



Molecular phylogenetic analysis of the *Paguristes tortugae* Schmitt, 1933 complex and selected other Paguroidea (Crustacea: Decapoda: Anomura)

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Abstract

Morphological characters, as presently applied to describe members of the *Paguristes tortugae* Schmitt, 1933 species complex, appear to be of limited value in inferring 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. This molecular analysis supported a polyphyletic Diogenidae Ortmann, 1892, although incomplete taxonomic sampling among the genera of Diogenidae limits the utility of this finding for resolving family level relationships. Several hypotheses regarding the evolutionary relationships among hermit crab genera were refuted by the Kishino-Hasegawa (KH), Shimodaira-Hasegawa (SH) and Approximately Unbiased (AU) tree topology tests, among them the hypothesis that *Areopaguristes* 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.

Key words: Diogenidae, 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; Ah Yong *et al.* 2009; 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).

One of the most species-rich genera of diogenid hermit crabs with diverse morphology and coloration as well as global distribution is *Paguristes* Dana, 1851. *Paguristes* is typified by the eastern Pacific species *Paguristes hir-*

tus Dana, 1851, a taxon 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 male pleopods modified as gonopods, 13 pairs of gills, and non-cheliform fourth pereopods (Dana 1851; Forest & McLaughlin 2000; Schweitzer & Feldmann 2001; Rahayu 2005).

In our opinion, two additional diogenid genera, *Pseudopaguristes* McLaughlin, 2002 and *Areopaguristes* Rahayu & McLaughlin, 2010, 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; WoRMS 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*, 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 analyses.

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 *Paguristes tortugae*, *P. hewatti* Wass, 1963, *P. angustithecus* McLaughlin & Provenzano, 1974, *P. perplexus* McLaughlin & Provenzano, 1974, *P. hernancortezii* McLaughlin & Provenzano, 1974, *P. anomalus* Bouvier, 1918, and *P. invisissacculus* 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 *Paguristes 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. invisissacculus* was transferred to the genus *Pseudopaguristes* on the basis of its 8 gill pairs (Rahayu 2005). We question both of these reassignments, especially with their being based solely on gill numbers.

Within the *P. 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; Vrijenhoek 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'Udekem 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), achelatan (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 (Macpherson & 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.* 2018; 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 *P. 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 *P. tortugae* complex, including suspected constituents of the complex that might have instead been assigned to the genera *Areopaguristes* and *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 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 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). 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 and four brachyuran representatives were included in the analysis as outgroups.

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

TABLE 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
<i>Albuneidae</i>			
<i>Albunea gibbesii</i>	ULLZ 7376/USNM 1541769	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	KF182698/KF182373/KF182558
<i>Lepidopa dexterae</i>	ULLZ 4867/USNM 1540594	Belize: Stann Creek, northwestern Caribbean	KF182704/KF182375/KF182561
<i>Calappidae</i>			
<i>Calappa gallus</i>	KC3083	Japan: Shirihama, northwestern Pacific	EU921049/EU920886/EU920916
<i>Diogenidae</i>			
<i>Areopaguristes hewatti</i>	ULLZ 6861/USNM 1543164	USA: Texas, northwestern Gulf of Mexico	KF182735/KF182378/pending
<i>Areopaguristes hewatti</i>	ULLZ 6876/USNM 1542683	USA: Texas, northwestern Gulf of Mexico	KF182733/KF182377/KF182535
<i>Areopaguristes hewatti</i>	ULLZ 7710/USNM 1543169	USA: Florida, northeastern Gulf of Mexico	MW160345/MW160971/MW167179
<i>Areopaguristes hewatti</i>	ULLZ 7133/USNM 1542127	USA: Texas, northwestern Gulf of Mexico	MW160347/MW160994/MW167183
<i>Areopaguristes hewatti</i>	ULLZ 7134/USNM 1542128	USA: Texas, northwestern Gulf of Mexico	MW160346/MW160969/MW167215
<i>Areopaguristes hummi</i>	ULLZ 6880/USNM 1542630	USA: Texas, northwestern Gulf of Mexico	KF182730/KF182379/KF182541
<i>Areopaguristes hummi</i>	ULLZ 6926/USNM 1541590	USA: Florida, Fort Pierce, western Atlantic	KF182731/KF182380/KF182542
<i>Areopaguristes hummi</i>	ULLZ 13232/USNM 1546831	USA: Louisiana, northwestern Gulf of Mexico	MW160337/MW160968/MW167184
<i>Areopaguristes hummi</i>	ULLZ 14571/USNM 1547704	USA: Louisiana, northwestern Gulf of Mexico	MW160336/MW160961/MW167225
<i>Areopaguristes nr. hummi</i>	ULLZ 15009/USNM 1548225	Panama: Bocas del Toro, southwestern Caribbean	MW160335/MW160980/MW167181
<i>Areopaguristes oxyophthalmus</i>	ULLZ 10859/USNM 1545362	USA: Louisiana, northwestern Gulf of Mexico	MW160284/MW160975/MW167193
<i>Areopaguristes oxyophthalmus</i>	ULLZ 13746/USNM 1547232	USA: Louisiana, northwestern Gulf of Mexico	MW160278/MW160973/MW167177
<i>Areopaguristes nr. oxyophthalmus</i>	ULLZ 14926/USNM 1548050	Panama: near Isla Cañas, northeastern Pacific	MW160283/MW160984/MW167252
<i>Areopaguristes nr. oxyophthalmus</i>	ULLZ 9676/USNM 1544504	Panama: Afuerita Channel, northeastern Pacific	MW160281/MW161021/MW167196
<i>Areopaguristes nr. oxyophthalmus</i>	ULLZ 9692/USNM 1544519	Panama: Afuerita Channel, northeastern Pacific	MW160279/MW160991/MW167197
<i>Areopaguristes tudgei</i>	ULLZ 12576/USNM 1547127	Belize: Carrie Bow Cay, northwestern Caribbean	MW160348/MW161008/MW167182
<i>Areopaguristes sp.</i>	ULLZ 9380/USNM 1544293	Costa Rica: Gulf of Papagayo, northeastern Pacific	MW160285/MW160990/MW167234
<i>Areopaguristes sp.</i>	ULLZ 9674/USNM 1544502	Panama: Afuerita Channel, northeastern Pacific	MW160277/MW161036/MW167250
<i>Areopaguristes sp.</i>	ULLZ 9675/USNM 1544503	Panama: Afuerita Channel, northeastern Pacific	MW160276/MW160959/MW167254

