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Decapod Crustacean Phylogenetics

edited by

Joel W. Martin, Keith A. Crandall, and Darryl L. Felder



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Molecular Phylogeny of Western Atlantic Representatives of the Genus *Hexapanopeus* (Decapoda: Brachyura: Panopeidae)

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ABSTRACT

Species of the brachyuran crab genus *Hexapanopeus* Rathbun, 1898, are common benthic inhabitants in coastal and nearshore waters of the Americas. Despite the frequency with which they are encountered, they are taxonomically problematic and commonly misidentified by non-experts. Little previous work has been undertaken to explain relationships among the 13 nominal species of *Hexapanopeus* or their relationship to other phenotypically similar genera of the family Panopeidae. In the present study we examine partial sequences for 16S and 12S mitochondrial rDNA for 71 individuals representing 46 species of Panopeidae and related families of the Brachyura. Phylogenies inferred from both of these datasets are largely congruent and show, with one exception, the included genera and species of the Panopeidae to represent a monophyletic grouping. Within this group, *Hexapanopeus* is polyphyletic, being distributed among several separate major clades and clearly warranting taxonomic subdivision.

1 INTRODUCTION

As part of ongoing studies of the superfamily Xanthoidea *sensu* Martin & Davis (2001), we have undertaken a reexamination of phylogenetic relationships among genera assigned to the family Panopeidae Ortmann, 1893, on molecular and morphological bases. Early in the course of our morphological studies, we saw reason to conclude that the genus *Hexapanopeus* Rathbun, 1898, as currently defined, was polyphyletic. Differences in the characters of the carapace, chelipeds, and male first pleopod (gonopod) served to obscure what, if any, relationship existed among the species in the genus. The present study serves as the first step towards restricting species composition of the genus *Hexapanopeus s.s.* (*sensu stricto*) and defining its phylogenetic relationships.

Presently, the genus *Hexapanopeus* consists of 13 species distributed on both coasts of the Americas; six species are known from the western Atlantic ranging from Massachusetts to Uruguay, while seven more range in the eastern Pacific from Mexico to Ecuador (Table 1). Representatives of *Hexapanopeus* are commonly encountered in environmental studies and inhabit a variety of nearshore environments ranging from sand-shell bottoms to rubble and surface fouling accumulations, where they often reside amongst sponges and ascidians (Rathbun 1930; Felder 1973; Williams 1984; Sankarankutty & Manning 1997). Even so, available illustrations and morphological descriptions are of limited detail and quality for many species, and little can be deduced from present literature to clarify their phylogenetic relationships.

Herein, we provide evidence for polyphyly in the genus *Hexapanopeus* on the basis of two mitochondrial genes (16S rDNA and 12S rDNA). We also examine relationships among species

Table 1. Known species presently assigned to *Hexapanopeus* with authority and known distribution. Those preceded by an asterisk (*) are included in the present phylogenetic analyses, along with one putative new species of the genus from the western Gulf of Mexico, yet to be described.

Taxon Name	Distribution
* <i>Hexapanopeus angustifrons</i> (Benedict & Rathbun, 1891)	Western Atlantic; from Massachusetts to Brazil
<i>Hexapanopeus beebei</i> Garth, 1961	Eastern Pacific; Nicaragua
* <i>Hexapanopeus caribbaeus</i> (Stimpson, 1871)	Western Atlantic; southeast Florida to Brazil
<i>Hexapanopeus cartagoensis</i> Garth, 1939	Eastern Pacific; Galapagos Islands, Ecuador
<i>Hexapanopeus costaricensis</i> Garth, 1940	Eastern Pacific; Costa Rica
* <i>Hexapanopeus lobipes</i> (A. Milne-Edwards, 1880)	Western Atlantic; Gulf of Mexico
* <i>Hexapanopeus manningi</i> Sankarankutty & Ferreira, 2000	Western Atlantic; Rio Grande do Norte, Brazil
<i>Hexapanopeus nicaraguensis</i> (Rathbun, 1904)	Eastern Pacific; Nicaragua
<i>Hexapanopeus orcutti</i> Rathbun, 1930	Eastern Pacific; Mexico
* <i>Hexapanopeus paulensis</i> Rathbun, 1930	Western Atlantic; South Carolina to Uruguay
<i>Hexapanopeus quinquedentatus</i> Rathbun, 1901	Western Atlantic; Puerto Rico
<i>Hexapanopeus rubicundus</i> Rathbun, 1933	Eastern Pacific; Gulf of California
<i>Hexapanopeus sinaloensis</i> Rathbun, 1930	Eastern Pacific; Mexico

currently assigned to *Hexapanopeus* and relationships of this genus to other genera and species encompassed within the family Panopeidae. This serves to further clarify the species composition of *Hexapanopeus* s.s., and to confirm its phylogenetic proximity to other taxa constituting a putative panopeid lineage.

