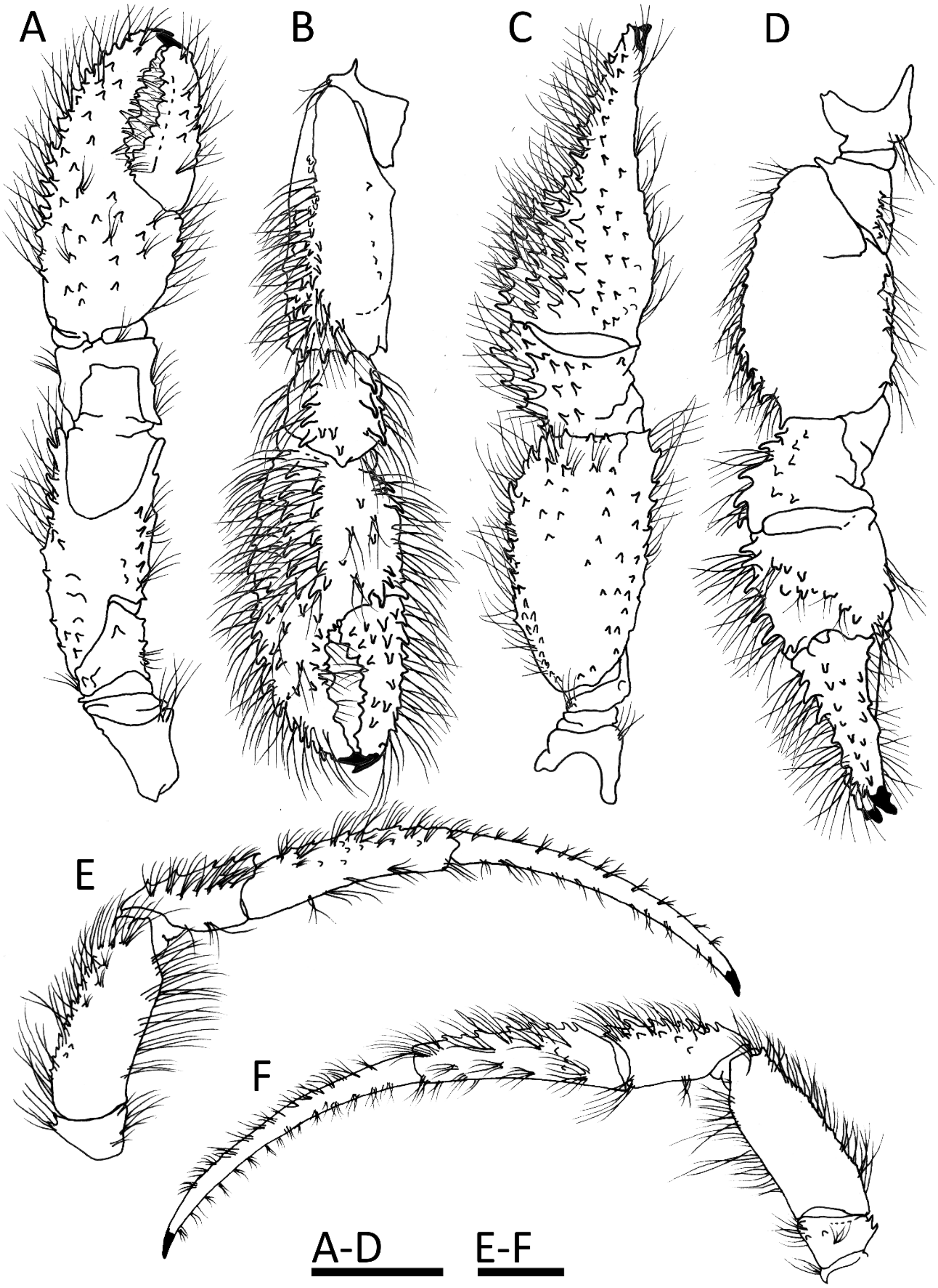

Figure 2.3. *Areopaguristes* "nr. *hummi* **n. sp.**" A–F, holotype male, s.l. 2.5 mm (ULLZ 15009 / USNM 1548225), Panama, southwestern Caribbean. A, right cheliped, ventral surface; B, right cheliped, dorsal surface; C, right cheliped, lateral surface; D, right cheliped, mesial surface; E, right second pereopod, lateral surface; F, right second pereopod, mesial surface. Scale bars = 1.0 mm (A–F).

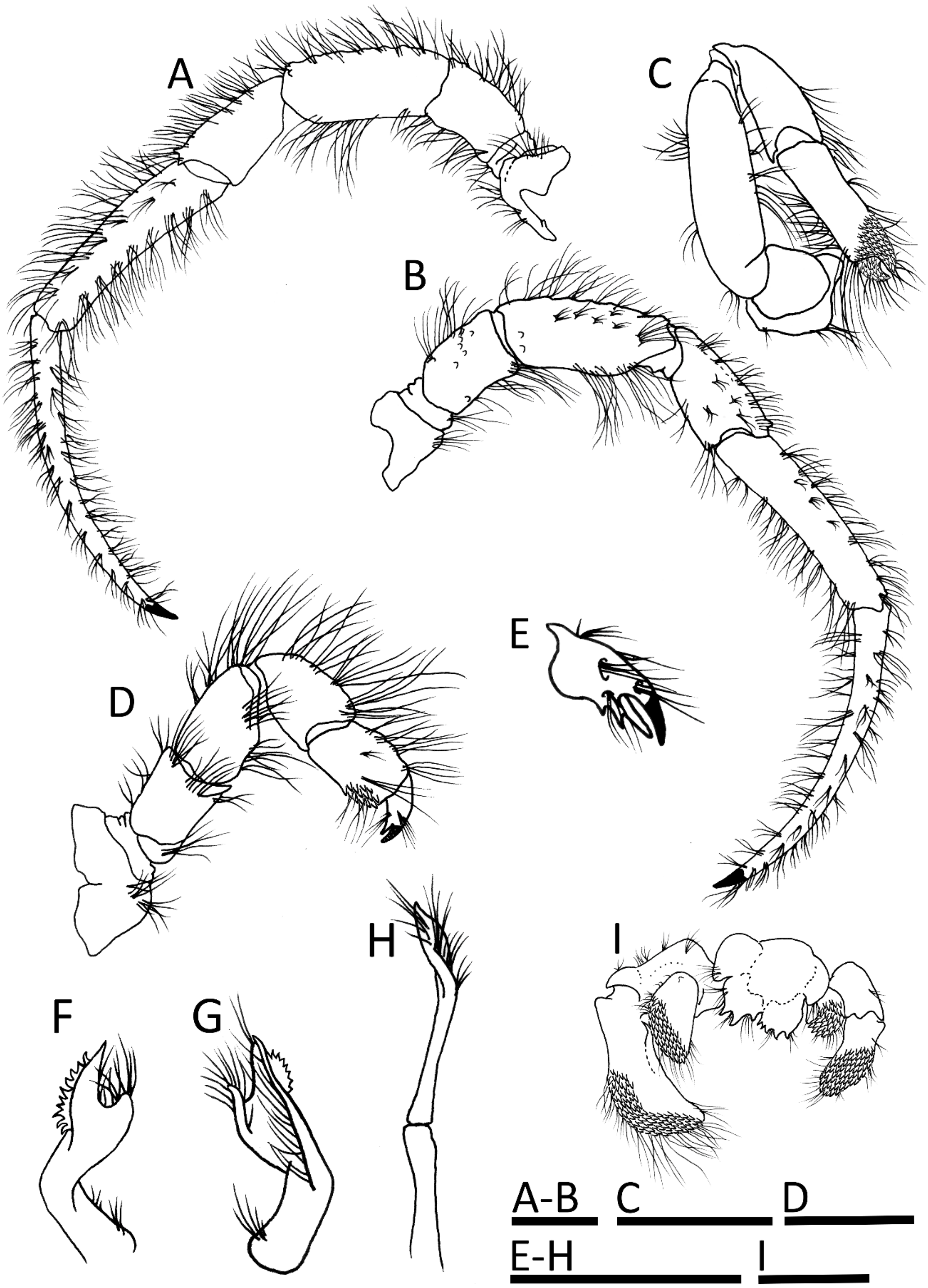

Figure 2.4. *Areopaguristes* "nr. *hummi* **n. sp.**" A–I, holotype male, s.l. 2.5 mm (ULLZ 15009 / USNM 1548225), Panama, southwestern Caribbean. A, right third pereopod, mesial surface; B, right third pereopod, lateral surface C, right fifth pereopod, lateral surface; D, right fourth pereopod, lateral surface; E, right fourth pereopod dactyl; F, right first pleopod, mesial surface; G, right first pleopod, internal surface; H, right second pleopod; I, telson and uropods, dorsal surface. Scale bars = 1.0 mm (A–I).

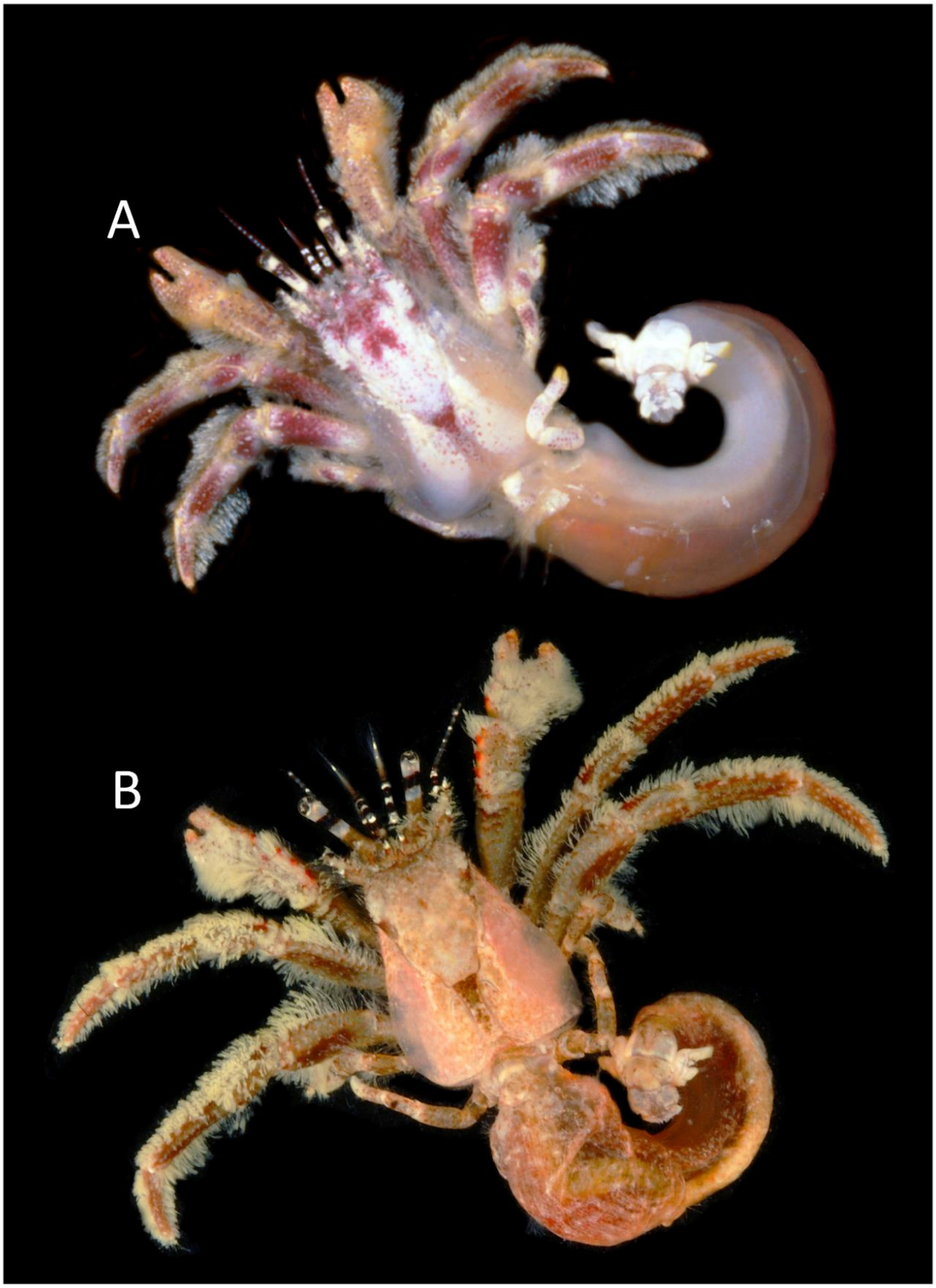

Figure 2.5. Color patterns of A, *Paguristes tortugae* s.s., male, s.l. 7.2 mm (ULLZ 4783 / USNM 1540547), Florida Keys, Gulf of Mexico; B, *P*. "nr. *tortugae* **n. sp.**", paratype male, s.l. 4.9 (ULLZ 8578 / USNM 1543769), Gulf of Mexico. A, carapace, dorsal view; B, carapace, dorsal view.

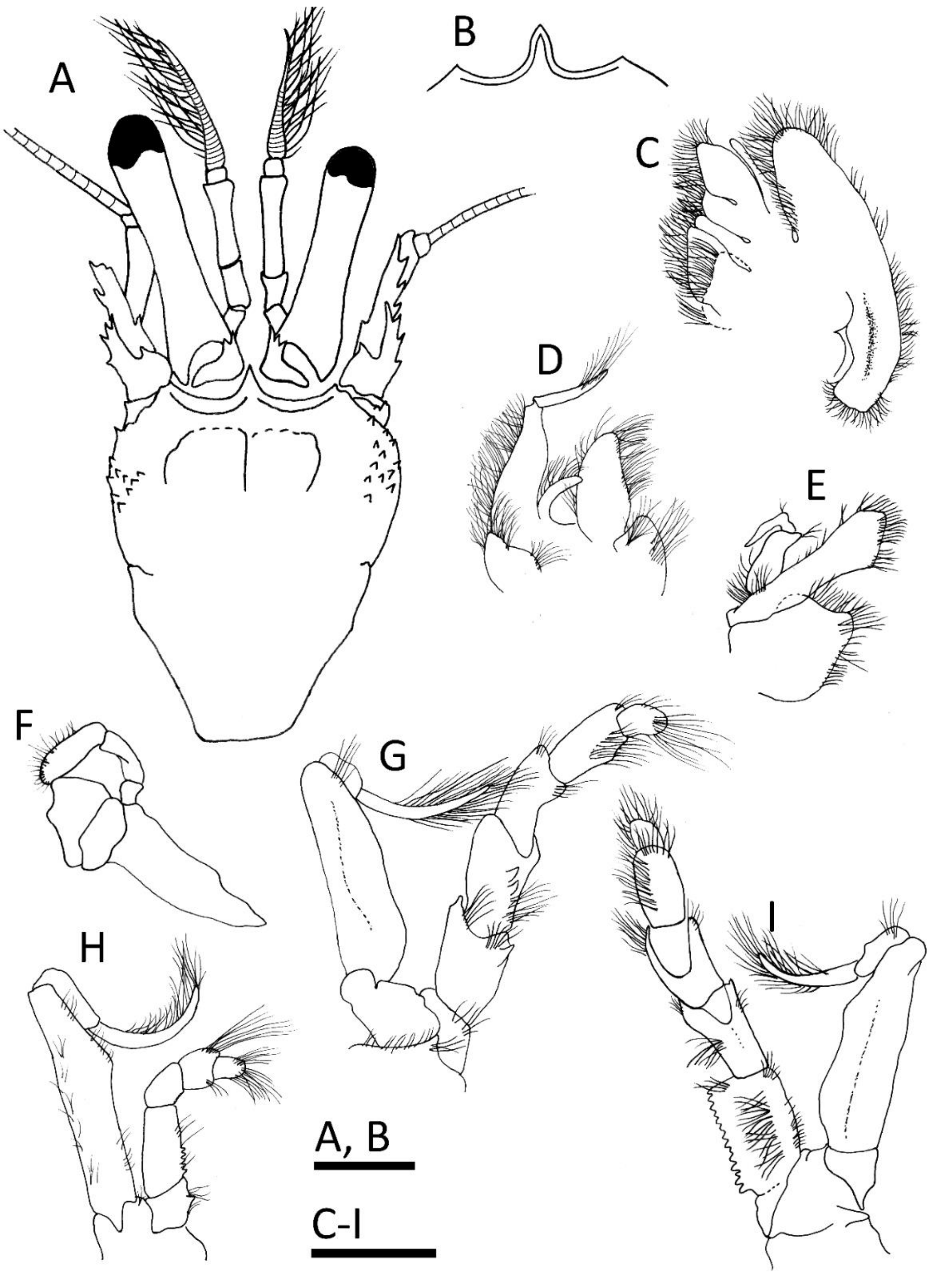

Figure 2.6. *Paguristes* "nr. *tortugae* **n. sp.**" A, C–I, paratype male, s.l. 4.9 mm (ULLZ 8578 / USNM 1543769), Gulf of Mexico; B, *P. tortugae* s.s., female, s.l. 4.1 mm (ULLZ 11148 / USNM 1545610), Belize, northwestern Caribbean. A, shield and head appendages, dorsal view, setae omitted; B, shield anterior margin showing rostrum; C, maxilla, internal surface; D, first maxilliped, external surface; E, maxillule, external surface; F, mandible, internal surface; G, third maxilliped, external surface; H, second maxilliped, external surface; I, third maxilliped, internal surface; Scale bars = 1.0 mm (A–I).