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TABLE 1. (Continued)

Taxon Name	Catalog No.	Country: Locality	Accession Number
<i>Areopaguristes</i> sp.	ULLZ 9678/USNM 1544506	Panama: Afuerita Channel, northeastern Pacific	MW160275/MW161005/MW167233
<i>Areopaguristes</i> sp.	ULLZ 9680/USNM 1544508	Panama: east of Isla Los Venaditos, northeastern Pacific	MW160334/MW160988/MW167185
<i>Areopaguristes</i> sp.	ULLZ 9688/USNM 1544516	Panama: Afuerita Channel, northeastern Pacific	MW160280/MW160982/MW167251
<i>Areopaguristes</i> sp.	ULLZ 9691/USNM 1544518	Panama: east of Isla Los Venaditos, northeastern Pacific	MW160282/MW160997/MW167192
<i>Areopaguristes</i> sp.	ULLZ 9693/USNM 1544520	Panama: east of Isla Los Venaditos, northeastern Pacific	MW160327/MW161003/MW167223
<i>Areopaguristes</i> sp.	ULLZ 14921/USNM 1548565	Panama: Panama Bay, northeastern Pacific	MW160287/pending/MW167188
<i>Areopaguristes</i> sp.	ULLZ 14922/USNM 1548044	Panama: Perlas Island, northeastern Pacific	MW160340/MZ442289/MW167236
<i>Areopaguristes</i> sp.	ULLZ 14923/USNM 1548046	Panama: Perlas Island, northeastern Pacific	MW160333/MW160987/MW167208
<i>Areopaguristes</i> sp.	ULLZ 14925/USNM 1548049	Panama: near Isla Cañas, northeastern Pacific	MW160286/MW161000/MW167190
<i>Bathynarius anomalus</i>	USNM 1297334	Curaçao: southeastern Caribbean	MW160288/MW161012/MW167238
<i>Birgus latro</i>	KC 6694	unavailable	KF182696/KF182421/KF182532
<i>Calcinus laevimanus</i>	NTOU A01100	Taiwan: western Pacific	KJ133080/KJ132385/KJ132524
<i>Calcinus obscurus</i>	ULLZ 14924/USNM 1548047	Panama: Perlas Island, northeastern Pacific	MW160293/MW160972/MW167195
<i>Calcinus tibicen</i>	ULLZ 8528/USNM 1543755	USA: Florida, Fort Pierce, western Atlantic	MW160294/MW160967/MW167194
<i>Calcinus tibicen</i>	ULLZ 9973/USNM 1544616	Belize: Carrie Bow Cay, northwestern Caribbean	MW160296/MW160963/MW167249
<i>Calcinus tibicen</i>	ULLZ 12528/USNM 1546374	Belize: Southwater Cay, northwestern Caribbean	MW160292/MW161037/MW167247
<i>Calcinus tibicen</i>	ULLZ 14920/USNM 1548043	Panama: Perlas Island, northeastern Pacific	MW160295/MW161032/MW167198
<i>Calcinus</i> sp.	UF 020715	Juan de Nova Island: Mozambique Channel, Indian Ocean	pending/MW161016/MW167245
<i>Clibanarius antillensis</i>	ULLZ 9433/USNM 1544313	USA: Florida, Fort Pierce, western Atlantic	KF182693/KF182424/KF182529
<i>Clibanarius corallinus</i>	ULLZ 10121/USNM 1544831	French Polynesia: Tuamotu Archipelago, southern Pacific	KF182694/KF182423/KF182528
<i>Clibanarius vittatus</i>	ULLZ 4781/USNM 1540545	USA: Florida, northeastern Gulf of Mexico	KF182692/KF182422/KF182527
<i>Coenobita clypeatus</i>	ULLZ 9968/USNM 1544612	Belize: Carrie Bow Cay, northwestern Caribbean	KF182695/KF182420/KF182531
<i>Coenobita perlatus</i>	MNHN Pg-8024	New Caledonia: Chesterfield Island, western Pacific	HQ241557/HQ241501/HQ241512
<i>Dardanus insignis</i>	CUR115203/USNM 1297351	Curaçao: southeastern Caribbean	MW160289/MW160996/MW167242
<i>Dardanus venosus</i>	ULLZ 6711/USNM 1541655	USA: Florida, northeastern Gulf of Mexico	KF182697/KF182428/KF182533
<i>Dardanus venosus</i>	CUR115156/USNM 1297404	Curaçao: southeastern Caribbean	MW160291/MW161009/MW167221

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TABLE 1. (Continued)