2 MATERIALS AND METHODS

2.1 Taxon sampling

Seventy-one individuals representing 46 species, 30 genera, and 10 families were subjected to molecular analyses. Of the 142 sequences used in this study, 132 were generated for this project, while the remaining 10 were obtained from GenBank (Table 2). Since the identity of the sister group to the family Panopeidae remains debatable (see Martin & Davis 2001, Karasawa & Schweitzer 2006, and Ng et al. 2008 for discussion), we included 22 taxa that represent the families Xanthidae MacLeay, 1838, Pseudorhombilidae Alcock, 1900, Pilumnidae Samouelle, 1819, Chasmocarcinidae Serène, 1964, Euryplacidae Stimpson, 1871, Goneplacidae MacLeay, 1838, Carpiliidae Ortmann, 1893, Eriphiidae MacLeay, 1838, and Portunidae Rafinesque, 1815.

Specimens used in this study were collected during research cruises and field expeditions and 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. Additional materials were obtained on loan from the National Museum of Natural History—Smithsonian Institution (USNM). When possible, identifications of specimens were confirmed by two or more of the investigators to limit the chance of misidentifications.

Table 2. Crab species used for phylogeny reconstruction, showing catalog number, collection locality, and GenBank accession numbers for partial sequences of 16S and 12S, respectively (ULLZ = University of Louisiana at Lafayette Zoological Collection, Lafayette, Louisiana; USNM = United States National Museum of Natural History, Smithsonian Institution, Washington D.C.).

Taxon	Catalog. No.	Collection Locality	16S	12S
Carpiliidae Ortmann, 1893				
<i>Carpilius maculatus</i> (Linnaeus, 1758)	GenBank		AF501732	AF501705
Chasmocarcinidae Serène, 1964				
<i>Chasmocarcinus chacei</i> Felder & Rabalais, 1986	ULLZ 8018	Northern Gulf of Mexico; 2006	EU863401	EU863335
<i>Chasmocarcinus mississippiensis</i> Rathbun, 1931	ULLZ 7346	Southwestern Gulf of Mexico; 2005	EU863406	EU863340
Eriphiidae MacLeay, 1838				
<i>Eriphia verrucosa</i> (Forskål, 1775)	ULLZ 4275	Eastern Atlantic; Spain; Cadiz, 1998	EU863398	EU863332
Euryplacidae Stimpson, 1871				
<i>Frevillea barbata</i> A. Milne-Edwards, 1880	ULLZ 8369	Southeastern Gulf of Mexico; 2004	EU863399	EU863333
<i>Sotoplax robersi</i> Guinot, 1984	ULLZ 7857	Northern Gulf of Mexico; 2006	EU863400	EU863334
Goneplacidae MacLeay, 1838				