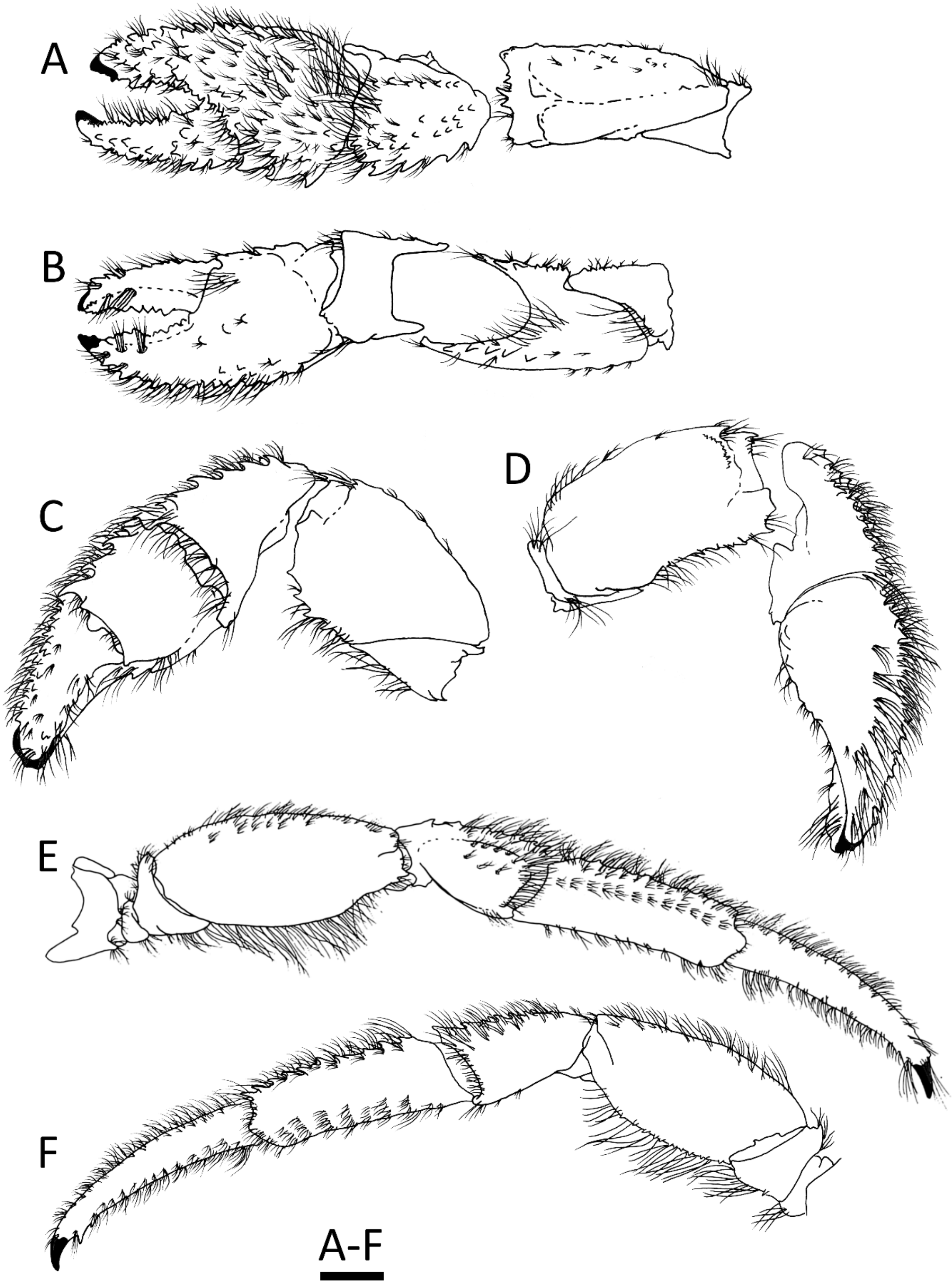

Figure 2.7. *Paguristes* “nr. *tortugae* **n. sp.**”, A–F, paratype, male, s.l. 4.9 mm (ULLZ 8578 / USNM 1543769), Gulf of Mexico. A, right cheliped, dorsal surface; B, right cheliped, ventral surface; C, right cheliped, mesial surface; D, right cheliped, lateral surface; E, right second pereopod, lateral surface; F, right second pereopod, mesial surface. Scale bar = 1.0 mm (A–F).

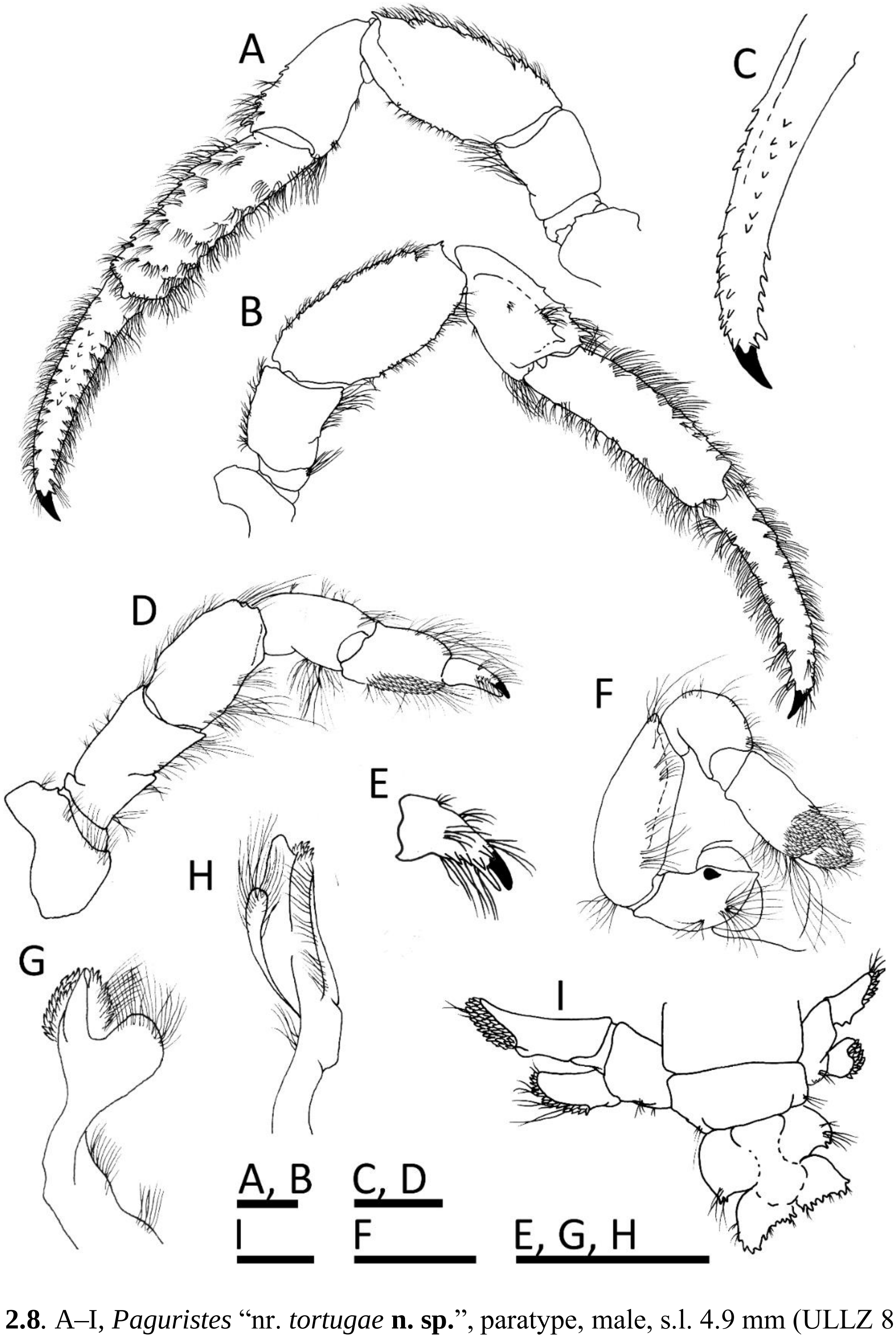

Figure 2.8. A–I, *Paguristes* “nr. *tortugae* **n. sp.**”, paratype, male, s.l. 4.9 mm (ULLZ 8578 / USNM 1543769), Gulf of Mexico. A, right third pereopod, mesial surface; B, right third pereopod, lateral surface; C, right third pereopod dactyl, mesial surface, setae omitted; D, right fourth pereopod, lateral surface; E, fourth pereopod dactyl; F, right fifth pereopod, lateral surface; G, gonopod, mesial surface; H, gonopod, internal surface; I, telson and uropods, dorsal surface. Scale bars = 1.0 mm (A–I).

Chapter 3: Molecular Phylogenetic Analysis of Slected Paguroidea (Crustacea: Decapoda: Anomura) With a Focus on the Diogenid Genera *Paguriestes* Dana, 1851, *Areopaguristes* Rahayu, 2005, and *Pseudopaguristes* McLaughlin, 2002.

Abstract

Among the genera of the hermit crab family Diogenidae Ortmann, 1892, *Paguristes* Dana, 1851 is among the most speciose and morphologically diverse. Over time, a series of taxonomic revisions resulted in the reassignment of some *Paguristes* taxa to the allied genera *Areopaguristes* Rahayu, 2005 or *Pseudopaguristes* McLaughlin, 2002. For these three genera, divergent morphology among complexes of constituent species has long telegraphed a lack of monophyly, which was confirmed by findings in a previous molecular phylogenetic analysis. Based on results from three Maximum Likelihood phylogenetic analyses of H3, 12SS, and 16S DNA sequences, the present study reveals as many as 11 genetic breaks that appear to be correlated with morphological characters within the group of thre genera *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*. The generic assignment to which each genetic clade most appropriately corresponded was unclear, but strong bootstrap support and potentially diagnostic characters may indicate that some of these clades warrant new generic status. The phylogenetic affinity of a *Paguristes* s.s. was inferred by the placement of its type species, *P. weddellii* H. Milne Edwards, 1848, as geneticly related to *A. hummi* Wass, 1955 and a few Pacific relatives that share some morphological similarities. The scope and constituency of a restricted *Areopaguristes* remained unresolved due to limited taxon sampling in allied clades, but the genus was determined to be a close relative of several even-handed diogenid species currently assigned to *Pseudopaguristes*. Although gill formula has been cited as lacking utility for diagnosis of *Paguristes*, *Areopaguristes*, and

Pseudopaguristes (Craig & Felder, in review), this character may be correlated with some of our genetic clades. Genetic data for *Pseudopaguristes janetkae* McLaughlin, 2002 placed that taxon with other species bearing feather-like setae on pereopod 4 and 8 quadriserial gill pairs.

Key Words: Anomura, systematics, mtDNA, 16S, 12S, Histone 3, Diogenidae

Introduction

In Dana's (1851) seminal account of the genus *Paguristes* Dana, 1851, descriptions of *Paguristes hirtus* Dana, 1851 from Chile and a second species, *Paguristes longirostris* Dana, 1851, are given. Although both descriptions are brief and included limited illustrations, Dana (1851, 1852) did note presence of external gonopods in the male holotype specimens of both species, and established that morphological feature as the primary distinguishing character for his new genus. Over time, a suite of characters has been developed for the genus that currently includes a non-chelate fourth pereopod and 13 gill pairs, as well as accommodations for variability in form and prominence of male gonopods (Forest *et al*., 2000). Adhering to these criteria, currently recognized *Paguristes* species now number more than 200 (McLaughlin *et al*., 2010; WoRMS, 2020). Two additional diogenid genera, *Pseudopaguristes* McLaughlin, 2002 and *Areopaguristes* Rahayu, 2005, are considered to be close allies of *Paguristes*, sharing with that genus many morphological characters including external gonopods in males and usually paired first pleopods in females. While recent molecular phylogenetic work has supported the alliance among these three genera, it has also revealed that none are monophyletic (Bracken-Grissom *et al*., 2013; Craig & Felder, in review).

In 2002 some male hermit crab specimens bearing gonopods were collected from Guam and subsequently described as a species new to science, *Pseudopaguristes janetkae*

McLaughlin, 2002. Considered “aberrant” at the time (McLaughlin, 2002), this species resembled some species of Parapaguridae Smith, 1882, but were excluded from that family due to the presence of a flagellum on the exopod of maxilliped two. Although consistent in some ways with a broad diagnosis of *Paguristes* (Dana, 1851; Forest *et al*., 2000; Komai, 2001), many characters of the new species were considered somewhat uncommon among *Paguristes* species (McLaughlin, 2002; Rahayu, 2005, 2006). One notable deviation of the new taxon from the diagnosis of *Paguristes* was a reduction of gill-pair number to 8 pairs from the 13 pairs typical for *Paguristes*. This character became one foundational character of *Pseudopaguristes*, with *P. janetkae* as the type species. Since the establishment of the genus, the number of species assigned to *Pseudopaguristes* has increased to 15, diagnosed primarily by the criterion of reduced gill-pair number (McLaughlin *et al*., 2010). Today, the majority of known *Pseudopaguristes* species are distributed in western Pacific waters, with only two *Pseudopaguristes* species so far recorded from the western Atlantic (Felder, 1973; Provenzano & McLaughlin, 1974; Strasser & Price, 1999; Rahayu, 2005; Felder *et al*., 2009; McLaughlin *et al*., 2010,).

The deviation of *Pseudopaguristes*’ gill formula from that of its presumed ally *Paguristes*, raised the possibility that other species with atypical gill formulas may have been assigned to *Paguristes* based primarily on the presence of external gonopods. This prompted Rahayu (2005) to reevaluate the gill formula of numerous species assigned to *Paguristes,* resulting in the discovery of a third gill-formula among constituents of this genus. Rahayu (2005) noted that in this third gill-pair configuration, gills on the anterior appendages were well developed but a missing pleurobranch above pereopod two resulted in a total of 12 gill pairs,. Numerous species previously assigned to *Paguristes* were found to exhibit this gill formula and subsequently reassigned to *Stratiotes* Thomson, 1899, a genus resurrected to accommodate them as typified by *Stratiotes setosus* H. Milne Edwards, 1848 from western New Zealand (Rahayu, 2005). Subsequently, the generic nominative *Stratiotes* was determined to be preoccupied by a genus of beetles, requiring establishment of the replacement name *Areopaguristes* (Rahayu & McLaughlin, 2010). Currently, the number of species assigned to *Areopaguristes* is increasing, although as previously mentioned, molecular phylogenetic evidence suggesting that the genus is not monophyletic is accumulating (Bracken Grissom *et al.*, 2013; Craig & Felder, in review).

In the past, determining the taxonomic memberships of *Pseudopaguristes*, *Areopaguristes*, and *Paguristes* was accomplished based on the morphological characters for the type species of those genera. In the case of *Pseudopaguristes*, the diagnosis is readily derived from a contemporary species description with an existing holotype (McLaughlin, 2002). For *Areopaguristes*, some recent emendments (Ayon-Parente & Hendrickx, 2015) to the generic diagnosis remain tentative, but modern work has refined the original morphological account of *A. setosus* (Forest *et al.*, 2000; Rahayu, 2005). Defining the scope of *Paguristes* holds some uncertainty due to recent taxonomic revisions that call into question the provenance of *Paguristes weddellii* H. Milne Edwards, 1848, the senior synonym of *P. hirtus* Dana, 1851 (Haig, 1955), the generic type species of *Paguristes* as designated by Stimpson (1858).

Many persistent and targeted attempts at deriving suites of morphological characters for these three genera have been made (Stimpson, 1858; A. Milne-Edwards, 1880; Henderson, 1888, 1896; A. Milne-Edwards & Bouvier, 1893, 1892, 1900; Ortmann, 1892; Benedict, 1901; Alcock, 1905; Makarov, 1938; Forest, 1854; Haig, 1955; McLaughlin &

Provenzano, 1974; Miyake, 1978; McLaughlin, 2004a; Rahayu, 2005). Such studies have noted intraspecific variation and speculated as to convergence in key characters that may be confounding efforts to establish robust diagnoses. Genetic data sets provide an opportunity to view evolutionary relationships differently by eliminating concerns that convergence in diagnostic characters is obscuring underlying evolutionary relationships. Evidence provided by recent work based on genetic data has demonstrated that *Paguristes* and related genera are not monophyletic (Bracken-Grissom *et al.*, 2013; Craig & Felder, in preparation). The present study builds upon that work through broader taxonomic sampling, including key genetic data to assist in defining and resolve the core constituencies of *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*.

Materials and Methods

Sampling included representatives of over 200 specimens from across Anomura for which high quality and recently collected material was available (Table 3.1). Specimens sequenced for this study were accessed from the University of Louisiana Lafayette Zoological Collection, Lafayette, Louisiana (ULLZ); the Florida Museum of Natural History Invertebrate Zoology Collection, University of Florida, Gainesville, Florida (UF); the United States National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); the National Institute of Water and Atmospheric Sciences, New Zealand (NIWA); and the Lee Kong Chian Museum of Natural History, Singapore (ZRC). Specimens used in this study were either directly preserved in 70–80% ethyl alcohol (EtOH), or first frozen in either seawater or glycerol at −80°C before later being transferred to 80% EtOH.

Genomic DNA was extracted from gill, abdominal tissue, eggs (when available), or whole appendages when necessary, using the Qiagen DNeasy DNA extraction kit (Qiagen, Cat. No. 69504). The DNA purity and concentration was evaluated using the NanoDrop Lite Spectrophotometer (ThermoFisher Scientific, Cat. No. ND-LITE-PR). Partial sequences of the 12S mtDNA, 16S mtDNA, and H3 nuclear DNA were amplified using primers and temperature profiles presented in Table 3.2. Reactions were performed using established protocols (Thoma *et al.* 2014) with primer concentrations varying from 0.2µM to 0.8 µM and 1 µL 1% Bovine Serum Albumin (BSA) substituted for Betaine in some reactions. PCR products were purified using SureClean Plus (Bioline USA Inc, SKU 37047). Cycle sequencing reactions and clean-up were largely based on established protocols (Thoma et al. 2014; Craig & Felder in preparation) with the protocol for cycle sequencing modified to accommodate the use of BDX64 Big-Dye Enhancing Buffer (Molecular Cloning Labs, Cat. No. BDX-100) for some samples.

Sequence contigs were trimmed and assembled in Sequencher version 4.1.2 (GeneCodes Corporation, Ann Arbor, MI). A multiple sequence alignment was generated for each marker individually in MAFFT under G-INS-I criteria for H3, and E-INS-i criteria for 12S12S and 16S16S (Katoh *et al.* 2017). Ambiguously aligned regions were trimmed from each alignment with gBlocks (Castresana 2000), using default parameters for the H3 marker, and the following modifications for the 12S12S and 16S16S alignments: 1) minimum length of block = 8; 2) allowed gap positions = half. The resulting single-gene alignments were concatenated into a single aligned matrix in BioEdit (Hall 1999). Model partitions were assigned each of the three individual markers, with the H3 marker further partitioned by codon position (Rodriguez et al. 1990). A Maximum Likelihood (ML) phylogeny with 1000 bootstrap replicates was inferred using the rAxML (Stamatakis 2006) Black-Box tool available on the CIPRES Science Gateway (Miller *et al*. 2010) with the GTR + Gamma model of nucleotide substitution applied to each partition (Rodriguez *et al.* 1990).

To assess the general topologies and relative statistical support at various levels of taxon sampling, three phylogenetic analyses, each with different levels of taxon sampling, were performed. Our Tree 1 analysis (Fig. 3.1) represents an initial iteration based on an incomplete sequence matrix that combined DNA sequence fragments of H3, 12S12S, and 16S16S for 389 individuals of 212 named or putative species across Anomura. Of the paguroids included in the Tree 1 iteration, approximately 30 species are currently assigned to *Paguristes*, approximately 17 species are assigned to *Areopaguristes*, and 5 species are assigned to *Pseudopaguristes*. The final data matrix is approximately 67.6% complete, 70.2% complete, and 88.7% complete for the H3, 12S, and 16S markers respectively. There are 1028 total sites in the alignment, with 337 sites, 294 sites, and 397 sites for the H3, 12S, and 16S fragments respectively.

A second phylogenetic analysis, Tree 2 (Fig. 3.2), examined a more restricted taxon sample, with a strong bias in taxonomic sampling toward *Paguristes, Areopaguristes*, and *Pseudopaguristes* species. The distribution of species among the three genera was similar to that in the first analysis. Likewise, our sequence data matrix combined fragments of three markers (H3, 12S, and 16S), this time for 194 individuals of approximately 87 named or putative paguroid species. There are 1064 total sites in the concatenated alignment, with 336 sites for H3, 310 sites for 12S, and 418 sites for 16S.