Taxon Name	Catalog No.	Country: Locality	Accession Number
<i>Dardanus</i> sp.	ULLZ 9694/USNM 1544521	Panama: Perlas Island, northeastern Pacific	MW160290/MW161010/MW167258
<i>Dardanus</i> sp.	ULLZ 9486/USNM 1535468	Panama: Perlas Island, northeastern Pacific	MW847147/MW160993/MW167253
<i>Paguristes acanthomerus</i>	UF 029439	Taiwan: Yilan County, northwestern Pacific	pending/MW161018/MW167256
<i>Paguristes anomalus</i>	ULLZ 7536/USNM 1543121	Mexico: Yucatan Peninsula: southwestern Gulf of Mexico	MW160349/MW160966/MW167212
<i>Paguristes anomalus</i>	ULLZ 14495/USNM 1547686	Dutch Antilles: Saba Bank, northeastern Caribbean	MW160351/MW160995/MW167189
<i>Paguristes grayi</i>	ULLZ 9963/USNM 1544609	Belize: Carrie Bow Cay, northwestern Caribbean	MW160320/MW160958/MW167191
<i>Paguristes grayi</i>	ULLZ 11744/USNM 1545936	Panama: Zapatillas Island, southwestern Caribbean	KF182728/KF182382/KF182537
<i>Paguristes grayi</i>	ULLZ 12533/USNM 1546377	Belize: Carrie Bow Cay, northwestern Caribbean	MW160319/MW160965/MW167211
<i>Paguristes hernancortezii</i>	ULLZ 16085/USNM 1618808	USA: Florida, northeastern Gulf of Mexico	MW160344/MW161025/MW167210
<i>Paguristes inconstans</i>	USNM 1297248	Curaçao: southeastern Caribbean	MW160303/MW161023/MW167200
<i>Paguristes jalur</i>	UF 005421	Mascarene Islands: Reunion Island, southern Indian Ocean	pending/MW161039/MW167218
<i>Paguristes moorei</i>	ULLZ 10860/USNM 1545363	USA: Louisiana, northwestern Gulf of Mexico	MW160302/MW160970/MW167214
<i>Paguristes moorei</i>	ULLZ 14050/USNM 1547438	USA: Louisiana, northwestern Gulf of Mexico	MW160301/MW161030/MW167248
<i>Paguristes moorei</i>	USNM 1297281	Curaçao: southeastern Caribbean	MW160309/MW161038/MW167219
<i>Paguristes moorei</i>	USNM 1297282	Curaçao: southeastern Caribbean	MW160310/MW160978/MW167230
<i>Paguristes moorei</i>	ULLZ 8172/USNM 1543433	USA: northeastern Gulf of Mexico	MW160300/MW160960/pending
<i>Paguristes planatus</i>	USNM 1297344	Curaçao: southeastern Caribbean	MW160339/MW161022/MW167220
<i>Paguristes puncticeps</i>	ULLZ 6801/USNM 1541861	southwestern Gulf of Mexico	KF182727/KF182383/KF182538
<i>Paguristes puncticeps</i>	ULLZ 8271/USNM 1543851	USA: Sackett Bank, northeastern Gulf of Mexico	MW160315/MW161006/MW167207
<i>Paguristes puncticeps</i>	ULLZ 11742/USNM 1545934	Panama: Zapatillas Island, southwestern Caribbean	MW160314/MW160962/MW167186
<i>Paguristes puncticeps</i>	ULLZ 13331/USNM 1546875	Panama: Bocas del Toro, southwestern Caribbean	MW160311/MW161033/MW167187
<i>Paguristes puncticeps</i>	ULLZ 14301/USNM 1547659	USA: Florida, southeastern Gulf of Mexico	MW160316/MW160964/MW167240
<i>Paguristes sericeus</i>	ULLZ 6525/USNM 1541664	USA: Florida, southeastern Gulf of Mexico	MW160318/MW160979/MW167213
<i>Paguristes sericeus</i>	ULLZ 7118/USNM 1541753	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	MW160322/MW161015/MW167199
<i>Paguristes sericeus</i>	ULLZ 7966/USNM 1543167	USA: northeastern Gulf of Mexico	MW160321/MW161007/MW167216
<i>Paguristes spinipes</i>	ULLZ 14487/USNM 1547681	Dutch Antilles: Saba Bank, northeastern Caribbean	MW160299/MW160992/MW853776
<i>Paguristes spinipes</i>	USNM 1297376	Curaçao: southeastern Caribbean	MW160306/MW161020/MW167206

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TABLE 1. (Continued)

Taxon Name	Catalog No.	Country: Locality	Accession Number
<i>Paguristes spinipes</i>	USNM 1297338	Curaçao: southeastern Caribbean	MW160307/MW161011/MW167231
<i>Paguristes tortugae</i>	ULLZ 4783/USNM 1540547	USA: Florida, southeastern Gulf of Mexico	MW160341/MW160989/MW167203
<i>Paguristes tortugae</i>	ULLZ 6800/USNM 1541858	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	KF182732/KF182676/KF182534
<i>Paguristes tortugae</i>	ULLZ 11148/USNM 1545610	Belize: Carrie Bow Cay, northwestern Caribbean	MW160329/MW161014/MW167180
<i>Paguristes tortugae</i>	UF 032577	French Antilles: northeastern Caribbean	pending/MW161001/MW167222
<i>Paguristes nr. tortugae</i>	ULLZ 4782/USNM 1540546	USA: Florida, southeastern Gulf of Mexico	MW160343/MW160976/MW167246
<i>Paguristes nr. tortugae</i>	ULLZ 13665/USNM 1547026	Panama: Bocas del Toro, southwestern Caribbean	MW160342/MZ442290/MW167205
<i>Paguristes nr. tortugae</i>	UF 015380	USA: Florida, Tampa Bay, northeastern Gulf of Mexico	pending/MW161019/MW167239
<i>Paguristes triangulatus</i>	ULLZ 6892/USNM 1541875	Mexico: Yucatan Peninsula: southwestern Gulf of Mexico	KF182729/KF182384/KF182539
<i>Paguristes triangulatus</i>	ULLZ 7719/USNM 1543174	USA: northeastern Gulf of Mexico	MW160305/MW160981/MW167204
<i>Paguristes triangulatus</i>	ULLZ 8250/USNM 1543418	USA: northeastern Gulf of Mexico	MW160298/MW160977/MW167227
<i>Paguristes wassi</i>	ULLZ 7326/USNM 1541761	Mexico: Yucatan Peninsula: southwestern Gulf of Mexico	MW160312/MZ442291/MW167255
<i>Paguristes wassi</i>	ULLZ 9371/USNM 1544277	Mexico: Yucatan Peninsula, southwestern Gulf of Mexico	MW160313/MW161031/MW167201
<i>Paguristes wassi</i>	UF 031881	French Antilles: northeastern Caribbean	pending/MW161004/MW167257
<i>Paguristes</i> sp.	ULLZ 14919/USNM 1548041	Panama: Perlas Island, northeastern Pacific	MW160308/MW160998/MW167226
<i>Paguristes</i> sp.	ULLZ 15256/USNM 1548292	Panama: Perlas Island, northeastern Pacific	MW160297/MW161029/MW167228
<i>Paguristes</i> sp.	ULLZ 15920/USNM 1618807	Curaçao: southeastern Caribbean	MW160338/MW161027/MW167244
<i>Paguristes</i> sp.	USNM 1297247	Curaçao: southeastern Caribbean	MW160317/MW161002/MW167224
<i>Paguristes</i> sp.	USNM 1297274	Curaçao: southeastern Caribbean	MW160304/MW161013/MW167229
<i>Paguristes</i> sp.	USNM 1622332	Curaçao: southeastern Caribbean	MW847152/MZ442293/MW853778
<i>Paguristes</i> sp.	USNM 1622333	Curaçao: southeastern Caribbean	MW847150/MZ442294/MW853779
<i>Paguristes</i> sp.	USNM 1622334	Curaçao: southeastern Caribbean	MW847149/MZ442295/MW853780
<i>Paguristes</i> sp.	USNM 1622335	Curaçao: southeastern Caribbean	MW847153/ MZ442296/MW853781
<i>Paguristes</i> sp.	USNM 1622336	Curaçao: southeastern Caribbean	MW847154/MZ442297/MW853782
<i>Paguristes</i> sp.	USNM 1622337	Curaçao: southeastern Caribbean	MW847151/MZ442298/MW853783
<i>Pseudopaguristes invisisacculus</i>	ULLZ 11115/USNM 1545589	Belize: Twin Cays, northwestern Caribbean	MW160350/MW161034/MW167178
<i>Pseudopaguristes</i> sp.	UF 016878	Australia: Queensland, southwestern Pacific	pending/MW161035/MW167241