<i>Bathyplox typhlus</i> A. Milne-Edwards, 1880	ULLZ 8032	Northwestern Gulf of Mexico; 2006	EU863397	EU863331
Panopeidae Ortmann, 1893				
<i>Acantholobulus bermudensis</i> (Benedict & Rathbun, 1891)	ULLZ 5843	Gulf of Mexico; Mexico; Campeche, 2002	EU863355	EU863289
<i>Acantholobulus bermudensis</i> (Benedict & Rathbun, 1891)	ULLZ 6558	Western Atlantic; Florida, Ft. Pierce, 2005	EU863354	EU863288
<i>Acantholobulus bermudensis</i> (Benedict & Rathbun, 1891)	ULLZ 6924	Western Atlantic; Florida, Ft. Pierce, 2006	EU863372	EU863306
<i>Acantholobulus schmitti</i> (Rathbun, 1930)	ULLZ 6613	Western Atlantic; Brazil; Sao Paulo, 1999	EU863364	EU863298
<i>Acantholobulus schmitti</i> (Rathbun, 1930)	ULLZ 8367	Western Atlantic; Brazil; Sao Paulo, 1999	EU863357	EU863291
<i>Cyrtoplax</i> nr. <i>spiniolata</i> (Benedict, 1892)	ULLZ 8423	Western Atlantic; Florida, Ft. Pierce, 2001	EU863369	EU863303
<i>Dyspanopeus sayi</i> (Smith, 1869)	ULLZ 7227	Western Atlantic; Florida, Ft. Pierce, 2006	EU863395	EU863329
<i>Eucratops crassimanus</i> (Dana, 1851)	ULLZ 6427	Western Atlantic; Florida, Ft. Pierce, 2006	EU863392	EU863326
<i>Eurypanopeus abbreviatus</i> (Stimpson, 1860)	ULLZ 3753	Western Atlantic; Florida, Ft. Pierce, 1998	EU863388	EU863322
<i>Eurypanopeus depressus</i> (Smith, 1869)	ULLZ 3976	Northern Gulf of Mexico; Mississippi, 1998	EU863391	EU863325
<i>Eurypanopeus depressus</i> (Smith, 1869)	ULLZ 6077	Eastern Gulf of Mexico; Tampa Bay, 2005	EU863390	EU863324
<i>Eurypanopeus dissimilis</i> (Benedict & Rathbun, 1891)	ULLZ 5878	Western Atlantic; Florida, Ft. Pierce, 1997	EU863396	EU863330
<i>Eurypanopeus dissimilis</i> (Benedict & Rathbun, 1891)	ULLZ 8424	Western Atlantic; Florida, Ft. Pierce, 1997	EU863387	EU863321
<i>Eurypanopeus planissimus</i> (Stimpson, 1860)	ULLZ 4140	Eastern Pacific; Mexico; Baja California, 1999	EU863386	EU863320
<i>Glyptoplax smithii</i> A. Milne-Edwards, 1880	ULLZ 6793	Southwestern Gulf of Mexico; 2005	EU863342	EU863276
<i>Glyptoplax smithii</i> A. Milne-Edwards, 1880	ULLZ 7686	Northern Gulf of Mexico; 2006	EU863379	EU863313
<i>Glyptoplax smithii</i> A. Milne-Edwards, 1880	ULLZ 8142	Northern Gulf of Mexico; 2006	EU863350	EU863284
<i>Glyptoplax smithii</i> A. Milne-Edwards, 1880	ULLZ 8335	Northern Gulf of Mexico; 2006	EU863371	EU863305
<i>Glyptoplax smithii</i> A. Milne-Edwards, 1880	ULLZ 9020	Western Atlantic; Florida, Ft. Pierce, 2003	EU863384	EU863318