The third analysis, Tree 3 (not figured), was taxonomically restricted to include only those individuals for which all three of our DNA markers were available. This subsample of our total data included 99 individuals of 57 named and putative species across Paguroidea.

Of these, approximately 20 species are currently assigned to *Paguristes*, with 14 species assigned to *Areopaguristes*, and 1 species assigned to *Pseudopaguristes*. The resulting matrix is complete, with 1037 total sites: 343 for H3, 251 for 12S, and 443 for 16S.

Results

While incongruities among phylogenetic inferences have many causes (Som, 2015), a consensus has emerged that increasing taxon sampling rather than increasing the number of characters sampled, (DNA bases in the case of this study), is crucial to avoiding errors in phylogenetic inference (Nabhan & Sarkar, 2012). For this reason, discussion of tree topology and clade support values herein draws primarily on our analyses including larger subsets of paguroid taxa; Tree 1 (Fig. 3.1) and Tree 2 (Fig. 3.2), with supplementary support provided by Tree 3 regarding broader relationships related to family level clades (Table 3.3) and subclades (Table 3.4).

The present study was able to expand somewhat on findings of previous molecular phylogenetic studies of Paguroidea; however, uncertainty about internal relationships within many families, genera, and species complexes remain . In the present study, family level groupings (Table 3.3) largely matched those of previous phylogenetic studies (Cunningham *et al*., 1992; Richter & Scholtz, 1994; Mantelatto *et al*., 2006; Tsang *et al*., 2008; Bracken-Grissom *et al*., 2013; Craig & Felder, in preparation). The overall similarities of the present outcomes to those of Craig & Felder (in preparation) prompted the continuation of nomenclature used therein to reference major phylogenetic subdivisions of Paguroidea (Table 3.3).

Some superficial observations about the broader phylogeny of Paguroidea can be drawn from the Tree 1 analysis (Fig. 3.1). There, Lithodidae was nested within Paguridae, forming a monophyletic clade (bootstrap 69) sister to the combined Diogenidae Clade 2, Diogenidae Clade 3, and Coenobitidae (bootstrap 70). The Paguridae+Lithodidae clade was characterized by a high degree of internal genetic structure, and some subdivisions at the generic level showed significant bootstrap support (Fig. 3.1). Low bootstrap support for most pagurid relationships above the generic level urges caution in the interpretation of Tree 1 outcomes, however. Parapaguridae was monophyletic at the family level, but of the two parapagurid genera represented in the study, neither was monophyletic (Fig. 3.1).

Across the three phylogenetic inferences considered herein, three primary diogenid subclades were noted (Table 3.3). Clade support values for Diogenidae Clade 1, Clade 2, and Clade 3 were greatest in Tree 3, when taxonomic sampling was greatly reduced overall and a complete genetic sequence matrix was employed. In general, Diogenidae Clade 2 and Clade 3 were more closely associated with Coenobitidae than they were with Diogenidae Clade 1, with Coenobitidae found auxiliary to a united Clade 2+Clade 3 (Tree 1, bootstrap <50), sister to Diogenidae Clade 2 (Tree 3, bootstrap 93), or embedded in Diogenidae Clade 2 (Tree 2, bootstrap <50). Diogenidae Clade 1 was present across analyses, and showed significant bootstrap support in two of the three phylogenetic inferences (Table 3.3). Tree 1 revealed that many of the genera grouped in Diogenidae Clade 2, (excepting *Diogenes* Dana, 1851), are likely monophyletic (Fig. 3.1), although taxonomic sampling across Diogenidae was incomplete at the generic level.

Across the three tree inferrences considered here, the constituents of Diogenidae Clade 1 were exclusively species currently assigned to *Paguristes*, *Areopaguristes*, or *Pseudopaguristes*. Diogenidae Clade 1 was partitioned into three major sub-clades, with Group A and Group B as sister clades, and Group C auxiliary to those. Although significant bootstrap values for Groups A and B were observed only in Tree 3 (Table 3.4), the two clades emerged in all three tree topologies inferred. In all cases Group B encompassed only species with 13 gill pairs, and in our most targeted approach to the phylogeny of Diogenidae Clade 1 (Fig. 3.2), the clade was composed primarily (but not exclusively) of western Atlantic species with unarmed telsons. In contrast, Group A counted among its members species of various gill formulas distributed among as many as 9 genetic subclades, with most subclades supported by significant bootstrap values in one or more analyses (Table 3.4).

Discussion

While it was not the purpose of the present work to fully resolve the scope and membership of the three subclades of Diogenidae, incorporation of 4 representative species of *Diogenes* into the present analyses provides insight into the constituencies of Diogenidae Clades 1 and 2. As can be derived from Tree 1 (Fig. 3.1), *Diogenes* species were relegated to Diogenidae Clade 2, but ultimately, they did not form a single monophyletic clade. Evaluation of morphological trends among species of *Diogenes* provides one means by which the phylogenetic relationships of *Diogenes* species not available for genetic analysis, including the generic type *D. miles* (Fabricius, 1787), can be predicted within Diogenidae Clade 2. As many as nine *Diogenes* species of the "*Trogolopagurus* group" (Morgan & Forest, 1991; Rahayu & Forest, 1995; McLaughlin, 2005) can be speculatively designated as allies of *Clibanarius* Dana, 1852 based on the phylogenetic placement of the group constituent *D. jubatus* Nobili, 1903 (Fig. 3.1). Similarly, drawing on their morphological association to *D. pallescens* Whitlegge, 1897, around 8 species of the "*pallescens* group" (McLaughlin & Cente, 2002; Asakura & Godwin, 2006; Asakura, 2020) can be placed as near relatives of *Isocheles* Stimpson, 1858 and *Loxopagurus* Forest, 1964 (Fig. 3.1). *Diogenes mixtus* Lanchester, 1902 provides an example of a species with a multispinose or “serrate” (Asakura & Tachikawa, 2010) intercalary process, a character it shares with the generic type species *D. miles*, among others. This morphological link between *D. miles* and *D. mixtus* provides a tentative expectation that a revised scope for Diogenidae might need to be restricted to Diogenidae Clade 2, primarily those hermit crab species most closely related to *Ciliopagurus* Forest, 1995 and *Calcinus* Dana, 1851.

Based on the consideration of combined evidence from the three tree topologies generated for this study, many Diogenidae Clade 1 Group A genetic subdivisions show significant bootstrap support at one or more levels of taxonomic sampling (Table 3.4). Although a subdivision consistent with Diogenidae Clade 1 Subclade 1a sensu Craig & Felder (in preparation) is supported across all three phylogenetic iterations of the present study, a genetic break is observed among those Subclade 1a taxa. When coupled with morphological discrepancies between taxa across that break, the previously defined Subclade 1a can be tentatively subdivided into Group A Clade 1 (A1) and Group A Clade 2 (A2). Species presently considered part of the *Paguristes tortugae* Schmitt, 1933 complex are distributed between A1 and A2 such that neither clade individually is directly analogous to the complex as it is commonly diagnosed (Provenzano & Rice, 1961; McLaughlin & Provenzano, 1974). Species designated herein as A1 taxa include the *P. tortugae* complex constituents genetically closest to *P. tortugae; P.* nr. *tortugae*, *A. hewatti* Wass, 1963, and *P. hernancortezi* McLaughlin & Provenzano, 1974. CladeSpeculatively, A1 lacks significant bootstrap support overall (Table 3.4), but segregation of the component taxa from those of A2 could assist in the development of putative diagnostic criteria for the core *P. tortugae* complex. Tentatively, A1 can be diagnosed by a small suite of characters including: short setae on the antennal flagellum, a well-developed brood pouch that is subquadrate to subovate in shape, and banded or spotted eyestalks.

The present molecular analyses support *P. anomalus* Bouvier, 1918, *A. tudgei* Lemaitre & Felder, 2012, and *Pseudopaguristes invisisacculus* McLaughlin & Provenzano, 1974, as close allies of A1, sharing with those taxa dense setation on the thoracic appendages, short setae on the antennal flagellum, and an acute rostrum exceeding lateral projections. They differ in potentially diagnostic ways however, having eyestalks with somewhat swollen bases and blue (in whole or in part) head appendages that lack distinct spots, bands, or stripes (Craig & Felder, in preparation). Although the diagnostic significance of brood pouch presence and shape above the species level in Diogenidae Clade 1 remains relatively unexplored, all genetically confirmed constituents of A2 either lack brood pouches entirely (*A. anomalus* and *A. tudgei*), or exhibit a greatly reduced, subtriangular brood pouch (*P. invisisacculus*). In consideration of these morphological discrepancies, as well as consistent phylogenetic support across this study (Table 3.4) and in previous work (Bracken-Grissom *et al*., 2013; Craig & Felder, in preparation), the present study considers these species distinct from A1 while withholding any conclusion regarding the taxonomic significance of this subdivision.

The present study lacks genetic data for a broad subset of the *Paguristes* species from the western Atlantic. Among those missing taxa are several species that have been attributed to the *Paguristes tortugae* complex, or are hypothetical allies as determined by various authors based primarily on the dense setation of their thoracic appendages and presence in western Atlantic waters (McLaughlin & Provenzano, 1974; Campos & Sanchez, 1995; Ayon-Parente & Hendrickx, 2016; Lima & Santana, 2017). Some such taxa include *P. scarabinoi* Lima & Santana, 2017, *P. angustithecus* McLaughlin & Provenzano, 1974, *P. werdingi*

Campos & Sanchez, 1995, *P. zebra* Campos & Sanchez, 1995, and potentially *P. espectacioni* Ayon-Parente & Hendrickx, 2016. Disregarding its eastern Pacific distribution, *A. espectacioni*, a species with remarkable similarity to *A. tudgei* (Ayon-Parente & Hendrickx, 2016), could be speculatively considered an A2 ally based on the putative diagnosis of A2 put forth herein. Other candidate constituents for A2 include individuals denoted as "*P. anhuacus*" by Westervelt (1967), for which the morphology and color described is similar to those of A2 constituents. However, care must be taken when considering "*P. anhuacus*", as Westervelt's account (1967) equates his collections of that taxon with *P. anahuacus* Glassell, 1938, a species showing morphological inconsistencies when compared with Westervelt's record and with our Clade A2 (Glassell, 1938; Westervelt, 1967; Haig, 1970). Most recently, it was hypothesized that the specimens of Westervelt (1967) may more appropriately be attributed to *A. lemaitrei* (Ayon-Parente & Hendrickx, 2012), a likely Clade 9 ally.

Clear arguments can be made for the consideration of some western Atlantic *Paguristes*, *Areopaguristes*, and *Pseudopaguristes* species as either A1 or A2 constituents, but the proposition of constituency in either clade remains questionable for some taxa. Though they are most likely firmly within Diogenidae Clade 1 owing to the possession of external gonopods in males, *Paguristes angustithecus* and *P. scarabinoi* are two species that remain difficult to classify further. Their constituency in the *P. tortugae* complex has been questioned previously on morphological grounds (Craig & Felder, in preparation), and that criticism holds in the face of our speculative morphological diagnoses of clade A1 and clade A2.

In all analyses presented herein, A1+A2 is allied with the well-supported A3 (Table

3.4), showing a significantly supported relationship in Tree 1 (Fig. 3.1). In the present genetic data set, A3 includes two named specimens, one of *P. planatus* A. Milne-Edwards & Bouvier, 1893 and one of *P. inconstans* McLaughlin & Provenzano, 1975, as well as two specimens from Curaçao noted in the field as potentially new species. We find that both specimens from Curaçao are genetically indistinguishable from *P. inconstans*, a taxon initially described based on material from Cuba (Fig. 3.2). The genetic affinity of *P. inconstans* for *P. planatus* is indisputable across our analyses (Table 3.4), but the presence of A3 in close phylogenetic proximity to the *P. tortugae* complex is unexpected and somewhat suspect. Although diagnostic morphological characters proposed for A1 and A2 have yet to be rigorously evaluated across western Atlantic *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*, applying the tentative criteria derived herein to *Paguristes planatus* and *P. inconstans* does little to urge the incorporation of A3 into either A1 or A2. Both *P. planatus* and *P. inconstans* possess a brood pouch, as do constituents of A1, but the two A3 species lack the fringe of setae, banded eyestalks, armed telson, and, in the case of *P. planatus*, a well-developed rostrum.

In two of the analyses herein, one additional individual identified as *P. inconstans* is recovered in Group B as a close genetic relative of *P. spinipes* A. Milne-Edwards, 1880 and *P. triangulatus* A. Milne-Edwards & Bouvier, 1893 (Figs 3.1, 3.2). *Paguristes planatus* is most frequently said to resemble the genetically confirmed Group B taxa *P. spinipes* and *P. moorei* Benedict, 1901 (McLaughlin & Provenzano, 1975), along with morphologically similar species such as *P. depressus* Stimpson, 1859 (A. Milne-Edwards & Bouvier, 1893), and *P. holguinensis* Majon-Cabeza, Garcia Raso & Martinez-Iglesias, 2002. Such discrepancies in the present analyses indicate that A3 requires more extensive morphological and genetic evaluation before any definitive conclusions can be drawn about its constituency, phylogenetic placement, or taxonomic significance.

Clades A1–A3 form one of the three major divisions of Group A, with A4 and A5 forming the second, and A6–A9 the third. Based on trees inferred herein, A4 and A5 are close genetic allies and quite distant from other Group A clades (Figs 3.1, 3.2). Clade A4 is herein considered a single genetic unit based primarily on its persistence across tree topologies and significant bootstrap support in all analyses for which representative data is included (Table 3.4). Across analyses, four species are genetically indicated as constituents of A4, with *A. ngochoae* Rahayu, 2005 close to *A. michelae* Rahayu, 2005, and *P. gamianus* H. Milne Edwards, 1836, sister to *P. agulhasensis* Forest, 1954. *Paguristes gamianus* and *P. agulhasensis* are thought to be endemic to South Africa (Kensley, 1981), and despite the absence of additional South African taxa in the present genetic data set, genetic evidence from a complimentary barcoding study supports extending the scope of A4 to *P. barnardi* Forest, 1954, a taxon denoted *P.* aff. *agulhasensis*, and as many as 3 more putative species assignable to *Paguristes* (Landschoff & Gouws, 2018). Such conclusions are supported by existing morphological evaluations of *P. gamianus* and *P. barnardi* that discuss the two species as morphologically similar to *P. agulhasensis* and *P. macrotrichus* Forest, 1954 (Forest 1954). In the aforementioned barcoding study, Landschoff & Gouws (2018) closely ally *P. gamianus* with two non-*Paguristes* taxa, *A. engyops* (Barnard, 1947) and a putative species assignable to *Pseudopaguristes* by present diagnosis. The putative *Pseudopaguristes* species of Landschoff & Gouws (2018) remains unpublished and thus unavailable for comment herein, but there are multiple discrepancies between *A. engyops* as figured by Barnard (1950) and our clade A4. In particular, the setation of the ambulatory appendages, distinctive “flask-shaped” eyestalks, medially curving antennal acicles, and ocular acicles with nearly adjacent mesial borders, are not consistent with the morphology of the other species genetically confirmed or postulated herein to be constituents of A4.

The second pair of A4 species is *A. ngochoae* and *A. michelae*, from the western Pacific. Previous accounts have proposed other *Paguristes* and *Areopaguristes* species as A4 realatives, including *A. orbis* Komai, 2009, *A. taenia* Komai, 1999, *A. breviantennatus,* Rahayu 2005, *A. japonicus* Miyake, 1961, *A. hirsutimanus* (Kobjakova, 1971), and *A. setosus* (Miyake, 1961; Komai, 1999, 2009; Rahayu, 2005; Asakura, 2006). Morphological commonalities provide support for the alliance of *A. ngochoae, A. michelae,* and *A. breviantennatus*, but a close resemblance of *A. breviantennatus* to *A. hirsutimanus* or *A. japonicus* is less evident. In overall morphology, A. *hirsutimanus* and *A. japonicus* do not conform exactly to one another, but both have antennal flagella bearing short, dense setae (Miyake, 1961; Asakura, 2006). This configuration differs substantially from that described for our other genetically confirmed A4 taxa, instead resembling more closely the *A. hummi* (Wass, 1955) complex of Clade A9 (Table 3.4) or a pair of *Paguristes* species from the western Atlantic previously discussed herein as potentially peripheral members of A1, *P. angustithecus* and *P. scarabinoi*.

The conservative nature of some clade assignments made by the present work reflects corresponding low bootstrap support values obtained for those clades under phylogenetic analysis. The tentative separation of A5 from A4 is one example of this (Figs 3.1, 3.2). The sister clade of A4, A5 is comprised three currently unassigned *Paguristes* specimens from the waters surrounding Curaçao. Field identifications initially suggested that these three A5 individuals may belong to two distinct putative species, but morphological examination and genetic analysis of more individuals from each putative species is necessary to confirm this. Above the species level, future studies can further segregate A4 from A5 by combining more inclusive genetic sampling across projected A4 allies with extensive morphological evaluation of unassigned species from Curaçao.

In our analysis, Clade A6 includes the western Atlantic *A. oxyophthalmus* Holthuis, 1959 and several eastern Pacific cognates genetically segregated into three clusters. As a single phylogenetic unit, A6 shows significant bootstrap support across all levels of taxonomic sampling (Table 3.4). Genetically confirmed Clade A6 constituents show high levels of morphological similarity, with the antennular peduncles well exceeding the ocular peduncles, corneas tapered, ocular acicles simple and well separated, and 12 pairs of biserial gills. Most notably, genetically confirmed constituents of A6 lack an epipod at the base of maxilliped 1. This character was observed by Ayon-Parente & Hendrickx (2015) for *A. oxyophthalmus* and *A. praedator* Glassell, 1937 and subsequently incorporated into the overall generic diagnosis for *Areopaguristes* with little consideration for the morphology of additional *Areopaguristes* species. Our morphological comparisons among *A. oxyophthalmus* specimens, other A6 individuals, and specimens of A1, A2, A4, A8, and A9 *Areopaguristes* species strongly argue that the departure in mouthpart configuration is unique to *Areopaguristes* taxa of A6.

A primary concern of the present work is to establish the phylogenetically supported taxonomic scope of the three diogenid genera *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*. To that end, genetic sequences for individuals of the type species of all three genera are included in the present analyses. Among those is *A. setosus*, originally described as *Pagurus setosus* and reassigned subsequently to *Stratiotes* Thomson, 1899, a genus erected to accommodate *Paguristes*-like species with chelipeds closely resembling those of *Diogenes*. Additional constituents of *Stratiotes* at that time included *P. barbatus* Heller, 1862 and *P. subpilosus* Henderson, 1888, a constituency derived without reference to gill formula (Forest *et al*., 2000). *Areopaguristes setosus* is today considered a New Zealand species, but early reports were made of Japanese representatives (Ortmann, 1892), with those reports propagated by later authors (Yokoya, 1933; Makarov, 1935, 1962; Miyake, 1978) despite inconsistencies among descriptions included in those accounts (Forest & McLaughlin, 1998). The original description of *A. setosus* is brief, discussing only that is resembles very closely *A. pilosus* H. Milne Edwards, 1836 in most respects, except that the cheliped is more setose and the dactyl of P3 is more slender in *A. setosus* (H. Milne Edwards, 1848), and that the two differ in bathymetric range. Additional historical context for *A. setosus* and its treatment in the literature are well summarized elsewhere, (Forest & McLaughlin, 1998, Forest *et al*., 2000), although the redescriptions included in those accounts of both *A. setosus* and *A. pilosus* lack notation of the gill formula for either species (Forest & McLaughlin, 1998).