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TABLE 1. (Continued)

Taxon Name	Catalog No.	Country: Locality	Accession Number H3/12S/16S
Epiplatidae			
<i>Chorilia longipes</i>	KC3089	Japan: Okinoshima, northwestern Pacific	EU921052/EU920889/EU920919
Galatheidae			
<i>Galathea rostrata</i>	ULLZ 7681/USNM 1532702	USA: Florida, northeastern Gulf of Mexico	KF182684/KF182388/KF182523
Hippidae			
<i>Emerita talpoida</i>	ULLZ 9434/USNM 1544314	USA: Florida, Fort Pierce, western Atlantic	KF182702/KF182419/KF182557
Leucosaeidae			
<i>Praebebalia longidactyla</i>	KC3086	unavailable	EU921071/EU920904/EU920931
Lithodidae			
<i>Cryptolithodes</i> sp.	ULLZ 11844/USNM 1545963	USA: Alaska, Sitka Sound, northeastern Pacific	KF182669/KF182402/KF182574
<i>Lithodes santolla</i>	ULLZ 11875/USNM 1546000	Patagonia	KF182671/KF182400/KF182572
<i>Paralomis</i> sp.	KC3506	unavailable	KF182666/KF182399/KF182571
Munidae			
<i>Munida iris</i>	ULLZ 8366/USNM 1532757	USA: Florida, southeastern Gulf of Mexico	KF182685/KF182389/KF182521
<i>Munida pusilla</i>	ULLZ 8322/USNM 1543605	USA: northwestern Gulf of Mexico	KF182686/KF182390/KF182522
Paguridae			
<i>Agaricochirus</i> sp.	USNM 1297342	Curaçao: southeastern Caribbean	MK830040/MK848215/MK848231
<i>Catapagurus</i> sp.	USNM 1297635	Curaçao: southeastern Caribbean	MW160325/MW160986/MW167217
<i>Iridopagurus reticulatus</i>	ULLZ 10032/USNM 1544746	Belize: Southwater Cay, northwestern Caribbean	KF182688/KF182413/KF182581
<i>Pagurus brevidactylus</i>	ULLZ 7065/USNM 1541856	Yucatan Peninsula: southwestern Gulf of Mexico	KF182679/KF182407/KF182563
<i>Pagurus bullisi</i>	ULLZ 11056/USNM 1545566	USA: Louisiana, northwestern Gulf of Mexico	KF182668/KF182410/KF182568
<i>Pagurus maclaughlinae</i>	ULLZ 11975/USNM 1546071	USA: Florida, northeastern Gulf of Mexico	KF182680/KF182408/KF182566
<i>Pagurus marshi</i>	ULLZ 11110/USNM 1545586	Belize: Twin Cays, northwestern Caribbean	KF182682/KF182409/KF182564
<i>Pagurus pollicaris</i>	ULLZ 11954/USNM 1546054	USA: Louisiana, northwestern Gulf of Mexico	KF182737/KF182403/JN800550
<i>Pagurus</i> "provenzanoi"	ULLZ 9685/USNM 1544513	Panama: Perlas Island, northeastern Pacific	MW160332/MW160985/MW167259
<i>Pagurus</i> "provenzanoi"	ULLZ 9687/USNM 1544515	Panama: Afuerita Channel, northeastern Pacific	MW160331/MW161017/MW167202
<i>Pagurus</i> "provenzanoi"	ULLZ 9690/USNM 1544517	Panama: near Isla Cavada, northeastern Pacific	MW160328/MW160999/MW167235

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TABLE 1. (Continued)