Table 2. continued.

Taxon	Catalog No.	Collection Locality	16S	12S
<i>Hexapanopeus angustifrons</i> (Benedict & Rathbun, 1891)	ULLZ 6943	Western Atlantic; Florida, Ft. Pierce, 2006	EU863343	EU863277
<i>Hexapanopeus angustifrons</i> (Benedict & Rathbun, 1891)	ULLZ 7174	Western Atlantic; Florida, Ft. Pierce, 2003	EU863368	EU863302
<i>Hexapanopeus angustifrons</i> (Benedict & Rathbun, 1891)	ULLZ 7757	Western Atlantic; Florida, Ft. Pierce, 2006	EU863351	EU863285
<i>Hexapanopeus angustifrons</i> (Benedict & Rathbun, 1891)	ULLZ 8368	Eastern Gulf of Mexico; Florida, 2004	EU863380	EU863314
<i>Hexapanopeus angustifrons</i> (Benedict & Rathbun, 1891)	ULLZ 9019	Western Atlantic; Florida, Ft. Pierce, 2003	EU863385	EU863319
<i>Hexapanopeus caribbaeus</i> (Stimpson, 1871)	ULLZ 6859	Western Atlantic; Florida, Ft. Pierce, 2006	EU863381	EU863315
<i>Hexapanopeus caribbaeus</i> (Stimpson, 1871)	ULLZ 6859	Western Atlantic; Florida, Ft. Pierce, 2006	EU863348	EU863282
<i>Hexapanopeus caribbaeus</i> (Stimpson, 1871)	ULLZ 7743	Western Atlantic; Florida, Ft. Pierce, 2006	EU863353	EU863287
<i>Hexapanopeus lobipes</i> (A. Milne-Edwards, 1880)	ULLZ 4731	Northern Gulf of Mexico; Louisiana, 2001	EU863356	EU863290
<i>Hexapanopeus lobipes</i> (A. Milne-Edwards, 1880)	ULLZ 6909	Southeastern Gulf of Mexico; 2004	EU863365	EU863299
<i>Hexapanopeus lobipes</i> (A. Milne-Edwards, 1880)	ULLZ 7828	Northern Gulf of Mexico; 2006	EU863352	EU863286
<i>Hexapanopeus manningi</i> Sankaranakuty & Ferreira, 2000	USNM 260923	Western Atlantic; Brazil; Rio Grande do Norte, 1996	EU863383	EU863317
<i>Hexapanopeus</i> nov. sp.	ULLZ 8646	Northern Gulf of Mexico; Texas, 1998	EU863361	EU863295
<i>Hexapanopeus paulensis</i> Rathbun, 1930	ULLZ 3891	Northern Gulf of Mexico; Texas, 1998	EU863360	EU863294
<i>Hexapanopeus paulensis</i> Rathbun, 1930	ULLZ 6608	Western Atlantic; Brazil; Sao Paulo, 1996	EU863373	EU863307
<i>Hexapanopeus paulensis</i> Rathbun, 1930	ULLZ 6862	Northern Gulf of Mexico; Texas, 2006	EU863358	EU863292
<i>Hexapanopeus paulensis</i> Rathbun, 1930	ULLZ 6870	Northern Gulf of Mexico; Texas, 2006	EU863374	EU863308
<i>Hexapanopeus paulensis</i> Rathbun, 1930	ULLZ 6875	Northern Gulf of Mexico; Texas, 2006	EU863376	EU863310
<i>Hexapanopeus paulensis</i> Rathbun, 1930	ULLZ 6882	Northern Gulf of Mexico; Texas, 2006	EU863375	EU863309
<i>Hexapanopeus paulensis</i> Rathbun, 1930	ULLZ 8645	Northern Gulf of Mexico; Panama City, 2007	EU863377	EU863311
<i>Neopanope packardii</i> Kingsley, 1879	ULLZ 3772	United States; Florida, Ft. Pierce, 1998	EU863349	EU863283
<i>Panopeus africanus</i> A. Milne-Edwards, 1867	ULLZ 4273	Eastern Atlantic; Spain; Cadiz, 1999	EU863370	EU863304
<i>Panopeus americanus</i> Sausurre, 1857	ULLZ 8456	Western Atlantic; Florida, Ft. Pierce, 1996	EU863345	EU863279
<i>Panopeus herbstii</i> H. Milne Edwards, 1834	ULLZ 8457	Western Atlantic; South Carolina, 1997	EU863362	EU863296
<i>Panopeus lacustris</i> Desbonne, 1867	ULLZ 3818	Western Atlantic; Florida, Ft. Pierce, 1997	EU863363	EU863297
<i>Panopeus occidentalis</i> Sausurre, 1857	ULLZ 8640	Northern Gulf of Mexico; Panama City, 2007	EU863393	EU863327
<i>Panopeus occidentalis</i> Sausurre, 1857	ULLZ 8643	Northern Gulf of Mexico; Panama City, 2007	EU863394	EU863328
<i>Panoplax depressa</i> Stimpson, 1871	ULLZ 8056	Northern Gulf of Mexico; 2006	EU863347	EU863281
<i>Rhithropanopeus harrisi</i> (Gould, 1841)	ULLZ 3995	Northern Gulf of Mexico; Texas, 1998	EU863346	EU863280
Pilumnidae Samouelle, 1819				
<i>Lobopilumnus agassizii</i> (Stimpson, 1871)	ULLZ 7121	Southwestern Gulf of Mexico; 2005	EU863402	EU863336
<i>Pilumnus floridanus</i> Stimpson, 1871	ULLZ 7343	Southern Gulf of Mexico; 2005	EU863403	EU863337

Table 2. continued.