In the establishment of a modern taxonomy that is congruent with phylogenetic evidence, determination of the taxonomic scope of *Areopaguristes* s.s. is largely dependent on the phylogenetic placement of the generic type, *A. setosus*. In our most taxon-rich analyses, Tree 1 (Fig. 3.1) and Tree 2 (Fig. 3.2), *A. setosus* is sister to *A. pilosus*. These two species are treated herein as Clade A7, and shown to be closely related to Clade A8, a pair of species currently assigned to *Pseudopaguristes* (Table 3.4). The A7 and A8 species pairs are united when representatives of both clades are present in the analysis (Figs 3.1, 3.2) with significant bootstrap support in one instance (Fig. 3.2). Lending insight into the scope of

Areopaguristes s.s., there is a lack of molecular phylogenetic support for a close association between A6 and A7 independent of A8 (Figs 3.1, 3.2). Given a general morphological cohesiveness among A6 constituents and the presence of the first maxilliped epipod for members of A7 and A8, the phylogenetic justification for a segregation of A6 from A7 is supported by morphology.

In a recent emendation to the diagnosis of *Areopaguristes*, *A. praedator* and *A. oxyophthalmus* were considered as constituents of *Areopaguristes* s.s., with morphological characters observed in those species used to broaden the accepted diagnosis of the genus (Ayon-Parente & Hendrickx, 2015). The study presented here includes genetic data from representatives of *A. setosus,* as well as specimens of *A. oxyophthalmus* and its several unnamed Pacific allies. Iterations of our phylogenetic analyses do not recover the *A. oxyophthalmus* clade (A6) as the closest relative of A7, indicating that *A. oxyophthalmus*, and likely the morphologically similar *A. praedator,* are not appropriate proxies for *Areopaguristes* s.s. Morphological evidence supports this assertion, with re-descriptions of holotypes for *A. setosus* and *A. pilosus* specifying that an epipod is indeed present on the first maxilliped of each (Forest & McLaughlin, 1998). Given the combination of genetic and morphological evidence, the suggestion that the diagnosis of *Areopaguristes* be emended to accommodate species lacking an epipod on the first maxilliped should be disregarded. Concurrent with this, findings herein suggest a distinct phylogenetic independence of *A. setosus* from most constituents of *Areopaguristes* s.l. This points to a far more limited scope for *Areopaguristes* s.s. than has previously been asserted.

As close genetic associates of *A. setosus* and *A. pilosus*, Clade A8 species present potential candidates for consideration as constituents of *Areopaguristes* s.s. Constituents of

A8 in the present analysis include *Pseudopaguristes laurentae* (Morgan & Forest, 1991) and *P. monoporus* (Morgan, 1987), two taxa with eight biserial gill pairs that are currently assigned to *Pseudopaguristes* despite substantial deviation of both taxa from the generic type species, *P. janetkae*. In the phylogenetic results of the present study, included *Pseudopaguristes* species fall into one of four genetic units: A1, A2, A8, or Group C (Table 3.4). Clades A1 and A2 are each represented by the western Atlantic species, *P. calliopsis* and *P. invisisacculus* respectively, leaving A8 as the Pacific representatives of *Pseudopaguristes* in Group A. Other *Pseudopaguristes* species not currently available for genetic analysis may be associated with A8 as suggested by morphological comparisons. First among them is *P. maclaughlinae* Rahayu, 2008, a species long acknowledged to be similar to *P. laurentae* in most respects (Rahayu, 2008). *Pseudopaguristes monoporus* is also linked to many other likely Group A species including *P. hians* (Henderson, 1888), *A. perspicax* (Nobili, 1906), and *P. abbreviatus* Dechancé, 1963 by the peculiarity of a single left gonopore in females (Dechancé, 1963; Haig & Ball, 1988; Rahayu, 2005, 2008). Additional *Pseudopaguristes* species are present in our Tree 1 and Tree 2 analyses, being recovered as a third major division of Diogenidae Clade 1, Group C (Table 3.4). Phylogenetically confirmed Group C taxa so far include *P. keukenthali* (de Man, 1902), *P. bicolor* Asakura & Kosuge, 2004, and *P. janetkae*. As discussed subsequently herein, those three species share several morphological characters not exhibited by the *Pseudopaguristes* constituents of A1, A2, or A8.

Establishing the phylogenetic position of *Paguristes weddellii* H. Milne Edwards, 1848 is critical to establishing a firm morphological diagnosis and taxonomic scope for *Paguristes* s.s., a genus that currently includes between 100 and 200 species (WoRMS, 2020;

McLaughlin *et al.*, 2010). Even before the designation of *P*. *hirtus* as the type species of the genus by Stimpson (1858), morphological similarities between *P*. *hirtus* and the previously described *P*. *weddellii* were noted (Kinahan, 1857), although some authors continued to treat the two species separately (Rathbun, 1910). Despite the loss of the holotype specimen of *P. hirtus*, a synonymy was formalized by Haig (1955) based determination by Forest of morphological congruence between the *P*. *weddellii* holotype specimen from Peru and the original accounts by Dana of *P. hirtus* from Chile (1851, 1852). Recent work has questioned this synonymy, asserting that it was formalized based on insufficient evidence and calling for the reassignment of *P. weddellii* to *Tetralobistes* Ayon-Parente & Hendrickx, 2010, a taxon typified by *Tetralobistes bicentenarius* Ayon-Parente & Hendrickx, 2010 (Ayon-Parente & Hendrickx, 2013). From our own observations, the holotype of *P*. *weddellii* is morphologically consistent with the detailed evaluations of Chilean materials by Ayon-Parente & Hendrickx (2013) and the collection locality of that material matches the type locality for *P*. *hirtus*. This strongly suggests that the long-standing synonymy of Haig (1955) should stand and we therefore hesitate to accept the reassignment of *P*. *weddellii* at this time.

In the current molecular data set, a representative of *Paguristes weddellii* is included (CCDB 1809), and our molecular phylogenetic analysis places it in Clade A9 with significant bootstrap support in Tree 2 (Fig. 3.2). Other genetically confirmed constituents of Clade A9 are *Areopaguristes hummi* and *A*. nr. *hummi* from the western Atlantic, along with the as yet unnamed taxa ULLZ 14923, ULLZ 9680 and ULLZ 9693 from the eastern Pacific. The first of these unnamed taxa resembles most closely *P. weddellii* and *Tetralobistes bicentenarius*, although a division of the telson into four posterior lobes is substituted by a broad cleft. Much like ULLZ 14923, ULLZ 9680 and ULLZ 9693 bear remarkable morphological similarities to named taxa from the northern parts of the eastern Tropical Pacific, with individuals of ULLZ 9680 closest to *A. mclaughlinae* Ayon-Parente & Hendrickx, 2006, while individuals of ULLZ 9693 bear more similarity to *A. lemaitrei* Ayon-Parente & Hendrickx, 2012. Across the individuals of A9, several unifying features can be recognized. The chelipeds are equal or subequal in size and of similar armature, the ocular acicles are flushly abutted along their mesial margins with serrated lateral margins, the rostrum is greatly reduced or obsolete. In females, the brood pouch and first pair of pleopods are absent, while male gonopods are paired, stout, and have armed inferior lamellae.

Although sharing these features, *P. weddellii* shows morphological discrepancies in comparison to the remainder of A9. The gill formula of *P. weddellii* counts 13 pairs rather than 12 pairs and the telson of *P. weddellii* is subdivided into four posterior lobes, a character shared with only one other diogenid species so far described, *T. bicentenarius*. Nevertheless, incorporating phylogenetic results with the historical context specifying *P. weddellii* as the senior synonym of *P. hirtus* lays the groundwork for the potential establishment of A9 as a core component of *Paguristes* s.s. should more intensive taxonomic sampling and subsequent genetic analyses continue to support this finding. Despite this uncertainty regarding the status of A9 as *Paguristes* s.s., the genetic framework established herein is sufficient to propose the addition of several other morphologically consistent species to A9, including *A. mclaughlinae*, *A. lemaitrei*, and *A. waldoschmitti* Ayon-Parente & Hendrickx, 2012.

A broad subset of *Paguristes* species are relegated to the second main subdivision of Diogenidae Clade 1. First acknowledged as Subclade 1b in a more abbreviated phylogenetic study aimed at resolving the internal relationships of the *P. tortugae* complex in the western Atlantic (Craig & Felder, in preparation), it is established here as Diogenidae Clade 1, Group

B. Interpretation of the phylogenetic analyses presented herein proposes that Group B is comprised of at least two distinct subclades, though neither shows consistent significant bootstrap support across all tree inferences (Table 3.4). One of these subclades, B2, is so far comprised entirely of two western Pacific species while the other, B1, includes a small suite of western Atlantic species and three Pacific constituents. Clade B1 shows a loose alliance with a pair of western Pacific species, *P. frontalis* H. Milne Edwards, 1836 and *P. acanthomerus* Ortmann, 1892, for which definitive phylogenetic affinity remains elusive (Figs 3.1, 3.2). When these latter two peripherally allied taxa are not considered, taxonomic sampling for B1 is highly biased toward western Atlantic species with right and left chelipeds equal or subequal in size in both sexes. While the internal phylogenetic relationships of B1 are topologically consistent across phylogenetic analyses, most lack bootstrap support above the species level.

In Tree 1 and Tree 2 a few representatives of *Paguristes* from beyond the western Atlantic are included and recovered as members of our proposed Clade B1 (Figs 3.1, 3.2). These species, *P. longirostris* Dana, 1851, *P. eremita* (Linnaeus, 1767), and *P. palythophilus* Ortmann, 1892 tend towards heterochely (Komai, 2001). They are consistent in their phylogenetic affinity for Clade B1 and for one another in all of our molecular analyses, with some genetic separation evident between *P. palythophilus* and the sister-species pair of *P. longirostris*+*P. eremita* (Figs 3.1, 3.2). In both trees in which they are represented, they join B1 on relatively long branches. Although long branches can represent many artifacts in a phylogeny (Som, 2015), one potential explanation is that these three taxa are representatives of a currently undersampled taxonomic group of heterochelous species, a speculation that can best be resolved through future work inclusive of more heterochelous species.

In the present study, Clade B2 is so far comprised of two West Pacific hermit crab species, *Paguristes jalur* Morgan, 1992 and *P. runyannae* Haig & Ball, 1988. Our designation of *P. jalur*+*P. runyannae* as the second component of Group B is prompted by the topologies of both Tree 1 and Tree 2, although the relationship between B1 and B2 does not show significant bs support in either analysis (Table 3.4). In support of this, species united in the molecular phylogenetic analysis as constituents of B2 have been regarded as highly morphologically similar to *P. acanthomerus* Ortmann, 1892 (Osawa & Takeda, 2002), a taxon found sister to the significantly supported B2 and whose phylogenetic placement closely follows that of B2 across analyses (Figs 3.1, 3.2). Still, lack of significant bs support for a direct alliance between *P. acanthomerus* and *P. jalur* + *P. runyannae*, coupled with the long terminal branch of *P. acanthomerus*, suggests that *P. acanthomerus* may be a singleton representative of a third drastically under sampled Group B clade (Som, 2015). Thus, the combined findings of Tree 1 and Tree 2 analyses with respect to B2 urge caution when considering the constituency, morphological diagnosis, or geographic scope for either of the Group B subdivisions defined herein.

Hermit crab species currently assigned to the genus *Pseudopaguristes* can be found in A1, A2, A8, and Group C, four clades recovered in all trees inferred by the present study. Since the establishment of *Pseudopaguristes* (McLaughlin, 2002), the generic diagnosis has been emended to accommodate the absence of the enlarged right cheliped in males, as well as a wide variety of configurations of gonopores and other external reproductive structures for both males and females, resulting in a generic diagnosis largely reliant on gill formula (Rahayu, 2005). By application of this extensively emended generic diagnosis the genus has grown to include around 25 species (McLaughlin *et al*., 2010; WoRMS, 2020) that are suggested by this study and others to be polyphyletic (Bracken-Grissom *et al*., 2013; Craig & Felder, in preparation).

As referenced in previous discussion of A8, Group C as genetically represented herein encompasses three species, *P. bicolor*, *P. keukenthali*, and the generic type, *P. janetkae*. Although there are some morphological discrepancies among the three, they share some novel characters that are encompassed by the current diagnosis of *Pseudopaguristes* but are not found in any A1, A2, or A8 representatives of the genus. In particular, Group C *Pseudopaguristes* are characterized by a row of unusual paddle-shaped or feather-like setae on the fourth pereopod inferior margin. These distinctive setae are found in all three genetically confirmed Group C taxa as well as *P. bollandi* Asakura & McLaughlin, 2003 and *P. shidarai* Asakura, 2004. Although there are no published accounts of right-handed *P. bicolor* specimens, males of the remaining Group C species, along with *P. bollandi*, and *P. shidarai*, are right-handed. In accordance with the current generic diagnosis, all three genetically confirmed Group C taxa have 8 gill pairs, as do A1, A2, and A8 *Pseudopaguristes*. Unlike the *Pseudopaguristes* taxa of Group A however, the gills of Group C species are quadriserial rather than biserial. Quadriserial gills are not unheard of within Diogenidae Clade 1 (McLaughlin & de Saint Laurent, 1998), but in the current analysis, *Pseudopaguristes* species with quadriserial gills are genetically confined to Group C as supported by morphological comparison among currently accepted *Pseudopaguristes* species included in the genetic data set analyzed herein.

Conclusions

As touched on in previous work (Craig & Felder, in review) the confirmation that *Paguristes*, *Areopaguristes*, and *Pseudopaguristes* are not monophyletic is a reason to propose significant revisions of the three genera. The direction in which that taxonomic revision should proceed is determined by the level of taxonomy ascribed to the genetic clades recovered herein. It was known *a priori* (Bracken-Grissom *et al*., 2013; Craig & Felder, in preparation) that species assigned to *Paguristes* s.l., *Areopaguristes* s.l., and *Pseudopaguristes* s.l. together formed a monophyletic clade across multiple levels of taxonomic sampling. This is confirmed herein (Table 3.3), and given the emergence of this clade as one of three deep divisions of Diogenidae, it is reasonable to think that Diogenidae Clade 1 be assigned family level status. Whether Diogenidae Clade 2 and Clade 3 entail the same treatment is largely dependent on the outcomes of studies similar to this one that focus on the numerous genera projected to be constituents of those clades. Investigations into the phylogenetic underpinnings of other currently recognized families such as Paguridae and Lithodidae must likewise be deferred to future studies of appropriate scope.

For genetic clades with significant bootstrap support in one or more analyses and some preliminary diagnostic characters (Table 3.4), it is perhaps reasonable to assign generic level status. Our analyses derive as many as 9 genetic clades across Group A and at least 2 clades in Group B. As was discussed for Group A, segregation of these genetic clades from one another is supported by morphology in some cases. In the case of *Areopaguristes*, genetic evidence separates A6 and A7+A8, encouraging the establishment of a new genus for A6 with morphological support provided by the character of the missing epipod on the first maxilliped. There is little morphologically to link A7 and A8, thus potentially restricting *Areopaguristes* s.s. to *A. setosus* and *A. pilosus* for the time being (A7).

Regarding the establishment of *Paguristes* s.s., genetic support for *P*. *weddellii* as a constituent of A9 is provided by Tree 2 (Fig. 3.2). Bootstrap support for that alliance is relatively weak (Table 3.4), but the species is morphologically similar to *A. hummi* and associated *Areopaguristes* spp. in overall setation of the carapace and a reduction of the rostrum, along with commonalities in the shape and orientation of the ocular acicles. Despite this, we urge a conservative approach as many potential allies of *P. weddellii*, especially some from the eastern Pacific, are not yet included in the molecular phylogenetic analysis. Addition of *A. waldoschmitti*, *A. lemaitrei*, and *T. bicentenarius* to the genetic data set is absolutely critical for solidification of the scope, constituency, and morphological diagnosis of *Paguristes* s.s.

An important point is raised by our proposition to drastically restrict the scope of *Paguristes* s.s., *Areopaguristes* s.s., and *Pseudopaguristes* s.s.to the limited constituencies suggested herein by molecular phylogenetic analyses and morphological comparissons. To some degree, the number of genetic clades and the accompanying phylogenetic distances among them that emerged in our analyses was unanticipated. One consequence of this is that, in the present work, taxonomic sampling is not spread evenly among the 11 genetic clades comprising *Paguristes* s.l., *Areopaguristes* s.l., and *Pseudopaguristes* s.l. It is possible that these gaps in taxon sampling have given rise to artifacts whereby some genetically distinguishable lineages appear depauperate of species when they are, in fact, quite speciose. As initiated herein, continued proposition of morphological allies for each of these clades will illustrate that many genetic subunits are more speciose than can be demonstrated by the currently available molecular data. The continued accumulation of DNA sequence data for paguroid taxa is necessary for the expansion of phylogenetic analyses to aid in the development of a taxonomic framework reflective of the evolutionary replationships among hermit and king crab species.