Taxon Name	Catalog No.	Country: Locality	Accession Number
<i>Pagurus stimpsoni</i>	ULLZ 16546/USNM 1618809	Belize: Twin Cays, northwestern Caribbean	MW160330/MW161026/MW167243
<i>Phimochirus formani</i>	ULLZ 7685/USNM 1543129	USA: Florida, northeastern Gulf of Mexico	MK830050/~MK848221
<i>Phimochirus formani</i>	ULLZ 14352/USNM 1547566	USA: Florida, northeastern Gulf of Mexico	MK830053/MK848204/MK848222
<i>Phimochirus formani</i>	ULLZ 14572/USNM 1547705	USA: Louisiana, northwestern Gulf of Mexico	MK830048/MK848205/MK848223
<i>Phimochirus tunnelli</i>	ULLZ 5789/USNM 1541146	USA: Louisiana, northwestern Gulf of Mexico	MK830051/MK848206/MK848224
<i>Phimochirus tunnelli</i>	ULLZ 7825/USNM 1543233	USA: northwestern Gulf of Mexico	MK830052/MK848208/MK848225
<i>Phimochirus tunnelli</i>	ULLZ 7973/USNM 1543319	USA: northeastern Gulf of Mexico	KF182678/KF182415/KF182578
<i>Phimochirus operculatus</i>	ULLZ 13837/USNM 1547302	USA: Louisiana, northwestern Gulf of Mexico	~/MK848209/MK848226
<i>Phimochirus operculatus</i>	ULLZ 9917/USNM 1534602	Belize: Carrie Bow Cay, northwestern Caribbean	MK830046/MK848212/MK848229
<i>Phimochirus randalli</i>	ULLZ 7071/USNM 1541890	Yucatan Peninsula: southwestern Gulf of Mexico	KF182676/KF182417/KF182576
<i>Phimochirus randalli</i>	ULLZ 7345/USNM 1541699	Yucatan Peninsula: southwestern Gulf of Mexico	KF182677/KF182418/KF182577
<i>Phimochirus venustus</i>	ULLZ 9677/USNM 1544505	Panama: near Isla Cavada, northeastern Pacific	MK830045/MK848214/MK848230
<i>Protonopagurus bioperculatus</i>	USNM 1297246	Curacao: southeastern Caribbean	MW160326/MW161024/MW167232
<i>Pylopagurus mackegei</i>	ULLZ 7675/USNM 1543124	USA: northwestern Gulf of Mexico	KF182675/KF182405/KF182569
<i>Tomopagurus merimaculosus</i>	ULLZ 9441/USNM 1544315	Costa Rica: eastern Pacific Ocean	KF182673/KF182411/KF182567
<i>Tomopagurus</i> sp.	ULLZ 16203/USNM 1549571	USA: Florida, northeastern Gulf of Mexico	MW160324/MW161028/MW167237
<i>Xylopagurus cancellarius</i>	ULLZ 9443/USNM 1544319	Costa Rica: northeastern Pacific	KF182683/KF182406/KF182584
<i>Xylopagurus cancellarius</i>	ULLZ 9689/USNM 1544522	Panama: A fuerita Channel, northeastern Pacific	MW160323/MW160983/MW167209
Parapaguridae			
<i>Paragiopagurus pilimanus</i>	USNM 1253320	Curacao: southeastern Caribbean	MW847148/pending/MW853777
<i>Sympagurus acinops</i>	ULLZ 11020/USNM 1545560	USA: northwestern Gulf of Mexico	KF182701/KF182371/KF182526
Porcellanidae			
<i>Allopetrolisthes spinifrons</i>	ULLZ 5979/USNM 1541241	Chile: Pozo Toyo, southeastern Pacific	KF182714/KF182398/KF182550
<i>Pachycheles rugimanus</i>	ULLZ 6903/USNM 1541675	USA: Florida, northeastern Gulf of Mexico	KF182705/KF182392/KF182543
<i>Petrolisthes armatus</i>	ULLZ 10098/USNM 1544814	USA: Florida, southeastern Gulf of Mexico	KF182708/KF182396/KF182549
Raninidae			
<i>Cosmonotus grayi</i>	KC3092	Japan: Okinoshima, northwestern Pacific	EU921051/EU920888/EU920918

16s-CWC-01r. A fragment of the mitochondrial small subunit rDNA (12S) approximately 310 bp in length was amplified using primers 12Sf and 12Sr. 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 2. Reactions were performed in 25 μ L volumes using one of four basic mixtures: 1) 30–50 ng DNA template, 0.8 μ M each primer, 200 μ M dNTPs, 2.5 μ L DreamTaq Green Buffer, 1.5 units DreamTaq Green (ThermoFischer Scientific Inc., Cat. No. EP0712); 2) 30–50 ng DNA template, 0.5 μ M each primer, 200 μ M dNTPs, 2.5 μ L DreamTaq Green Buffer, 1 unit DreamTaq Green; 3) 30–50 ng DNA template, 0.8 μ M each primer, 200 μ M dNTPs, 2.5 μ L DreamTaq Green Buffer, 1.5 units DreamTaq Green, 1 μ L 1% Bovine Serum Albumin; 4) 30–50 ng DNA template, 0.4 μ M each primer, 200 μ M dNTPs, 2.5 μ L DreamTaq Green Buffer, 1 unit DreamTaq Green, 1 μ L 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 to 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 72°C; final extension of 10 min at 72°C (Table 2).

TABLE 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 <i>et al.</i> 1998
H3 reverse	H3r	5' - ATATCCTTRGGCATRGTGAC - 3'	50–54°C for 30–60 s	Colgan <i>et al.</i> 1998
12S forward	12Sf	5' - GAAACCAGGATTAGATACCC - 3'		Buhay <i>et al.</i> 2007
12S reverse	12Sr	5' - AGCGACGGCGATATGTATAG - 3'	50–54°C for 30–60 s	Buhay <i>et al.</i> 2007
16S forward	16S 1472	5' - AGATAGAAACCAACCTGG - 3'		Crandall & Fitzpatrick 1996
16S reverse	16SL2	5' - TGCCTGTTTATCAAAAACAT - 3'		Schubart <i>et al.</i> 2002
16S reverse	16Sar	5' - CGCCTGTTTATCAAAAACAT - 3'	50–54°C for 30–60 s	Palumbi <i>et al.</i> 1991
16S reverse	16S-CWC-01r	5' - CCGGTTTGAACCTCAAATCATGT - 3'		new
16S forward	16S-CWC-01f	5' - TAAAGTCTAGCCTGCCCACT - 3'	52–58°C for 30–60 s	new

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 through 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 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).