Taxon	Catalog No.	Collection Locality	16S	12S
Portunidae Rafinesque, 1815				
<i>Ovalipes punctatus</i> (De Haan, 1833)	GenBank		DQ062733	DQ060652
Pseudorhombilidae Alcock, 1900				
<i>Trapezioplax tridentata</i> (A. Milne-Edwards, 1880)	ULLZ 8054	Northern Gulf of Mexico; 2006	EU863344	EU863278
Xanthidae MacLeay, 1838				
<i>Atergatis reticulatus</i> (De Haan, 1835)	GenBank		DQ062726	DQ060646
<i>Batodaeus urinator</i> (A. Milne-Edwards, 1881)	ULLZ 8131	Southern Gulf of Mexico; 2005	EU863405	EU863339
<i>Eucratodes agassizii</i> A. Milne-Edwards, 1880	ULLZ 8400	Northern Gulf of Mexico; Louisiana, 1996	EU863389	EU863323
<i>Garthiops barbadensis</i> (Rathbun, 1921)	ULLZ 8170	Northern Gulf of Mexico; 2006	EU863367	EU863301
<i>Garthiops barbadensis</i> (Rathbun, 1921)	ULLZ 8183	Northern Gulf of Mexico; 2006	EU863366	EU863300
<i>Liomera cinctimana</i> (White, 1847)	GenBank		AF501736	AF501708
<i>Macromedaeus distinguendus</i> (De Haan, 1835)	GenBank		DQ062731	DQ060654
<i>Micropanope sculpipes</i> Stimpson, 1871	ULLZ 6603	Southeastern Gulf of Mexico; 2004	EU863404	EU863338
<i>Micropanope sculpipes</i> Stimpson, 1871	ULLZ 8025	Northern Gulf of Mexico; 2006	EU863378	EU863312
<i>Speocarcinus lobatus</i> Guinot, 1969	ULLZ 7820	Northern Gulf of Mexico; 2006	EU863407	EU863341
<i>Speocarcinus monotuberculatus</i> Felder & Rabalais, 1986	ULLZ 7562	Southwestern Gulf of Mexico; 2005	EU863359	EU863293
<i>Xanthias camaliculatus</i> Rathbun, 1906	ULLZ 4381	Indian Ocean; South Africa; Sodwana Bay, 2001	EU863382	EU863316

Table 3. Primers used in this study.

Gene	Primer	Sequence 5'→3'	Ref.
16S	16Sar	CGC CTG TTT ATC AAA AAC AT	(1)
16S	16Sbr	CCG GTC TGA ACT CAG ATC ACG T	(1)
16S	16L2	TGC CTG TTT ATC AAA AAC AT	(2)
16S	1472	AGA TAG AAA CCA ACC TGG	(3)
12S	12sf	GAA ACC AGG ATT AGA TAC CC	(4)
12S	12s1r	AGC GAC GGG CGA TAT GTA C	(4)

References: (1) Palumbi et al. 1991, (2) Schubart et al. 2002, (3) Crandall & Fitzpatrick 1996, (4) Buhay et al. 2007.

2.2 DNA extraction, PCR, and sequencing

Genomic DNA was extracted from muscle tissue of the pereopods of a total of 66 specimens of the family Panopeidae and related taxa of the Xanthoidea *sensu* Martin & Davis (2001) utilizing one of the following extraction protocols: Genomic DNA Extraction Kit for Arthropod Samples (Cartagen Molecular Systems, Cat. No. 20810-050), Qiagen DNeasy® Blood and Tissue Kit (Qiagen, Cat. No. 69504), or isopropanol precipitation following Robles et al. (2007).

Two mitochondrial markers were selectively amplified using polymerase chain reaction (PCR). A fragment of the 16S large subunit rDNA approximately 550 basepairs (bp) in length was amplified using the primers 1472 or 16Sbr in combination with 16L2 and 16Sar and a fragment of the 12S small subunit rDNA approximately 310 bp in length was amplified using the primers 12sf and 12s1r (see Table 3 for complete primer information). PCR reactions were performed in 25- μ l volumes containing: 0.5 μ M forward and reverse primer, 200 μ M each dNTP, 2.5 μ l 10x PCR buffer, 3 mM MgCl₂, 1 M betaine, 1 unit NEB Standard Taq polymerase (New England Biolabs, Cat. No. M0273S), and 30–50 ng of genomic DNA. Reactions were carried out using the following cycling parameters: initial denaturation at 94°C for 2 min; 40 cycles at 94°C for 25 sec, 40°C (16S) or 52°C (12S) for 1 min, 72°C for 1 min; final extension at 72°C for 5 min. PCR products were purified using EPOCH GenCatch PCR Clean-up Kit (EPOCH BioLabs, Cat. No. 13-60250) and sequenced in both directions using ABI BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA). Cycle sequencing products were purified using Sephadex G-50 columns (Sigma-Aldrich Chemicals, Cat. No. S6022). Sequencing products were run on an ABI PRISM® 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA).