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Table 3.1. Voucher specimens used for ML phylogenetic inferences, showing catalog number, collection locality, and NCBI GenBank accession numbers for partial sequences of H3, 12S mtDNA, and 16S mtDNA

Taxon Name	Catalog No.	Country: Locality	Accession Number H3 / 12S / 16S
Albuneidae			
Albunea gibbesii	ULLZ 7376/USNM 1541769	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	KF182698 / KF182373 / KF182558
Lepidopa dexterae	ULLZ 4867/USNM 1540594	Belize: Stann Creek, northwestern Caribbean	KF182704 / KF182375 / KF182561
Diogenidae			
Areopaguristes hewatti	ULLZ 6861/USNM 1543164	USA: Texas, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes hewatti	ULLZ 6876/USNM 1542683	USA: Texas, northwestern Gulf of Mexico	KF182733 / KF182377 / KF182535
Areopaguristes hewatti	ULLZ 7710/USNM 1543169	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Areopaguristes hewatti	ULLZ 7133/USNM 1542127	USA: Texas, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes hewatti	ULLZ 7134/USNM 1542128	USA: Texas, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes hummi	ULLZ 6880/USNM 1542630	USA: Texas, northwestern Gulf of Mexico	KF182730 / KF182379 / KF182541
Areopaguristes hummi	ULLZ 6926/USNM 1541590	USA: Florida, Fort Pierce, western Atlantic	KF182731 / KF182380 / KF182542
Areopaguristes hummi	ULLZ 13232/USNM 1546831	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes hummi	ULLZ 14571/USNM 1547704	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes nr. *hummi*	ULLZ 15009/USNM 1548225	Panama: Bocas del Toro, southwestern Caribbean	pending / pending / pending
Areopagrusites michelae	EBISCO-DW2618	Southwestern Pacific	- / - / pending
Areopaguristes ngochoae	EBISCO-DW2634	Southwestern Pacific	- / - / pending
Areopaguristes ngochoae	EBISCO-DW2513	Southwestern Pacific	- / - / pending
Areopaguristes oxyophthalmus	ULLZ 11006/USNM 1545553	USA: Sackett Bank, northeastern Gulf of Mexico	- / pending / pending
Areopaguristes oxyophthalmus	ULLZ 11054/USNM 1545565	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / -
Areopaguristes oxyophthalmus	ULLZ 10859/USNM 1545362	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Areopaguristes	ULLZ 13746/USNM	USA: Louisiana,	pending / pending /

oxyophthalmus	1547232	northwestern Gulf of Mexico	pending
Areopaguristes nr. *Oxyophthalmus*	ULLZ 14926/USNM 1548050	Panama: near Isla Cañas, northeastern Pacific	pending / pending / pending
Areopaguristes nr. *oxyophthalmus*	ULLZ 9676/USNM 1544504	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes nr. *oxyophthalmus*	ULLZ 9692/USNM 1544519	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes pilosus	NIWA 28030	New Zealand: western coast, Tasman Sea	- / - / pending
Areopaguristes setosus	NIWA 38019	southwestern Pacific	- / - / pending
Areopaguristes setosus	NIWA 29946	southwestern Pacific	- / - / pending
Areopaguristes tudgei	ULLZ 12530/USNM 1546477	Belize: Carrie Bow Cay, northwestern Caribbean	- / pending / pending
Areopaguristes tudgei	ULLZ 12576/USNM 1547127	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Areopaguristes tudgei	ULLZ 16498	Belize: Carrie Bow Cay, northwestern Caribbean	pending / - / pending
Areopaguristes tudgei	ULLZ 16505/USNM 1550441	Belize: Carrie Bow Cay, northwestern Caribbean	pending / - / pending
Areopaguristes sp.	ULLZ 9380/USNM 1544293	Costa Rica: Gulf of Papagayo, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9674/USNM 1544502	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9675/USNM 1544503	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9676/USNM 1544504	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9678/USNM 1544506	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9680/USNM 1544508	Panama: east of Isla Los Venaditos, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9688/USNM 1544516	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9691/USNM 1544518	Panama: east of Isla Los Venaditos, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9692/USNM 1544519	Panama: west of Isla Cébaco, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 9693/USNM 1544520	Panama: east of Isla Los Venaditos, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 14921/USNM 1548565	Panama: Panama Bay, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 14922/USNM 1548044	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 14923/USNM 1548046	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Areopaguristes sp.	ULLZ 14925/USNM 1548049	Panama: near Isla Cañas, northeastern Pacific	pending / pending / pending
Bathynarius anomalus	USNM 1297334	Curaçao: southeastern Caribbean	pending / pending / pending
Birgus latro	KC 6694	unavailable	KF182696 / KF182421 /

			KF182532
Birgus latro	NIWA 32328	south central Pacific	- / - / HQ380270
Calcinus laevimanus	UF 008445	USA: Wake Island, north central Pacific	FJ620424 / - / FJ620175
Calcinus laevimanus	UF 005426	Mascarene Islands: Reunion Island, western Indian Ocean	FJ620423 / - / FJ620174
Calcinus laevimanus	ULLZ 10120/USNM 1544830	French Polynesia: Manihi Atoll, southern central Pacific	KF182691 / KF182426 / -
Calcinus laevimanus	NTOU A01100	Taiwan: western Pacific	KJ133080 / KJ132385 / KJ132524
Calcinus obscurus	ULLZ 14924/USNM 1548047	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Calcinus obscurus	ULLZ 14920/USNM 1548043	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Calcinus obscurus	UF 008359	Panama: Perlas Island, northeastern Pacific	
Calcinus tibicen	ULLZ 8528/USNM 1543755	USA: Florida, Fort Pierce, western Atlantic	pending / pending / pending
Calcinus tibicen	ULLZ 9973/USNM 1544616	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Calcinus tibicen	ULLZ 12528/USNM 1546374	Belize: Southwater Cay, northwestern Caribbean	pending / pending / pending
Calcinus tibicen	ULLZ 16499 / USNM 1550387	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Calcinus tibicen	ULLZ 11755/USNM 1545944	Belize: Carrie Bow Cay, northwestern Caribbean	- / pending / pending
Calcinus sp.	UF 020715	Juan de Nova Island: Mozambique Channel, western Indian Ocean	pending / pending / pending
Ciliopagurus galzini	UF 001339	French Polynesia: Rangiroa Atoll, southern central Pacific	- / - / EU334654
Ciliopagurus hawaiiensis	H296 (Poupin & Malay 2009)	USA: Hawaii, French Frigate Shoals, northern central Pacific	- / - / EU334655
Ciliopagurus strigatus	UF 007115	Japan: Okinawa, Ie Island, northwestern Pacific	- / - / EU334650
Ciliopagurus strigatus	UF 008771	USA: Hawaii, Oahu Island, northern central Pacific	- / - / EU334649
Ciliopagurus tricolor	MNHN 7760	unavailable	- / - / EU334647
Ciliopagurus tricolor	UF 005422	Mascarene Islands: Reunion Island, western Indian Ocean	- / - / EU334648
Ciliopagurus vakovako	MNHN 5901	unavailable	- / - / EU334651
Ciliopagurus vakovako	MNHN 5898	unavailable	- / - / EU334652
Clibanarius albidigitus	unavailable	Panama: Panama City, northeastern Pacific	- / - / AF425323
Clibanarius antillensis	ULLZ 9433/USNM 1544313	USA: Florida, Fort Pierce, western Atlantic	KF182693 / KF182424 / KF182529
Clibanarius antillensis	CCDB 2651	Brazil: São Paulo State, southwestern Atlantic	- / - / MF490154
Clibanarius corallinus	ULLZ 10121/USNM 1544831	French Polynesia: Tuamotu Archipelago, southern Pacific	KF182694 / KF182423 / KF182528

Clibanarius vittatus	ULLZ 4781/USNM 1540545	USA: Florida, northeastern Gulf of Mexico	KF182692 / KF182422 / KF182527
Clibanarius vittatus	CCDB 1185	USA: Texas, northwestern Gulf of Mexico	- / - / JN671527
Clabanarius vittatus	CCDB 2907	Brazil: Bahia State, Ilhéus, southwestern Atlantic	- / - / JN671524
Coenobita clypeatus	ULLZ 9968/USNM 1544612	Belize: Carrie Bow Cay, northwestern Caribbean	KF182695 / KF182420 / KF182531
Coenobita compressus		northeastern Pacific	- / - / AF436059
Coenobita perlatus	MNHN IU200816162	New Caledonia: Chesterfield Island, western Pacific	HQ241557 / HQ241501 / HQ241512
Dardanus fucosus	ULLZ 7122/USNM 1542512	USA: Texas, northwestern Gulf of Mexico	- / KF182430 / KF182586
Dardanus fucosus	UF 013307	USA: Florida, Fort Pierce, northwestern Atlantic	- / pending / pending
Dardanus insignis	CCDB 774	Brazil: São Paulo State, Caraguatatuba, southwestern Atlantic	- / - / DQ369943
Dardanus insignis	ULLZ 7964/USNM 1543301	USA: Florida, northeastern Gulf of Mexico	- / KF182429 / -
Dardanus insignis	USNM 1297351	Curaçao: southeastern Caribbean	pending / pending / pending
Dardanus venosus	ULLZ 6711/USNM 1541655	USA: Florida, northeastern Gulf of Mexico	KF182697 / KF182428 / KF182533
Dardanus venosus	USNM 1297404	Curaçao: southeastern Caribbean	
Dardanus venosus	CCDB 766	Brazil: São Paulo State, Ubatuba, southwestern Atlantic	- / - / DQ369944
Dardanus sp.	ULLZ 9694/USNM 1544521	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Dardanus sp.	ULLZ 9486/USNM 1535468	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Diogenes fasciatus	ZRC 2016.0364	western Pacific	- / - / pending
Diogenes jubatus	ZRC 2016.0356	unavailable	- / - / pending
Diogenes jubatus	ZRC 2016.0355	unavailable	- / - / pending
Diogenes mixtus	ZRC 2016.0362	South China Sea	- / - / pending
Diogenes pallescens	UF 013977	Madagascar: Nosy Be, western Indian Ocean	- / - / pending
Isocheles pilosus	unavailable	Northeastern Pacific	- / - / AF436057
Isocheles sawayi	CCDB 308	Venezuela: Margarita Island, southeastern Caribbean	- / - / DQ369937
Isocheles sawayi	CCDB 302	Brazil: São Paulo State, Ubatuba, southwestern Atlantic	- / - / DQ369938
Isocheles wurdemanni	ULLZ 3890	USA: Texas, northwestern Gulf of Mexico	- / - / DQ369936
Isocheles wurdemanni	ULLZ 5683/USNM 1541095	USA: Texas, northwestern Gulf of Mexico	- / KF182425 / KF182530
Loxopagurus loxochelis	CCDB 765	Brazil: São Paulo State, Ubatuba, southwestern Atlantic	- / - / DQ369939

Paguristes acanthomerus	UF 029439	Taiwan: Yilan County, northwestern Pacific	pending / pending / pending
Paguristes agulhasensis	SA_PA2	South Africa: southeastern Atlantic	- / pending / pending
Paguristes anomalus	ULLZ 6747/USNM 1541930	Offshore: south central Gulf of Mexico	pending / pending / pending
Paguristes anomalus	ULLZ 7536/USNM 1543121	Mexico: Yucatan Peninsula,: southwestern Gulf of Mexico	pending / pending / pending
Paguristes anomalus	ULLZ 14495/USNM 1547686	Dutch Antilles: Saba Bank, northeastern Caribbean	pending / pending / pending
Paguristes cadenati	ULLZ 15922	Curaçao: Director’s Bay, southeastern Caribbean	- / pending / pending
Paguristes cadenati	ULLZ 7624/USNM 1543238	Offshore: south central Gulf of Mexico	- / pending / pending
Paguristes cadenati	UF 4602	Virgin Islands: Saint John’s, northeastern Caribbean	- / pending / pending
Paguristes cadenati	ULLZ 7043/USNM 1541826	Mexico: off Yucatan Peninsula, southwestern Gulf of Mexico	- / - / pending
Paguristes eremita	CCDB 1800	Portugal: Almería, Alboran Sea	- / - / FJ869140
Paguristes frontalis	UF 019016	Australia: South Australia, eastern Indian Ocean	- / pending / pending
Paguristes gamianus	SA_PG10	South Africa: southeastern Atlantic	- / - / pending
Paguristes grayi	ULLZ 9963/USNM 1544609	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Paguristes grayi	ULLZ 9967/USNM 1544611	Belize: Carrie Bow Cay, northwestern Caribbean	- / pending / pending
Paguristes grayi	ULLZ 11744/USNM 1545936	Panama: Zapatillas Island, southwestern Caribbean	KF182728 / KF182382 / KF182537
Paguristes grayi	ULLZ 12533/USNM 1546377	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Paguristes grayi	ULLZ 16335 / USNM 1549572	British Virgin Islands: northeastern Caribbean	- / pending / pending
Paguristes hernancortezi	ULLZ 6783/USNM 1541958	USA: Louisiana, northwestern Gulf of Mexico	- / - / pending
Paguristes hernancortezi	ULLZ 8574/USNM 1543776	USA: Louisiana, north central Gulf of Mexico	pending / - / pending
Paguristes hernancortezi	ULLZ 14044/USNM 1547432	USA: Louisiana, north central Gulf of Mexico	- / pending / pending
Paguristes hernancortezi	ULLZ 16085/USNM 1618808	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Paguristes inconstans	USNM 1297248	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes inconstans	USNM 1297254	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes jalur	ZRC 2016.0357	unavailable	- / - / pending
Paguristes jalur	UF 6515	Philippines: Luzon, Bolinao, South China Sea	- / pending / pending
Paguristes jalur	UF 005709	Northern Mariana Islands: Maug Island, western Pacific	pending / pending / -
Paguristes longirostris	ZRC 2000.0791	Thailand: Gulf of Thailand	- / - / pending
Paguristes moorei	ULLZ 10860/USNM 1545363	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending

Paguristes moorei	ULLZ 14050/USNM 1547438	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Paguristes moorei	ULLZ 15917	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes moorei	USNM 1297281	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes moorei	USNM 1297282	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes moorei	USNM 1622333	Curaçao: southeastern Caribbean	
Paguristes moorei	ULLZ 8172/USNM 1543433	USA: northeastern Gulf of Mexico	pending / pending / pending
Paguristes palythophilus	UF 034667	Taiwan: Yilan, East China Sea	- / pending / pending
Paguristes palythophilus	ZRC 2016.0367	South China Sea	- / - / pending
Paguristes planatus.	ULLZ 15920/USNM 1618807	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes planatus	USNM 1297344	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes planatus	USNM 1622332	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes puncticeps	ULLZ 6801/USNM 1541861	Mexico: Campeche, southwestern Gulf of Mexico	KF182727 / KF182383 / KF182538
Paguristes puncticeps	ULLZ 6728/USNM 1541944	Mexico: off Yucatan Peninsula, southwestern Gulf of Mexico	pending / pending / pending
Paguristes puncticeps	ULLZ 8271/USNM 1543851	USA: Sackett Bank, northeastern Gulf of Mexico	pending / pending / pending
Paguristes puncticeps	ULLZ 11742/USNM 1545934	Panama: Zapatillas Island, southwestern Caribbean	pending / pending / pending
Paguristes puncticeps	ULLZ 13331/USNM 1546875	Panama: Bocas del Toro, southwestern Caribbean	pending / pending / pending
Paguristes puncticeps	ULLZ 14301/USNM 1547659	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Paguristes runyannae	ZRC.2011.0136	South China Sea	- / - / pending
Paguristes sericeus	ULLZ 6525/USNM 1541664	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Paguristes sericeus	ULLZ 7118/USNM 1541753	Mexico: off Yucatan Peninsula, southwestern Gulf of Mexico	pending / pending / pending
Paguristes seriseus	ULLZ 7531/USNM 1543119	Mexico: off Yucatan Peninsula, south central Gulf of Mexico	- / pending / pending
Paguristes sericeus	ULLZ 12828/USNM 1546948	USA: Louisiana, north central Gulf of Mexico	- / pending / pending
Paguristes sericeus	ULLZ 15864/USNM 1549514	USA: Dry Tortugas, southeastern Gulf of Mexico	- / pending / pending
Paguristes spinipes	ULLZ 14487/USNM 1547681	Dutch Antilles: Saba Bank, northeastern Caribbean	pending / pending / pending
Paguristes spinipes	ULLZ 15928	Curaçao: southeastern Caribbean	- / pending / pending
Paguristes spinipes	USNM 1297376	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes spinipes	USNM 1297338	Curaçao: southeastern Caribbean	pending / pending / pending

Paguristes spinipes	CURI 12142	Curaçao: southeastern Caribbean	pending / - / pending
Paguristes tortugae	ULLZ 4783/USNM 1540547	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Paguristes tortugae	ULLZ 6800/USNM 1541858	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	KF182732 / KF182676 / KF182534
Paguristes tortugae	ULLZ 7064/USNM 1541855	Mexico: off Yucatan Peninsula, southwestern Gulf of Mexico	pending / - / pending
Paguristes tortugae	ULLZ 11148/USNM 1545610	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Paguristes tortugae	ULLZ 16485	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Paguristes tortugae	UF 032577	French Antilles: northeastern Caribbean	pending / pending / pending
Paguristes nr. *tortugae*	ULLZ 4782/USNM 1540546	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Paguristes nr. *tortugae*	ULLZ 8578/USNM 1543769	USA: Florida, northeastern Gulf of Mexico	pending / - / -
Paguristes nr. tortugae	ULLZ 11743/USNM 1545935	Panama: Bocas del Toro, southwestern Caribbean	pending / - / pending
Paguristes nr. *tortugae*	ULLZ 13330/USNM 1546874	Panama: Bocas del Toro, southwestern Caribbean	pending / pending / -
Paguristes nr. *tortugae*	ULLZ 13665/USNM 1547026	Panama: Bocas del Toro, southwestern Caribbean	pending / pending / pending
Paguristes nr. *tortugae*	ULLZ 16975	Panama: Bocas del Toro, southwestern Caribbean	pending / - / -
Paguristes nr. *tortugae*	UF 015380	USA: Florida, Tampa Bay, northeastern Gulf of Mexico	pending / pending / pending
Paguristes triangulatus	ULLZ 6892/USNM 1541875	Mexico: Yucatan Peninsula: southwestern Gulf of Mexico	pending / pending / pending
Paguristes triangulatus	ULLZ 7719/USNM 1543174	USA: northeastern Gulf of Mexico	pending / pending / pending
Paguristes triangulatus	ULLZ 8250/USNM 1543418	USA: northeastern Gulf of Mexico	pending / pending / pending
Paguristes ulreyi	ULLZ 17363	Mexico: Baja, San Felipe, Gulf of California	pending / pending / pending
Paguristes wassi	ULLZ 7326/USNM 1541761	Mexico: Yucatan Peninsula,: southwestern Gulf of Mexico	pending / pending / pending
Paguristes wassi	ULLZ 9371/USNM 1544277	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	pending / pending / pending
Paguristes wassi	UF 031881	French Antilles: northeastern Caribbean	pending / pending / pending
Paguristes weddellii	CCDB 1809	Chile: Valdavia, southeastern Pacific	- / - / FJ869141
Paguristes sp.	ULLZ 9683/USNM 1544511	Panama: east from Coiba Islnad, northeastern Pacific	pending / pending / -
Paguristes sp.	UF 006532	Philippines: Luzon, Baligasay, South China Sea	pending / - / -
Paguristes sp.	ULLZ 14919/USNM 1548041	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Paguristes sp.	ULLZ 14922/USNM 1548044	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Paguristes sp.	ULLZ 15256/USNM 1548292	Panama: Perlas Island, northeastern Pacific	pending / pending / pending