TABLE 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 <i>Areopaguristes</i>	31238.640	0	0	5.12e ⁻⁴⁴
<i>Areopaguristes</i> and <i>Paguristes</i> as monophyletic sister clades	31666.816	0	0	2.15e ⁻⁴⁷

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 a reliable measures of clade support (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). Nodal bootstrap support values of 50 or greater were considered to represent progressively higher levels of quantitative support for the inferred tree topology. Such nodes were consequently treated in subsequent interpretations of our results as credible accounts 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). 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*, *A. hewatti*, *P. hernancortezii*, *P. anomalus*, *Pseudopaguristes invisissacculus*, *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 oxyphthalmus*, *A. nr. oxyphthalmus*, and numerous morphologically similar individuals of unknown identity from the eastern Pacific (Subclade 1c, bootstrap 98), 4) *Areopaguristes hummi*, *A. nr. hummi*, and morphologically similar individuals of

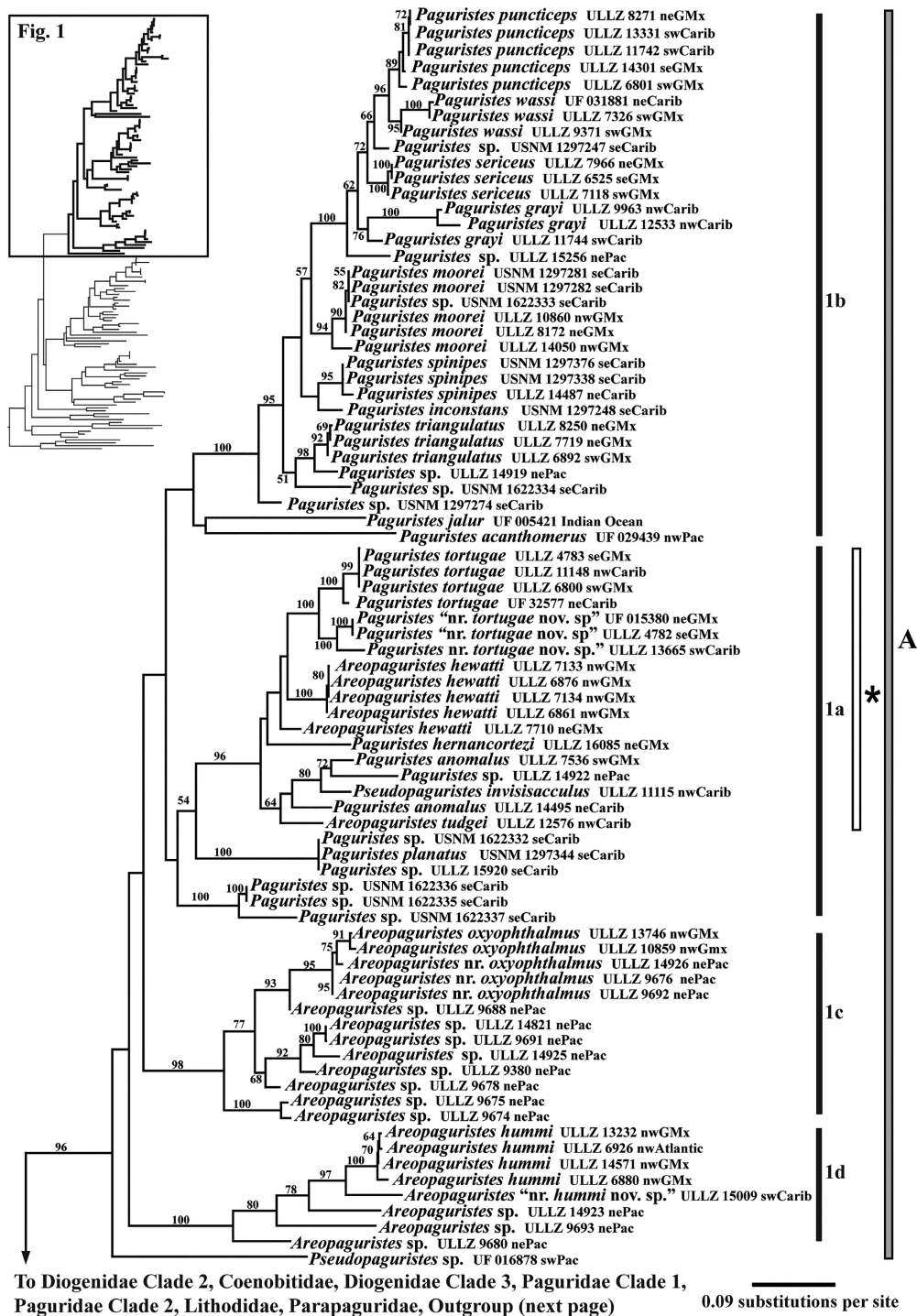


FIGURE 1. Maximum Likelihood phylogeny (-lnL: 26590.631) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions per 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). Abbreviations: nwAtlantic = northwestern Atlantic; neCarib = northeastern Caribbean; nwCarib = northwestern Caribbean; seCarib = southeastern Caribbean; swCarib = southwestern Caribbean; neGMx = northeastern Gulf of Mexico; nwGMx = northwestern Gulf of Mexico; seGMx = southeastern Gulf of Mexico; swGMx = southwestern Gulf of Mexico; nePac = northeastern Pacific; wPac = western Pacific; nwPac = northwestern Pacific; sePac = southeastern Pacific; swPac = southwestern Pacific.