2.3 Phylogenetic analyses

Sequences were assembled using Sequencher 4.7 (GeneCodes, Ann Arbor, MI, USA). Once assembled, sequences were aligned using MUSCLE (MULTiple Sequence Comparison by Log-Expectation), a computer program found to be more accurate and faster than other alignment algorithms (Edgar 2004). Alignments were further refined using GBlocks v0.91b (Castresana 2000) to omit poorly aligned or ambiguous positions. Default parameters were used for GBlocks except: 1) minimum length of a block = 4, 2) allowed gap positions = half. We conducted a partition heterogeneity test or incongruence length difference test (ILD) (Bull et al. 1993), as implemented in PAUP* v4b10 (Swofford 2003), to determine if the two gene regions could be combined.

The model of evolution that best fit each of the datasets was determined by likelihood tests as implemented in Modeltest version 3.6 (Posada & Crandall 1998) under the Akaike Information

Criterion (AIC). The maximum likelihood (ML) analyses were conducted using PhyML Online (Guindon et al. 2005) using the model parameters selected with free parameters estimated by PhyML. Confidence in the resulting topology was assessed using non-parametric bootstrap estimates (Felsenstein 1985) with 500 replicates.

The Bayesian (BAY) analyses were conducted in MrBayes (Huelsenbeck & Ronquist 2001) with computations performed on the computer cluster of the CyberInfrastructure for Phylogenetic REsearch project (CIPRES) at the San Diego Supercomputer Center, using parameters selected by Modeltest. A Markov Chain Monte Carlo (MCMC) algorithm with 4 chains and a temperature of 0.2 ran for 4,000,000 generations, sampling 1 tree every 1,000 generations. Preliminary analyses and observation of the log likelihood (L) values allowed us to determine burn-ins and stationary distributions for the data. Once the values reached a plateau, a 50% majority rule consensus tree was obtained from the remaining trees. Clade support was assessed with posterior probabilities (pP).

3 RESULTS

The initial sequence alignment of the 16S dataset, including gaps and primer regions, was 606 bp in length, while that of the 12S dataset was 384 bp in length. GBLOCKS was used to further refine the alignment, removing ambiguously aligned regions resulting in final alignments of 521 bp (86%) and 284 bp (74%) for 16S and 12S, respectively. Despite recent studies combining multiple loci into a single alignment (Ahyong & O'Meally 2004, Porter et al. 2005), we chose in this instance not to combine the datasets. The partition heterogeneity test or incongruence length difference test, as implemented in PAUP*, indicated that the combination of the two gene regions was significantly rejected ($P = 0.0240$). Furthermore, preliminary analysis of the combined dataset resulted in lower support for some of the tip branches than was the case in the single gene trees. This is due to different branching patterns (16S vs. 12S) at this level of the tree, which will be discussed later in this paper. This information would be lost in a combined tree.

Application of the likelihood tests as implemented in Modeltest revealed that the selected model of DNA substitution by AIC for the 16S dataset was HKY+I+G (Hasegawa et al. 1985) with an assumed proportion of invariable sites of 0.3957 and a gamma distribution shape parameter of 0.4975. The selected model for the 12S dataset was GTR+I+G (Rodríguez et al. 1990) with an assumed proportion of invariable sites of 0.3228 and a gamma distribution shape parameter of 0.6191.

Phylogenetic relationships among 71 individuals representing 46 species of the Xanthoidea *sensu* Martin & Davis (2001) were determined using Bayesian and ML approaches for both the 16S and 12S datasets. For the Bayesian analyses, the first 1,000 trees were discarded as burn-in and the consensus tree was estimated using the remaining 3,000 trees (= 3 million generations). Topologies resulting from the Bayesian analyses of both the 16S and 12S datasets were largely congruent (Figs. 1 and 2). A number of monophyletic clades are supported by both datasets, as follow: 1) *Acantholobulus bermudensis*, *Acantholobulus schmitti*, and *Hexapanopeus caribbaeus* with pP (16S/12S) of 99/77, 2) *Hexapanopeus angustifrons* and *Hexapanopeus paulensis* with pP of 100/99, 3) *Eurypanopeus depressus*, *Eurypanopeus dissimilis*, *Dyspanopeus sayi*, *Neopanope packardii*, and *Rhithropanopeus harrisii* with pP of 97/99, 4) *Eurypanopeus abbreviatus* and *Eurypanopeus planissimus* with pP of 99/87. In general, Bayesian posterior probabilities have been shown to be higher than the corresponding bootstrap values, but, in many cases, posterior probabilities tend to overrate confidence in a topology while bootstrap values based on neighbor joining, maximum parsimony, or ML methods tend to slightly underestimate support (Huelsenbeck et al. 2001, Huelsenbeck et al. 2002, Suzuki et al. 2002). With this in mind, it is not surprising to find that ML bootstrap supports for the same four clades are lower than the pP. The bootstrap values of the above clades are as follows: 1) <50/<50, 2) 72/51, 3) <50/<50, and 4) < 50/<50.