Paguristes sp.	USNM 1297247	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1297274	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622332	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622333	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622334	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622335	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622336	Curaçao: southeastern Caribbean	pending / pending / pending
Paguristes sp.	USNM 1622337	Curaçao: southeastern Caribbean	pending / pending / pending
Petrochirus diogenes	ULLZ 8129/USNM 1543383	USA: Florida, northeastern Gulf of Mexico	KF182719 / KF182427
Petrochirus diogenes	CCDB 776	Brazil: São Paulo State, Ubatuba, southwestern Atlantic	- / - / DQ369942
Pseudopaguristes calliopsis	CCDB 768	Brazil: São Paulo State, Ubatuba, southwestern Atlantic	- / - / DQ369932
Pseudopaguristes invisisacculus	ULLZ 11115/USNM 1545589	Belize: Twin Cays, northwestern Caribbean	pending / pending / pending
Pseudopaguristes janetkae	UF 007316	USA: Mariana Islands, Guam, western Pacific	- / - / pending
Pseudopaguristes keukenthali	UF 009667	Papua New Guinea: Bismarck Archipelago, southwestern Pacific	- / pending / pending
Pseudopaguristes laurentae	UF 016855	Australia: Lizard Island, southwestern Pacific	pending / - / pending
Pseudopaguristes laurentae	UF 016878	Australia: Lizard Island, southwestern Pacific	pending / pending / pending
Pseudopaguristes monoporus	ZRC 2013.1761	South China Sea	
Strigopagurus poupini	H323 (Poupin & Malay 2009)	USA: Hawaii, French Frigate Shoals, central northern Pacific	- / - / EU334656
Epialtidae			
Chorilia longipes	KC3089	Japan: Okinoshima, northwestern Pacific	EU921052 / EU920889 / EU920919
Galatheidae			
Galathea rostrata	ULLZ 7681/USNM 1532702	USA: Florida, northeastern Gulf of Mexico	KF182684 / KF182388 / KF182523
Hippidae			
Emerita talpoida	ULLZ 9434/USNM 1544314	USA: Florida, Fort Pierce, western Atlantic	KF182702 / KF182419 / KF182557
Leucoseiidae			
Praebebalia longidactyla	KC3086	unavailable	EU921071 / EU920904 / EU920931
Lithodidae			

Cryptolithodes sp.	ULLZ 11844/USNM 1545963	USA: Alaska, Sitka Sound, northeastern Pacific	KF182669 / KF182402 / KF182574
Glyptolithodes cristatipes	(Zaklan & Cunningham, unpub.)	USA: California, Redondo Canyon, northeastern Pacific	AF425326
Lithodes santolla	ULLZ 11875/USNM 1546000	Patagonia	KF182671 / KF182400 / KF182572
Lithodes santolla	isolate 211 (Hall *et al.* unpub.)	unavailable	- / - / HM020955
Lithodes santolla	KAClisa	unavailable	DQ079679 / AY595546 / AY595927
Lithodes santolla	isolate 213 (Hall *et al.* unpublished)	unavailable	- / - / HM020956
Lopholithodes mandtii	(Zaklan & Cunningham unpub.)	Canada: British Columbia, northeastern Pacific	- / - / AF425333
Paralithodes brevipes	(Zaklan & Cunningham, unpub.)	Japan: Habomai, Nemura, northwestern Pacific	- / - / AF425337
Paralithodes camtschaticus	(Zaklan & Cunningham, unpub.)	Japan: Kitamiyamato Bank, northwestern Pacific	- / - / AF425338
Paralomis sp.	KC3506	unavailable	KF182666 / KF182399 / KF182571
Phyllolithodes papillosus	(Zaklan & Cunningham unpub.)	Canada: British Columbia, northeastern Pacific	- / - / AF425340
Munidae			
Munida iris	ULLZ 8366/USNM 1532757	USA: Florida, southeastern Gulf of Mexico	KF182685 / KF182389 / KF182521
Munida pusilla	ULLZ 8322/USNM 1543605	USA: northwestern Gulf of Mexico	KF182686 / KF182390 / KF182522
Munidopsidae			
Munidopsis rostrata	KC 3102	unavailable	- / EU920898 / -
Paguridae			
Agaricochirus alexandri	ULLZ 6891/USNM 1541873	Mexico: off Yucatan Peninsula, southwestern Gulf of Mexico	KF182672 / KF182404 / -
Agaricochirus boletifer	UF 007017	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Agaricochirus sp.	USNM 1297342	Curaçao: southeastern Caribbean	MK830040 / MK848215 / MK848231
Agaricochirus sp.	ULLZ 7970/USNM 1543305	USA: Florida, northeastern Gulf of Mexico	pending / pending / -
Anisopagurus pygmaeus	UF 032391	French Antilles: Saint Martin, northeastern Caribbean	- / pending / -
Bythiopagurus macrocolus	NIWA 29632	New Zealand: Gothic Hill, southwestern Pacific	- / - / EU821532
Catapaguroides foresti	UF 034424	USA: Mariana Islands, Guam Island, western Pacific	pending / pending / pending
Catapaguroides hooveri	UF 008033	USA: Hawaii, Maui Island, northern central Pacific	- / pending / pending
Catapaguroides hooveri	UF 020158	USA: Hawaii, Maui Island, northern central Pacific	pending / pending / pending
Catapaguroides microps	ULLZ 13984/USNM 1547399	USA: Louisiana, northeastern Gulf of Mexico	pending / pending / pending
Catapagurus sp.	USNM 1297635	Curaçao: southeastern Caribbean	pending / pending / pending

Catapagurus tuberculosus	UF 007192	Japan: Okinawa, Ie Island, northwestern Pacific	pending / pending / pending
Discorsopagurus schmitti	UF 031338	USA: Washington, San Juan Island, northeastern Pacific	Pending / pending / pending
Discorsopagurus schmitti	UF 31228	USA: Washington, Shaw Island, northeastern Pacific	pending / pending / pending
Elassochiruss tenuimanus	ULLZ 11871/USNM 1545996	USA: Alaska, Glacier Bay, northeastern Pacific	pending / pending / pending
Elassochirus tenuimanus	UF 031291	USA: Washington, Skipjack Island, northeastern Pacific	- / pending / pending
Enneobranchus flavioculatus	ULLZ 12293/USNM 1534598	USA: Offshore, northern Gulf of Mexico	pending / pending / pending
Enneobranchus sp.	ULLZ 10934/USNM 1545375	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Goreopagurus piercei	ULLZ 8570/USNM 1543775	USA: Alabama, northeastern Gulf of Mexico	KF182670 / KF182416 / -
Goreopagurus piecei	ULLZ 14582/USNM 1547712	USA: Texas, northwestern Gulf of Mexico	pending / pending / pending
Iridopagurus caribbensis	ULLZ 13528/USNM 1547269	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Iridopagurus caribbensis	ULLZ 6759/USNM 1541909	Mexico: off Yucatan Peninsula, southwestern Gulf of mexico	- / - / KF182580
Iridopagurus reticulatus	ULLZ 14632/USNM 1547813	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Iridopagurus sp.	ULLZ 12561/USNM 1546397	Belize: Southwater Cay, northwestern Caribbean	pending / pending / pending
Labidochirus splendescens	UF 019861	USA: Washington, San Juan Island, northeastern Pacific	- / pending / pending
Labidochirus splendescens	UF 038422	USA: Washington, San Juan Island, northeastern Pacific	pending / pending / pending
Manucomplanus longimanus	ULLZ 9444/USNM 1544321	Costa Rica: northeastern Pacific	pending / pending / pending
Manucomplanus ungulatus	ULLZ 14401/USNM 1547537	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Manucomplanus ungulatus	UF 028476	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Micropagurus acantholepis	ULLZ 12443/USNM 1546357	Australia: Tasmania, eastern Indian Ocean	pending / pending / pending
Micropagurus devaneyi	UF 015328	USA: Hawaii, French Frigate Shoals, north central Pacific	pending / pending / pending
Micropagurus devaneyi	UF 012297	USA: Hawaii, French Frigate Shoals, north central Pacific	pending / pending / pending
Nematopagurus fagei	ULLZ 8948/USNM 1544360	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Nematopagurus spinulosensoris	UF 029707	Taiwan: East China Sea	pending / pending / pending
Ostraconotus spatulipes	ULLZ 15843/USNM 1549510	USA: Florida, northeastern Gulf of Mexico	- / pending / -
Paguritta vittata	UF 026913	Japan: Okinawa, Ryukyu Islands, northwestern Pacific	pending / pending / pending
Paguritta sp.	UF 025242	Australia: Heron Island, southwestern Pacific	pending / pending / pending
Pagurixus laevimanus	UF 026609	USA: Mariana Islands, Guam Island, western Pacific	pending / pending / pending

Pagurixus maorus	UF 035291	French Polynesia: Tuamotu Archipelago, southern central Pacific	pending / pending / pending
Pagurixus nomurai	UF 016966	Australia: Lizard Island, southwestern Pacific	pending / pending / pending
Pagurodofleinia doerderleini	UF 029448	Taiwan: Daxi fishport, East China Sea	pending / pending / pending
Pagurus anachoretus	UF 039803	Spain: Girona Province, Balearic Sea	pending / pending / pending
Pagurus beringanus	UF 034552	USA: Washington, San Juan Island, northeastern Pacific	pending / pending / pending
Pagurus bernhardus	UF 039773	England: Plymouth, northeastern Atlantic	pending / pending / pending
Pagurus bernhardus	JSDUK 146	unavailable	- / - / JN107608
Pagurus bernhardus	(Zaklan & Cunningham unpub.)	France: Roscoff, northeastern Atlantic	- / - / AF425335
Pagurus brevidactylus	ULLZ 7065/USNM 1541856	Yucatan Peninsula: southwestern Gulf of Mexico	KF182679 / KF182407 / KF182563
Pagurus brevidactylus	ULLZ 7842/USNM 1543314	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Pagurus brevidactylus	ULLZ 7976/USNM 1543308	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Pagurus bullisi	ULLZ 11056/USNM 1545566	USA: Louisiana, northwestern Gulf of Mexico	KF182668 / KF182410 / KF182568
Pagurus bullisi	ULLZ 14475/USNM 1547757	USA: Louisiana, north central Gulf of Mexico	pending / pending / pending
Pagurus carolinensis	ULLZ 8576/USNM 1543770	USA: Florida, northeastern Gulf of Mexico	In the tree twice in two different places
Pagurus carolinensis	ULLZ 7836/USNM 1543227	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Pagurus carolinensis	ULLZ 7720/USNM 1543175	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Pagurus comptus	CCDB 1702	Argentina: southwestern Atlantic	- / - / FJ869144
Pagurus comptus	CCDB 1751	Chile: Bahía Gente Grande, Strait of Magellan	- / - / FJ869142
Pagurus criniticornus	ULLZ 13482/USNM 1546940	Panama: Boco del Drago, southwestern Caribbean	pending / pending / pending
Pagurus criniticornus	ULLZ 13714/USNM 1547072	Panama: Boco del Drago, southwestern Caribbean	pending / pending / pending
Pagurus criniticornus	CCDB 779	Brazil: São Paulo State, Ubatuba, southwestern Atlantic	- / - / DQ369947
Pagurus dalli	UF 034568	USA: Washington, SanJuan Island, northeastern Pacific	pending / pending / pending
Pagurus defensus	ULLZ 14570/USNM 1547703	USA: Louisiana, north central Gulf of Mexico	pending / pending / pending
Pagurus edwardsii	CCDB 2207	Chile: Antofagasta, southeastern Pacific	- / - / FJ869146
Pagurus edwardsii	ULLZ 5670/USNM 1542544	Chile: Antofagasta, Caleta Cobija, southeastern Pacific	pending / pending / pending
Pagurus exilis	CCDB 767	Brazil: São Paulo State, Ubatuba, southwestern Atlantic	- / - / FJ869147
Pagurus filholi	ULLZ 13963/USNM	South Korea: Jeju Island,	pending / pending /

	1547411	northwestern Pacific	pending
Pagurus forceps	CCDB 1806	Chile: Punta de Tralca, southeastern Pacific	- / - / FJ869149
Pagurus forceps	CCDB 2078	Chile: Coquimbo, southeastern Pacific	- / - / FJ869150
Paguristes gladius	ULLZ 5681/USNM 1541094	Mexico: Baja, San Felipe, Gulf of California	pending / pending / pending
Pagurus granosimanus	UF 011958	USA: Washington, San Juan Island northeastern Pacific	pending / pending / pending
Pagurus gymnodactylus	ULLZ 14541/USNM 1547731	USA: Mississippi, northeastern Gulf of Mexico	pending / pending / pending
Pagurus hirtimanus	UF 006993	Japan: Okinawa, Cape Zanpa, northwestern Pacific	pending / pending / pending
Pagurus hirtimanus	UF 027926	Australia: Ningaloo, eastern Indian Ocean	pending / pending / pending
Pagurus hirtimanus	UF 007148	Japan: Okinawa, Seragaki, northwestern Pacific	pending / pending / pending
Pagurus hirtimanus	UF 040210	Saudi Arabia: Yanbu, Red Sea	pending / pending / pending
Pagurus hirtimanus	UF 005960	USA: Mariana Islands, Guam Island, western Pacific	pending / pending / pending
Pagurus hirtimanus	UF 006239	Tuvalu Islands: Funafuti Atoll, southwestern Pacific	pending / pending / pending
Pagurus impressus	UF 034631	USA: North Carolina, northwestern Atlantic	pending / pending / pending
Pagurus kennerleyi	UF 038438	USA: Washington, San Juan Island, northeastern Pacific	pending / pending / pending
Pagurus longicarpus	UF 001067	USA: Florida, Seahorse Key, northeastern Gulf of Mexico	pending / pending / pending
Pagurus maclaughlinae	ULLZ 11975/USNM 1546071	USA: Florida, northeastern Gulf of Mexico	KF182680 / KF182408 / KF182566
Pagurus maclaughlinae	ULLZ 13890/USNM 1547322	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Pagurus maclaughlinae	ULLZ 13889/USNM 1547321	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Pagurus marshi	ULLZ 11110/USNM 1545586	Belize: Twin Cays, northwestern Caribbean	KF182682 / KF182409 / KF182564
Pagurus marshi	ULLZ 9771/USNM 1544591	Belize: Twin Cays, northwestern Caribbean	pending / pending / pending
Pagurus marshi	ULLZ 16501/USNM 1550439	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / -
Pagurus marshi	ULLZ 16520	Belize: Carrie Bow Cay, northwestern Caribbean	- / pending / -
Pagurus ochotensis-	UF 031326	USA: Washington, San Juan Island, northeastern Pacific	pending / pending / pending
Pagurus pollicaris	ULLZ 11954/USNM 1546054	USA: Louisiana, northwestern Gulf of Mexico	KF182737 / KF182403 / JN800550
Pagurus pollicaris	ULLZ 5673/USNM 1541088	USA: Louisiana, northwestern Gulf of Mexico	- / - / FJ869152
Pagurus pollicaris	UF 034642	USA: North Carolina, northwestern Atlantic	pending / pending / pending
Pagurus prideaux	CCDB 1798	Portugal: Almería, Alboran Sea	- / - / FJ869153
Pagurus prideaux	UF 039813	Spain: Girona Province, Balearic Sea	pending / - / pending

Pagurus provenzanoi	ULLZ 9770/USNM 1544590	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Pagurus provenzanoi	ULLZ 14652/USNM 1547849	Belize: Carrie Bow Cay, northwestern Caribbean	pending / pending / pending
Pagurus provenzanoi	MZUSP 13808	Brazil: Santa Caterina State, southwestern Atlantic	- / - / FJ869154
Pagurus “provenzanoi”	ULLZ 9685/USNM 1544513	Panama: Perlas Island, northeastern Pacific	pending / pending / pending
Pagurus “provenzanoi”	ULLZ 9687/USNM 1544515	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Pagurus “provenzanoi”	ULLZ 9690/USNM 1544517	Panama: near Isla Cavada, northeastern Pacific	pending / pending / pending
Pagurus rotundimanus	ULLZ 12765/USNM 1547367	USA: Mississippi, northeastern Gulf of Mexico	pending / pending / pending
Pagurus samuelis	UF 013319	USA: California, northeastern Pacific	pending / - / pending
Pagurus villosus	CCDB 1808	Chile: Valdavia, southeastern Pacific	- / - / FJ869155
Pagurus sp.	ULLZ 9687/USNM 1544515	Panama: east of Coiba Island, northeastern Pacific	pending / pending / pending
Pagurus stimpsoni	ULLZ 16546/USNM 1618809	Belize: Twin Cays, northwestern Caribbean	pending / pending / pending
Phimochirus formani	ULLZ 7685/USNM 1543129	USA: Florida, northeastern Gulf of Mexico	MK830050 / - / MK848221
Phimochirus formani	ULLZ 7847/USNM 1543313	USA: Florida, northeastern Gulf of Mexico	- / pending / pending
Phimochirus formani	ULLZ 14352/USNM 1547566	USA: Florida, northeastern Gulf of Mexico	MK830053 / MK848204 / MK848222
Phimochirus formani	ULLZ 14572/USNM 1547705	USA: Louisiana, northwestern Gulf of Mexico	MK830048 / MK848205 / MK848223
Phimochirus formani	UF 039527	USA: Florida, northeastern Gulf of Mexico	- / pending / -
Phimochirus tunnelli	ULLZ 5789/USNM 1541146	USA: Louisiana, northwestern Gulf of Mexico	MK830051/ MK848206 / MK848224
Phimochirus tunnelli	ULLZ 5814/USNM 1541669	Offshore: southeastern Gulf of Mexico	pending / pending / -
Phimochirus tunnelli	UF 006671	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Phimochirus tunnelli	ULLZ 7825/USNM 1543233	USA: northwestern Gulf of Mexico	MK830052 / MK848208 / MK848225
Phimochirus tunnelli	ULLZ 7973/USNM 1543319	USA: northeastern Gulf of Mexico	KF182678 / KF182415 / KF182578
Phimochirus tunnelli	ULLZ 13837/USNM 1547302	USA: Louisiana, northwestern Gulf of Mexico	- / MK848209 / MK848226
Phimochirus tunnelli	UF 031667	USA: Florida, northeastern Gulf of Mexico	pending / pending / -
Phimochirus operculatus	ULLZ 9917/USNM 1534602	Belize: Carrie Bow Cay, northwestern Caribbean	MK830046 / MK848212 / MK848229
Phimochirus operculatus	UF 026018	USA: Florida, southeastern Gulf of Mexico	pending / pending / pending
Phimochirus randalli	ULLZ 7071/USNM 1541890	Yucatan Peninsula: southwestern Gulf of Mexico	KF182676 / KF182417 / KF182576
Phimochirus randalli	ULLZ 7345/USNM 1541699	Yucatan Peninsula: southwestern Gulf of Mexico	KF182677 / KF182418 / KF182577
Phimochirus venustus	ULLZ 9677/USNM 1544505	Panama: near Isla Cavada, northeastern Pacific	MK830045 / MK848214 / MK848230