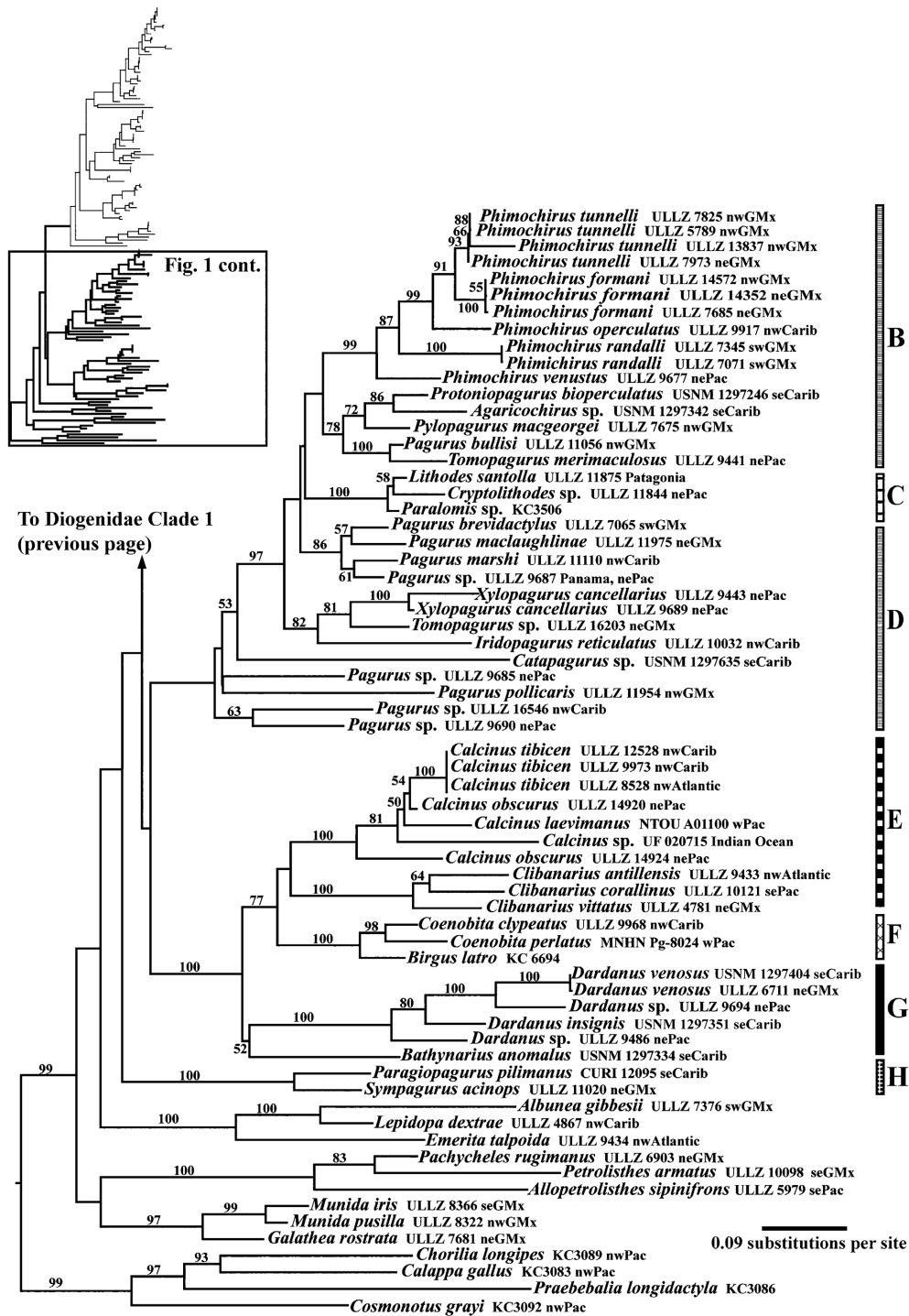


FIGURE 1 (cont'd). Maximum Likelihood phylogeny (-lnL: 26590.631) inferred in RAxML under the GTR + Gamma model of nucleotide substitution. Bootstrap proportions resulting from 1000 bootstrap replicates are displayed at tree nodes, with values under 50 omitted. Branch lengths are measured as substitutions 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 Lithodiidae. 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). Abbreviations: nwAtlantic = northwestern Atlantic; neCarib = northeastern Caribbean; nwCarib = northwestern Caribbean; seCarib = southeastern Caribbean; swCarib = southwestern Caribbean; neGMx = northeastern Gulf of Mexico; nwGMx = northwestern Gulf of Mexico; seGMx = southeastern Gulf of Mexico; swGMx = southwestern Gulf of Mexico; nePac = northeastern Pacific; wPac = western Pacific; nwPac = northwestern Pacific; sePac = southeastern Pacific; swPac = southwestern Pacific.

unknown identity from the eastern Pacific (Subclade 1d, bootstrap 100). The second major diogenid clade, Diogenidae Clade 2, counted among its constituent genera *Clibanarius* and *Calcinus* and showed significant support for a sister relationship to our representatives of Coenobitidae, *Coenobita clypeatus* and *Birgus latro* (bootstrap 77). However, Diogenidae Clade 2 was not supported as an independent clade. Comprised of the genera *Bathynarius* and *Dardanus*, 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). The multigene ML analysis did not recover a monophyletic *Areopaguristes*, and hypothetical trees that included such a clade were refuted by quantitative comparisons (Table 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 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).

Discussion

Diogenidae has been considered by many authors to be a monophyletic family 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; Landschoff & Gouws 2018; Tan *et al.* 2018; Wolfe *et al.* 2019). Our analysis concurs with the latter findings of a non-monophyletic Diogenidae 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). While the phylogenetic validity of these two major clades in our study and others is strongly supported, their generic composition is not congruent with currently accepted taxonomy for Paguroidea, but determination of appropriate revisions at the family level remains 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). That study recovered a polyphyletic Diogenidae having three groupings with constituencies congruent with those of our three diogenid clades. The convergence of our phylogenetic analysis with some 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 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). 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*, while a second subclade, Subclade 1b, encompasses only species of *Paguristes*. Two other assemblages, Subclade 1c and Subclade 1d, count only species of *Areopaguristes* as constituents. Correlations between the telson groupings applied to the genus *Paguristes* by McLaughlin & Provenzano (1975) and some Diogenidae Clade 1 genetic subclades are evident in the present study, with most species included in the monophyletic Subclade 1b belonging to the group of *Paguristes* spp. with unarmed telsons (Fig. 2A). However, no similar monophyletic genetic grouping in our analysis corresponds to the morphologically defined group with armed telsons (Fig. 2B). 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; Miyake 1978; Komai 2001; McLaughlin & Rahayu 2005; Rahayu 2006; Rahayu & McLaughlin 2006; McLaughlin 2008; Lemaitre & Felder 2012; Komai *et al.* 2015).