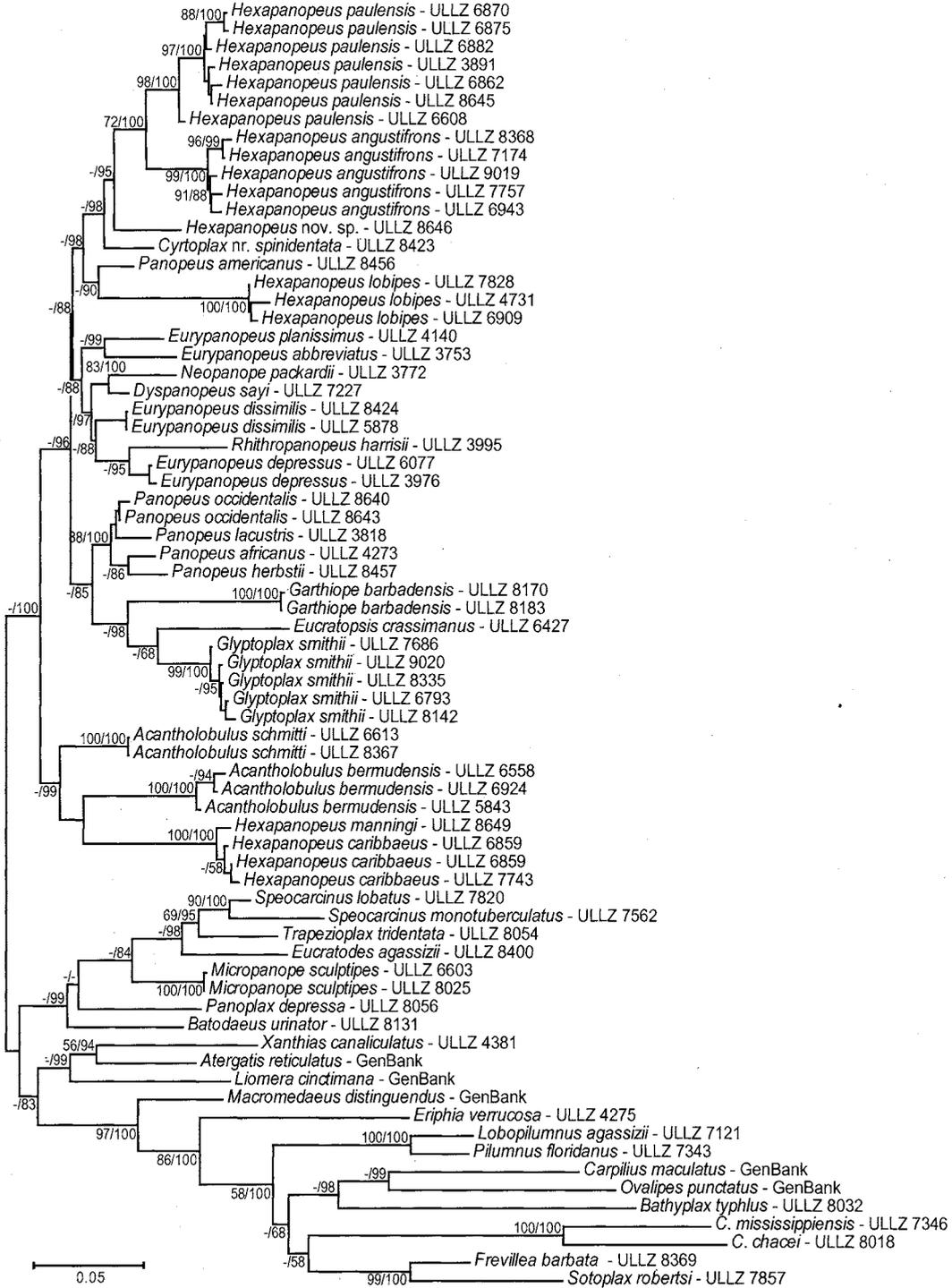


Figure 1. Phylogenetic relationships among panopeid crab species and selected representatives of the superfamily Xanthoidea *sensu* Martin & Davis (2001), inferred by Bayesian analysis from 521 basepairs of the 16S rDNA gene. Confidence intervals are from 500 bootstrap maximum likelihood analysis followed by Bayesian posterior probabilities. Genus shown as "C." = *Chasmocarcinus*. Values below 50 are indicated by "-".