Phimochirus cf. *venustus*	ULLZ 9679	Panama: Perlas Island, northeastern Pacific	- / pending / pending
Porcellanopagurus filholi	NIWA 29628	New Zealand: near Chatham Island, southwestern Pacific	- / - / HQ380267
Propagurus obtusifrons	UF 034675	Taiwan: Yilan County, East China Sea	pending / pending / pending
Propagurus obtusifrons	UF 034676	Taiwan: Yilan County, East China Sea	- / pending / pending
Protoniopagurus bioperculatus	USNM 1297246	Curaçao: southeastern Caribbean	pending / pending / pending
Pylopaguridium markhami	ULLZ 6780/USNM 1541901	Mexico: off Yucatan Peninsula, southwestern Gulf of Mexico	- / - / KF182570
Pylopagurus discoidalis	CURI 12107	Curaçao: southeastern Caribbean	pending / pending / -
Pylopagurus discoidalis	ULLZ 14483/USNM 1547761	Dutch Antilles: Saba Bank, northeastern Caribbean	pending / pending / pending
Pylopagurus discoidalis	ULLZ 15835	Curaçao: southeastern Caribbean	- / pending / -
Pylopagurus fimbriata	UF 26648	USA: Mariana Islands, Guam Island, western Pacific	pending / pending / pending
Pylopagurus macgeorgei	ULLZ 7675/USNM 1543124	USA: northwestern Gulf of Mexico	pending / pending / pending
Pylopagurus pustulosa	UF 029441	Taiwan: Daxi fishport, East China Sea	pending / pending / pending
Pylopagurus speciosa	UF 027173	Japan: Okinawa, Ryukyu Islands, northwestern Pacific	pending / pending / pending
Pylopagurus zebra	UF 029366	Taiwan, off Keelung City, East China Sea	pending / pending / pending
Rhodochirus rosaceus	ULLZ 13830/USNM 1547296	USA: Mississippi, northeastern Gulf of Mexico	pending / pending / pending
Solenopagurus lineatus	ULLZ 10861/USNM 1545364	USA: Louisiana, northwestern Gulf of Mexico	pending / pending / pending
Solenopagurus lineatus	ULLZ 13858/USNM 1547320	USA: Louisiana, northwestern Gulf of Mexico	- / pending / pending
Solitariopagurus trullirostris	UF 034683	French Polynesia: Moorea Island, south central Pacific	- / pending / -
Solitariopagurus sp.	UF 035482	French Polynesia: Gambier Islands, south central Pacific	- / pending / pending
Solitariopagurus sp.	UF 035387	French Polynesia: Tuamotu Archipelago, southern central Pacific	- / pending / pending
Spathapagurus collinae	ULLZ 12687/USNM 1546572	Costa Rica: eastern Pacific Ocean	pending / pending / pending
Trichopagurus trichophthalmus	UF 024498	French Polynesia: Moorea Island, south central Pacific	pending / pending / pending
Tomopagurus merimaculosus	ULLZ 9441/USNM 1544315	Costa Rica: eastern Pacific Ocean	KF182673 / KF182411 / KF182567
Tomopagurus sp.	ULLZ 16203/USNM 1549571	USA: Florida, northeastern Gulf of Mexico	pending / pending / pending
Xylopagurus cancellarius	ULLZ 9443/USNM 1544319	Costa Rica: northeastern Pacific	KF182683 / KF182406 / KF182584
Xylopagurus cancellarius	ULLZ 9689/USNM 1544522	Panama: Afuerita Channel, northeastern Pacific	pending / pending / pending
Parapaguridae			

Paragiopagurus pilimanus	USNM 1253320	Curaçao: southeastern Caribbean	pending / pending / pending
Paragiopagurus pilimanus	USNM 1253322	Curaçao: southeastern Caribbean	pending / pending / -
Paragiopagurus pilimanus	USNM 1253317	Curaçao: southeastern Caribbean	pending / pending / -
Sympagurus acinops	ULLZ 11020/USNM 1545560	USA: northwestern Gulf of Mexico	KF182701 / KF182371 / KF182526
Sympagurus dimorphus	NIWA 29594	New Zealand: Morgue Hill, southwestern Pacific	- / - / EU821533
Sympagurus pictus	ULLZ 10849/USNM 1545354	USA: Louisiana, northwestern Gulf of Mexico	- / - / KF182525
Sympagurus pictus	HBG4187	unavailable	- / - / MF197243
Sympagurus sp.	KC 7247	unavailable	- / - / KF182579
Porcellanidae			
Allopetrolisthes spinifrons	ULLZ 5979/USNM 1541241	Chile: Pozo Toyo, southeastern Pacific	KF182714 / KF182398 / KF182550
Allopetrolisthes spinifrons	unavailable	Chile: Las Cruces, southeastern Pacific	- / - / AF260617
Pachycheles pilosus	unavailable	Venezuela: Isla la Tortuga, southeastern Caribbean	- / - / DQ865329
Pachycheles rugimanus	ULLZ 6903/USNM 1541675	USA: Florida, northeastern Gulf of Mexico	KF182705 / KF182392 / KF182543
Petrolisthes armatus	ULLZ 10098/USNM 1544814	USA: Florida, southeastern Gulf of Mexico	KF182708 / KF182396 / KF182549
Petrolisthes galathinus	ULLZ 16965	USA: Texas, northwestern Gulf of Mexico	pending / - / -
Raninidae			
Cosmonotus grayi	KC3092	Japan: Okinoshima, northwestern Pacific	EU921051 / EU920888 / EU920918

Table 3.2. Histone 3 (H3), 12S mtDNA, and 16S mtDNA primers used in this study.

Gene	Primer	Primer Sequence	Annealing Temperatures	Reference
H3 forward	H3af	5' - ATGGCTCTGACCAAGCAGACVGC - 3'		Colgan *et al.* 1998
H3 reverse	H3r	5' - ATATCCTTRGGCATRGTGAC - 3'	50–54°C for 30–60 s	Colgan *et al.* 1998
12S forward	12Sf	5' - GAAACCAGGATTAGATACCC - 3'		Buhay *et al.* 2007
12S reverse	12S1r	5' - AGCGACGGGCGATATGTATAG - 3'	50–54°C for 30–60 s	Buhay *et al.* 2007
16S forward	16S 1472	5' - AGATAGAAACCAACCTGG - 3'		Crandall & Fitzpatrick 1996
16S reverse	16SL2	5' - TGCCTGTTTATCAAAAACAT - 3'		Schubart *et al*. 2002
16S reverse	16Sar	5' - CGCCTGTTTATCAAAAACAT - 3'	50–54°C for 30–60 s	Palumbi *et al*. 1991
16S reverse	16S-CWC-01r	5' - CCGGTTTGAACTCAAATCATGT - 3'		new
16S forward	16S-CWC-01f	5' - TAAAGTCTAGCCTGCCCACT - 3'	52–58°C for 30–60 s	new

Table 3.3. Summary of major genetic subdivisions recovered and their respective constituent genera across the three phylogenetic analyses. The bootstrap value from each analysis is presented for all clades aside from the individual clades Paguridae and Lithodidae where significant internal genetic structure made delineations between the two families tentative. Bootstrap values <50 were considered unsupported and denoted with "–". The symbol "*" denotes that no representatives of the indicated clade were present in the particular analysis.

			Bootstrap Value		
Family/Clade		Constituent Genera	Tree 1	Tree 2	Tree 3
Diogenidae 1		*Paguristes*, *Areopaguristes*, *Pseudopaguristes*	–	51	100
Diogenidae 2		*Calcinus*, *Ciliopagurus*, *Diogenes*, *Isocheles*, *Strigopagurus*, *Loxopagurus*, *Clibanarius*, *Bathynarius*	–	–	63
Diogenidae 3		*Dardanus*, *Petrochirus*	–	–	73
Coenobitidae		*Coenobita*, *Birgus*	99	–	98
Paguridae + Lithodidae			69	52	64
	Paguridae	*Phimochirus*, *Anisopagurus*, *Agaricochirus*, *Protoniopagurus*, *Pylopagurus*, *Manucomplanus*, *Tomopagurus*, *Pagurus*, *Goreopagurus*, *Pylopaguridium*, *Spathapagurus*, *Solenopagurus*, *Labidochirus*, *Elassochirus*, *Paguridofleinia*, *Discorsopagurus*, *Solitariopagurus*, *Nematopagurus*, *Paguritta*, *Propagurus*, *Bythiopagurus*, *Pagurixus*, *Porcellanopagurus*, *Tichopagurus*, *Micropagurus*, *Ostraconotus*, *Catapagurus*, *Iridopagurus*, *Enneobranchus*, *Catapaguroides*			
	Lithodidae	*Paralithodes*, *Phyllolithodes*, *Glyptolithodes*, *Lopholithodes*, *Paralomis*, *Cryptolithodes*, *Lithodes*			
Parapaguridae		*Sympagurus*, *Paragiopagurus*	95	100	*

Table 3.4. Summary of major genetic subdivisions recovered within Diogenidae and their respective constituent genera across the three phylogenetic analyses. Bootstrap values <50 were considered unsupported and denoted with "–". The final column lists general morphological characters that may prove to be of diagnostic utility for the clades presented herein. For analyses marked with "†" *Paguristes weddellii* was not included among taxa in the data set analyzed. The "‡" in the Bootstrap Values column denotes that the indicated clade was not represented in the phylogenetic analysis.

			Bootstrap Value			
Group	Clade	Constituent Species	Tree 1	Tree 2	Tree 3	Potentially Diagnostic Characters
A			–	–	65	
	1	*Paguristes tortugae*, *P.* nr. *tortugae*, *P. ulreyi*, *Areoapguristes hewatti*	–	–	–	Antennal flagellum with short setae; Brood pouch well-developed; Banded or spotted eyestalks;
	2	*Paguristes anomalus*, *A. tudgei*, *Pseudopaguristes invisisacculus*	63	53	82	Brood pouch reduced or absent; Eyestalks with broad bases; Eyestalks without bands, stripes, or spots
	3	*Paguristes planatus*, *P. inconstans*	100	100	100	Unconfirmed
	4	*Areopaguristes michelae*, *A. ngochoae*, *A. agulhasensis*, *A. gamianus*	–	87	‡	Unconfirmed
	5	*Paguristes* sp. (Caribbean)	100	100	100	Unconfirmed
	6	*Areopaguristes oxyophthalmus*, *Areopaguristes* sp. (Pacific)	–	65	97	12 pairs biserial gills*; Maxilliped 1 lacking epipod; Tapering ocular peduncles; Elongate antennular peduncles; Simple, well-separated ocular acicles
	7	*Areopaguristes setosus*, *A. pilosus*	96	99	‡	Unconfirmed
	8	*Pseudopaguristes laurentae*, *P. monoporous*	98	100	‡	8 pairs biserial gills*; Chelipeds equal or subequal in size; Female gonopore unpaired (most)
	9	*Areopaguristes hummi*, *A.* nr. *hummi*, *Areoapguristes* sp. (Pacific), *Paguristes weddellii*†	52†	50	100†	Occular acicles flushly abutted at midline; Rostrum reduced or obsolete; Antennal flagellum short with long setae; Female first pleopods absent
B		*Paguristes grayi*, *P. moorei*, *P. palythophilus*, *P. eremita*, *P. longirostris*, *P. spinipes*, *P. cadenati*, *P. puncticeps*, *P. triangulatus*, *P. erythrops*, *P. sericeus*, *P. wassi*, *P. jalur*, *P. runyannae*	–	–	100	Undetermined

C	*Pseudopaguristes keukenthali*, *P. bicolor*, *P. janetkae*	89	93	‡	8 pairs quadriserial gills*; Heterochelous males (most); Fourth pereopod with feathered setae
Taxa of uncertain affinity	*Paguristes acanthomerus*, *P. frontalis*	–	–	‡	

* Although not diagnostic for *Paguristes*, *Areopaguristes*, or *Pseudopaguristes*, the utility of gill formula for the diagnosis of the genetic clades delineated in the present study is so far unknown

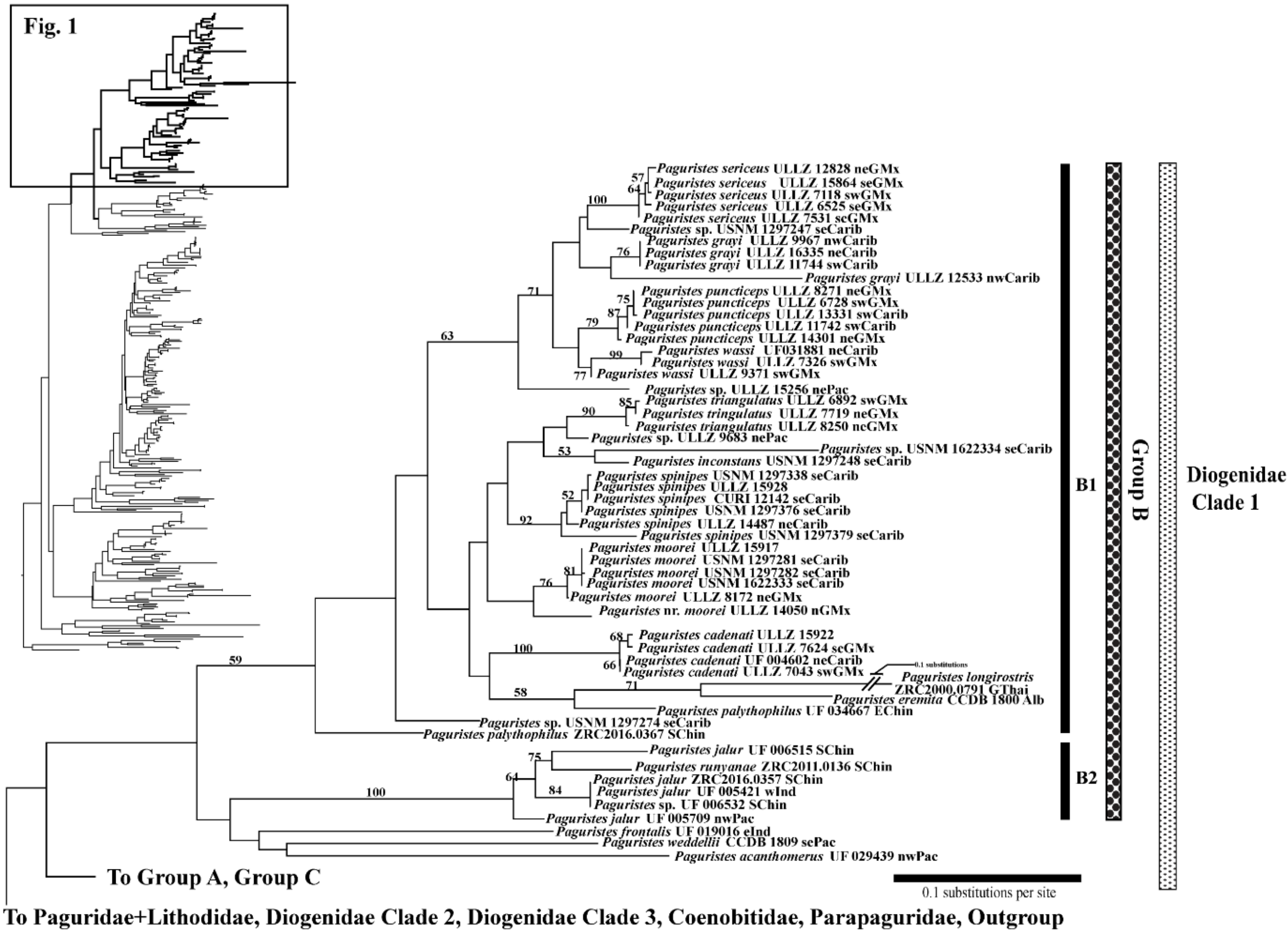


Figure 3.1, continued next page. Tree1: Maximum Likelihood phylogeny (−lnL: 37079.716) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions per site. For branch labels, taxon name is followed by voucher catalog number and abbreviated collection locality (Table 3.1).

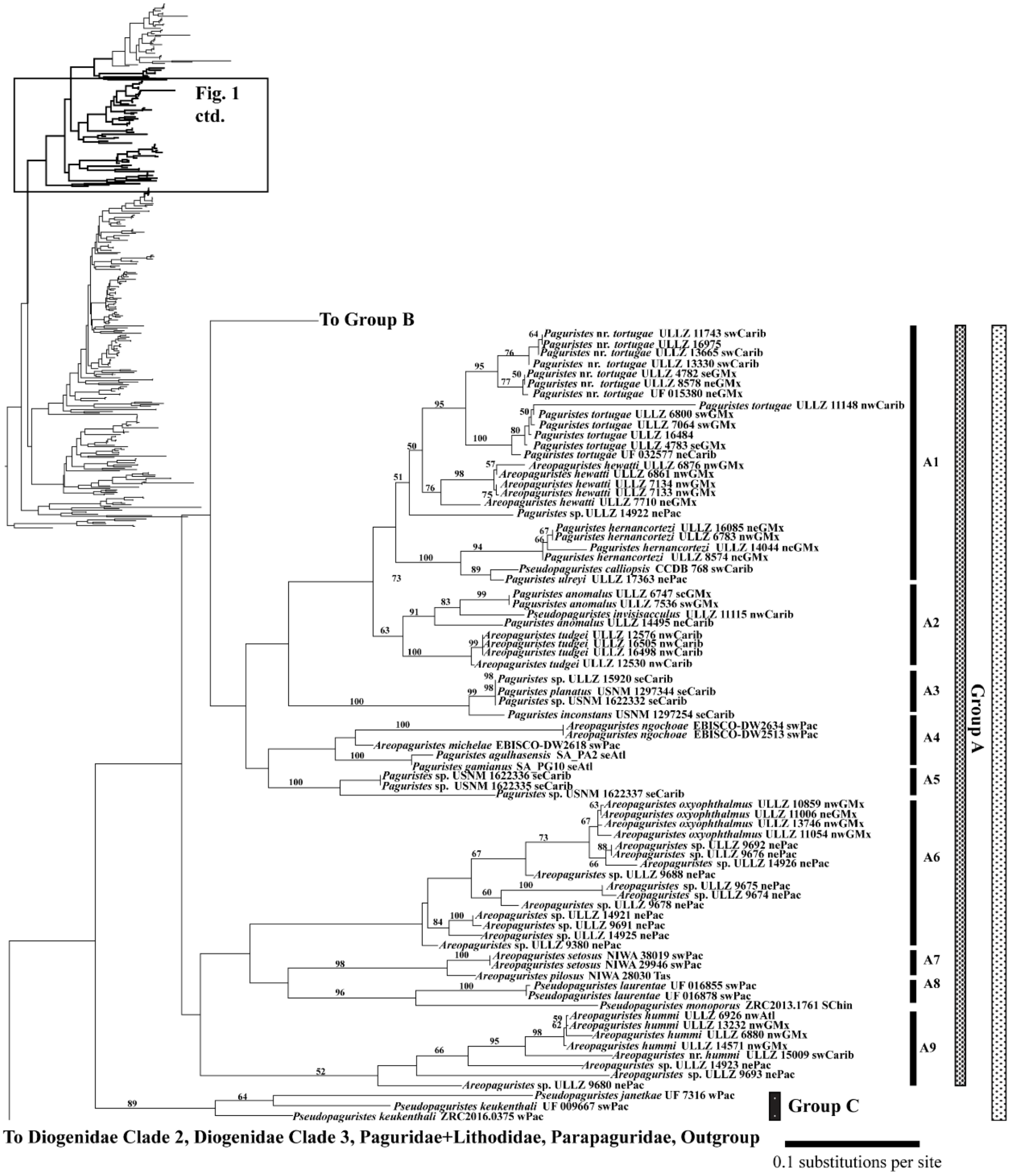


Figure 3.1, continued from previous page. Tree1: Maximum Likelihood phylogeny (−lnL: 37079.716) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions per site. For branch labels, taxon name is followed by voucher catalog number and abbreviated collection locality (Table 3.1).