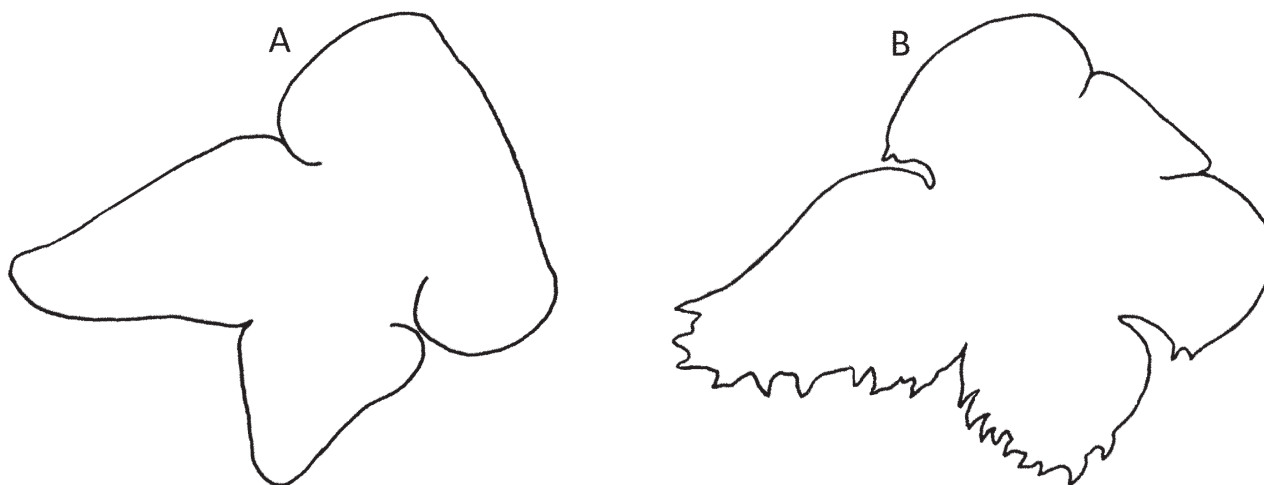


FIGURE 2. Schematic illustrations of unarmed (A) and armed (B) telsons.

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 do not form a monophyletic grouping within the *P. tortugae* complex, nor within other subclades of Diogenidae Clade 1 (Fig. 1). The results of the KH, SH, and AU tests provide substantial quantitative support for the distribution of species assigned to *Areopaguristes*, *Pseudopaguristes*, and *Paguristes*, 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 reciprocally monophyletic sister clades (Table 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 similarities likely represent 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 for now remain 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.

From the results of this study, specific taxonomic revisions of *Areopaguristes*, *Paguristes*, and *Pseudopaguristes* cannot be proposed but the genetic breaks within and among the three genera indicate that taxonomic revisions will be necessary if paguroid taxonomy is to reflect evolutionary relationships. For *Paguristes*, *Areopaguristes*, and *Pseudopaguristes*, one approach to revisions would be to subdivide the existing genera and redistribute the constituent species among new genera erected to reflect phylogenetic relationships. Such an undertaking would likely yield several genera and morphological characters will play a key role in determining the scope of those proposed genera.

Results reported herein and preliminary results from a broader genetic analysis currently underway support this approach, indicating that character suites applied currently to some informal species complexes correspond to distinct genetic subclades in several cases. An alternative approach would be the treatment of *Paguristes*, *Areopaguristes*, and *Pseudopaguristes* as a single large genus of more than 200 species. This approach avoids the establishment new genera and the introduction of potentially confounding taxonomic complexity but would limit the utility of the necessarily broad morphological diagnosis that would accompany such a revision.

Establishing the limits of *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 regarded *P. hirtus* and *P. weddellii* to be separate species, of which the latter was moved to *Tetralobistes* Ayon-Parente & Hendrickx, 2010. We currently 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 species of the *A. hummi* complex 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). 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 *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 but undescribed species close to *P. tortugae* (Strasser & Price 1999), 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 a cryptic 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* 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 is insignificantly supported. In our ML phylogeny, the *A. hummi* complex includes specimens with unclear diagnoses, many of which are from the Pacific coast of Panama. With these unidentified Pacific specimens included, the *A. hummi* complex is strongly monophyletic (bootstrap 100). Multiple individuals of *A. hummi* s.s. from the Gulf of Mexico cluster together with high support (boot-

strap 100), and *A. nr. hummi*, our new species from Atlantic coast of Central America, is sister to our assemblage of *A. hummi* s.s. representatives (bootstrap 97).

Definitive morphological characters for *A. nr. hummi* are not readily apparent, but support for its separation is found in the coloration of fresh specimens. As described by Wass (1955), *A. hummi* s.s. 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* 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*, in contrast to the blue hue of *A. hummi* s.s. Adding support for the establishment of *A. nr. hummi*, the geographic distribution for the two species does not overlap. *Areopaguristes hummi* s.s. is found broadly across the Gulf of Mexico (Wass 1955; Strasser & Price 1999; Felder *et al.* 2009a), while our new species, *A. nr. hummi*, is currently known only from the Atlantic coast of Central America. As with *P. nr. tortugae*, full comparative treatment of morphology and color characters is deferred to a companion paper formally describing *A. nr. hummi* 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 *P. 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*, *A. hewatti*, and *P. hernancortezi*, encompasses only species with banded or spotted eyestalks. In the other subclade, composed of *Aeropaguristes tudgei*, *Pseudopaguristes invisissacculus*, 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. Species of the *Paguristes tortugae* complex 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 using eyestalk patterning and color to delineate subclades within the *P. tortugae* complex limits definitive conclusions about subclade constituency, but evidence of this phenomenon all the more compels hermit crab systematists to include color of fresh specimens as a character of potential value not only for species distinctions but for determination of phylogenetic groupings of species as well.

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