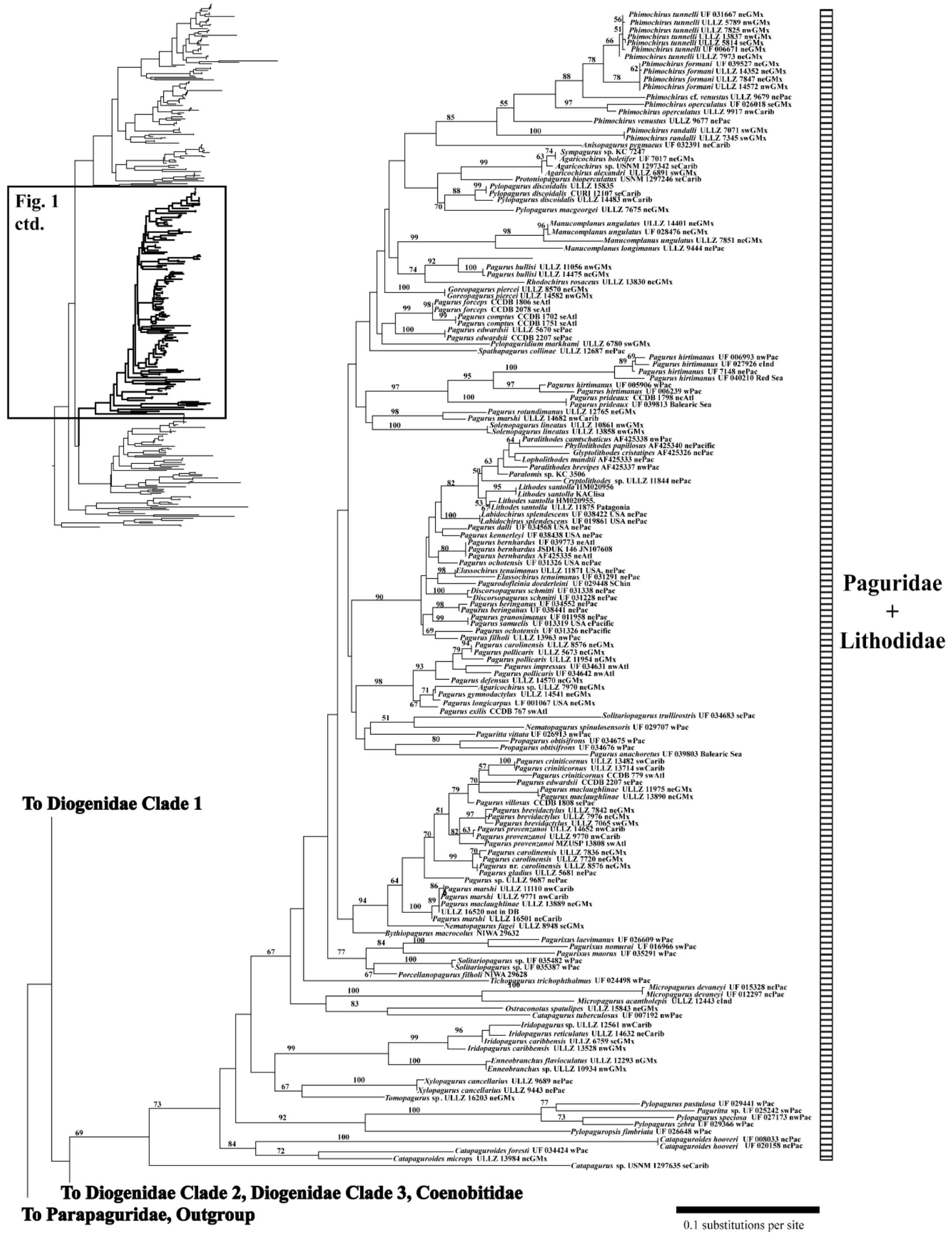


Figure 3.1, continued from previous page. Tree1: Maximum Likelihood phylogeny (−lnL: 37079.716) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions per site. For branch labels, taxon name is followed by voucher catalog number and abbreviated collection locality (Table 3.1).

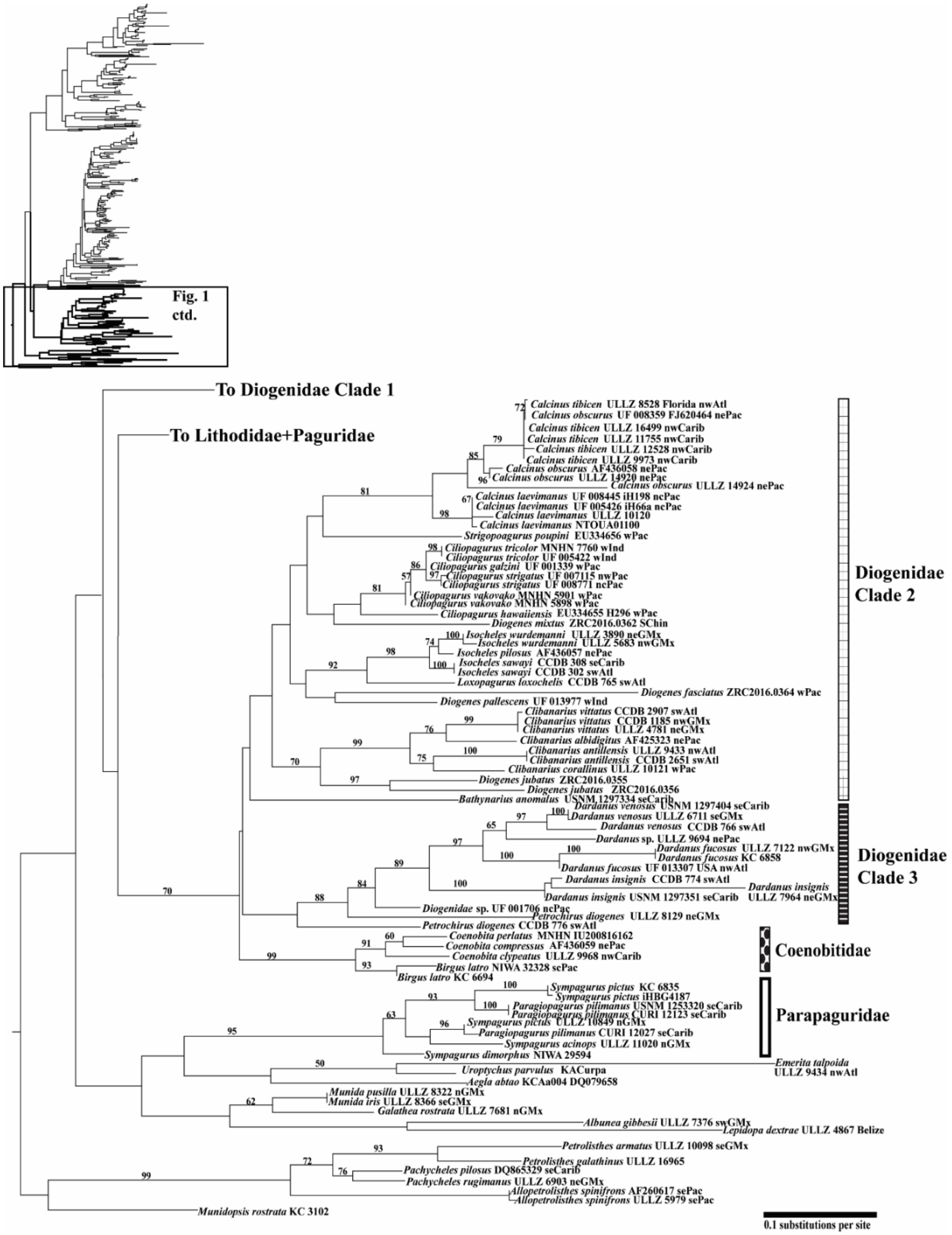


Figure 3.1, continued from previous page. Tree1: Maximum Likelihood phylogeny (−lnL: 37079.716) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions per site. For branch labels, taxon name is followed by voucher catalog number and abbreviated collection locality (Table 3.1).

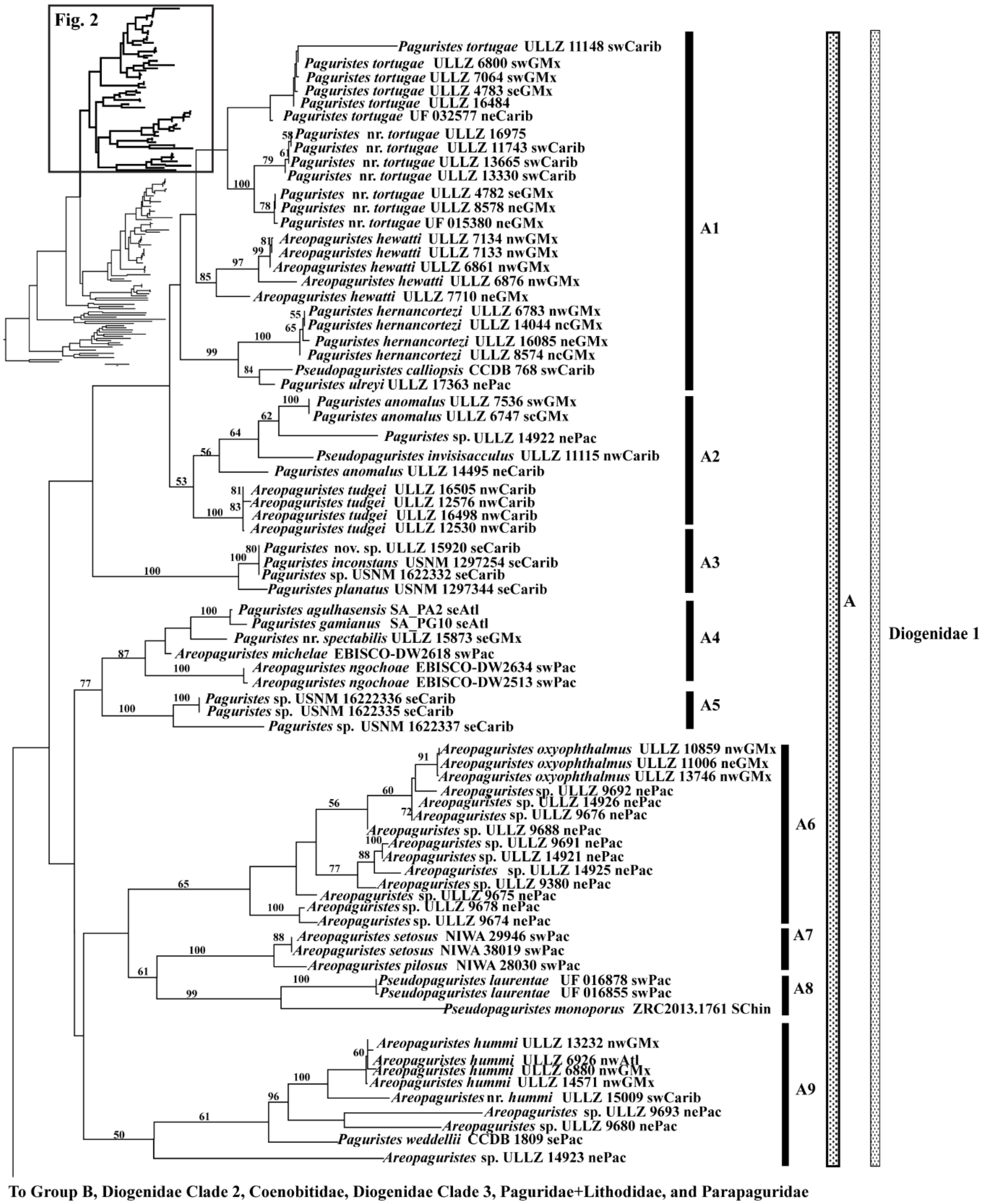
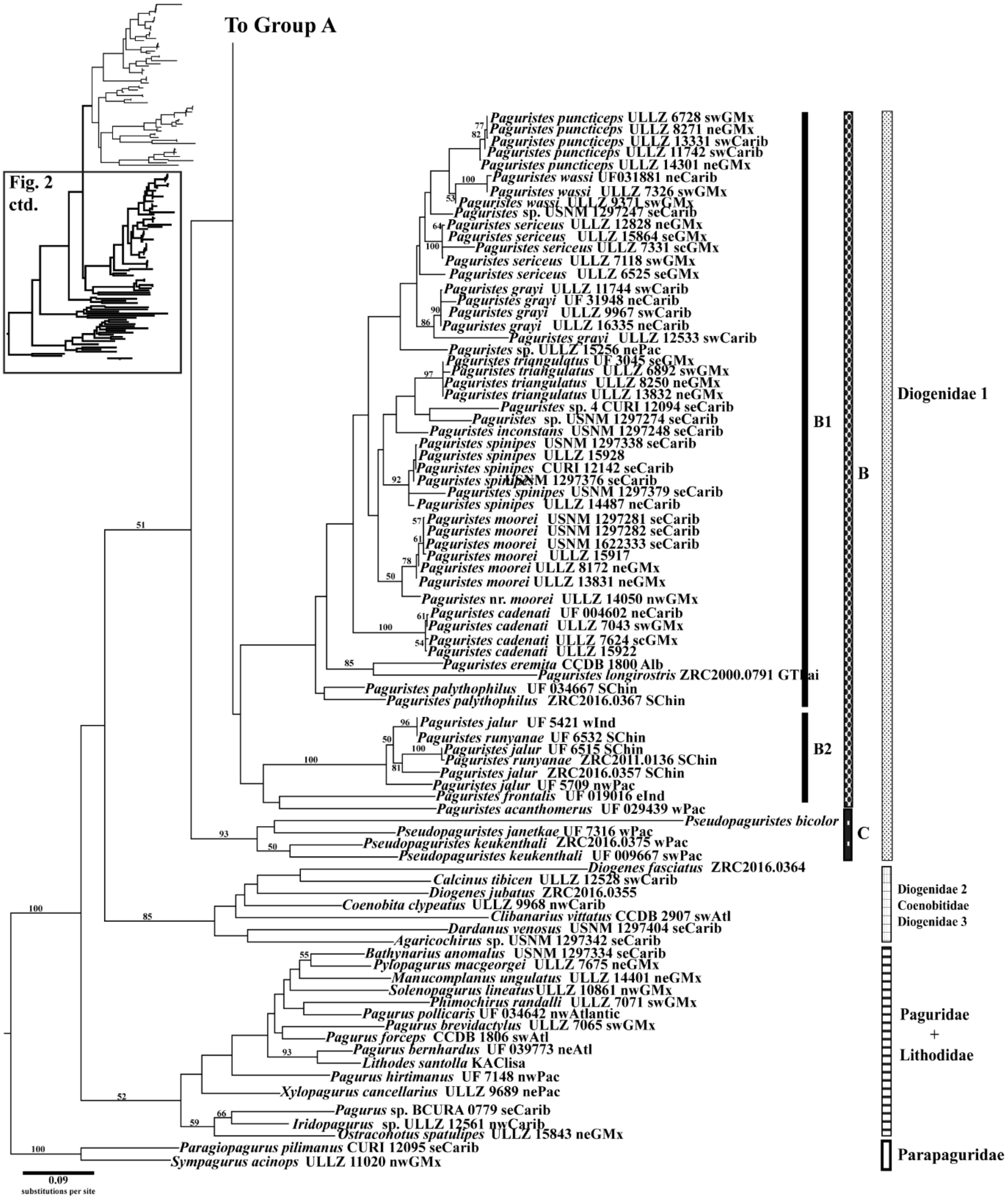


Figure 3.2, continued next page. Tree 2: Maximum Likelihood phylogeny (−lnL: 23101.248) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions per site. For branch labels, taxon name is followed by voucher catalog number and abbreviated collection locality (Table 3.1).



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Craig, Catherine W. Associate of Liberal Arts, Spokane Community College, Spring 2004; Bachelor of Science, Montana State University, Spring 2007; Master of Science, Washington State University, Summer 2011; Doctor of Philosophy, University of Louisiana at Lafayette, Spring 2021
Major: Environmental and Evolutionary Biology
Title of Dissertation: Molecular Phylogenetics of the Hermit Crab Genera PAGURISTES Dana, 1851, AREOPAGURISTES Rahayu, 2005, and PSEUDOPAGURISTES McLaughlin, 2002 (Crustacea: Decapoda: Anomura) with Descriptions of Two New Species
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Abstract

Hermit and king crabs represent a considerable portion of decapod biodiversity, yet the evolutionary relationships among them remain poorly understood. Much of this uncertainty results from intraspecific variation and convergence in morphological characters historically used for diagnosis of species and higher-level taxonomic groupings. The utility of Maximum Likelihood (ML) phylogenetic methods for analyses based on genetic data has been acknowledged by many systematic studies of decapods at a variety of taxonomic levels. This dissertation employed ML phylogenetic analyses based on nuclear and mitochondrial DNA data to elucidate the evolutionary relationships among hermit and king crabs at various levels of taxonomic sampling. The work is presented as a compilation of articles for future publication, the first of which focused on a subset of *Paguristes, Areopaguristes,* and *Pseudopaguristes* species from the western Atlantic. That study demonstrated a lack of monophyly for all three genera and identified two new species previously suggested by morphology. Further results confirmed that color is a key character for species diagnosis and has potential to delineate broader taxonomic subgroups. Morphological descriptions for these new species were provided in the second article of this volume, along with a comparative discussion of potentially allied species. The final article in this volume expanded the number

Paguristes, *Areopaguristes*, and *Pseudopaguristes* species in the phylogenetic analysis and included gene sequences for the type species of the three genera of primary interest were obtained, thereby enabling broader conclusions about the constituency of the genera. Major findings indicated numerous genetic clades within the generic complex, although the taxonomic scope and status of these clades was not definitively determined. Still, many of the clades recovered could be tentatively diagnosed by morphological characters that may prove useful for future taxonomic revisions. Based on such observations, it was suggested that *Paguristes* s.s. may be best represented by those taxa most closely allied with *A. hummi* and morphologically similar Pacific species such as *A. lemaitrei*, and *A. waldoschmitti*. The constituency and affiliation of *Areopaguristes* s.s. remained poorly defined, but phylogenetic outcomes suggested that *Pseudopaguristes* s.s. is composed of species with 8 quadriserial gill pairs and enlarged right chelipeds.

Biographical Sketch

Catherine W. Craig was born in Spokane, Washington, USA in 1982. She received a bachelor's degree in organismal biology from Montana State University in 2007 and a Master of Science in zoology from Washington State University in 2011. In Fall 2011 she enrolled in the doctoral program at the University of Louisiana at Lafayette, completing a Doctor of Philosophy in environmental and evolutionary biology under the supervision of Dr. Darryl L. Felder in Spring 2021.

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