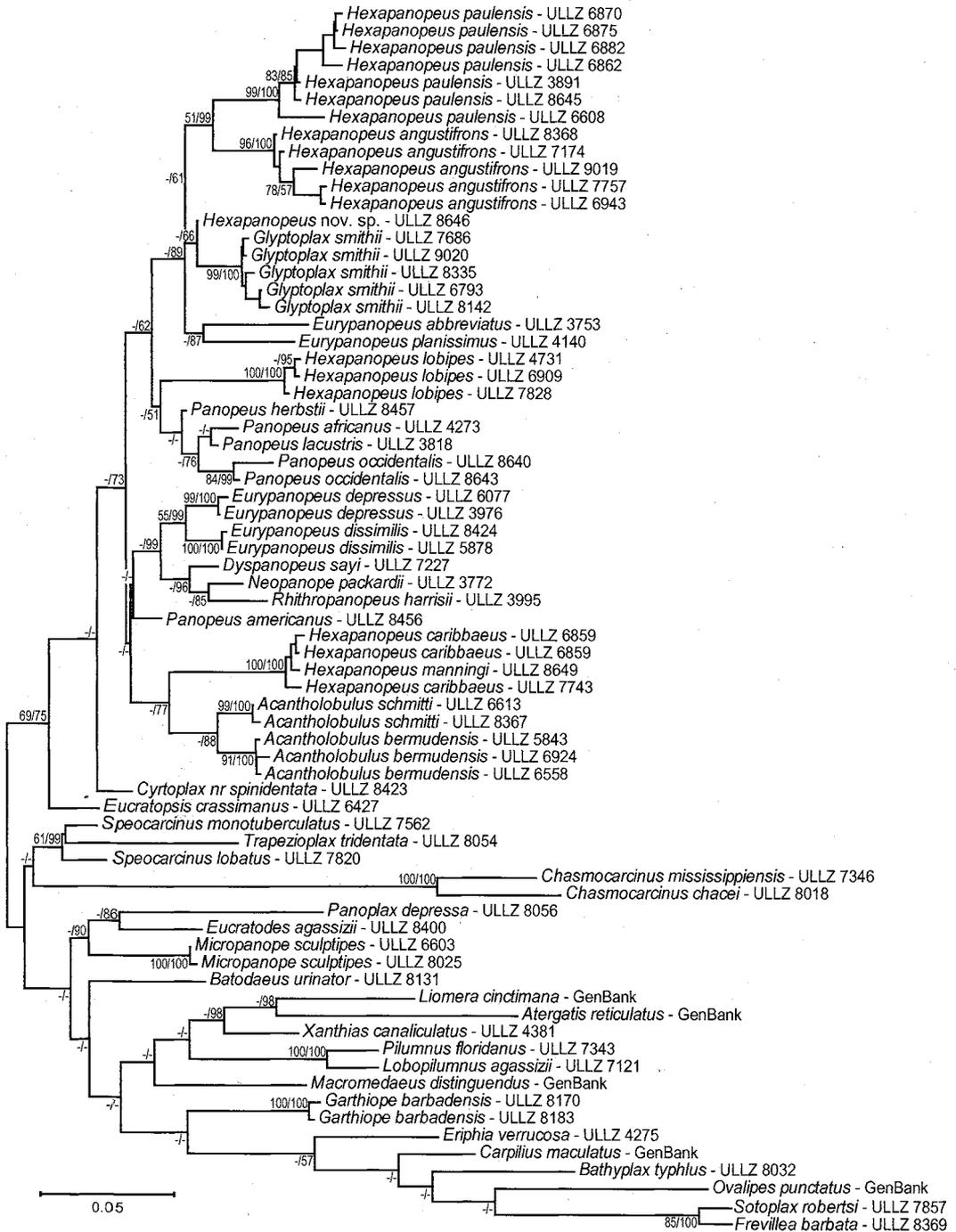


Figure 2. Phylogenetic relationships among panopeid crab species and selected representatives of the superfamily Xanthoidea *sensu* Martin & Davis (2001), inferred by Bayesian analysis from 284 basepairs of the 12S rDNA gene. Confidence intervals are from 500 bootstrap maximum likelihood analysis followed by Bayesian posterior probabilities. Values below 50 are indicated by “-”.

4 DISCUSSION

Here we report two molecular phylogenies of the genus *Hexapanopeus* and related genera of the family Panopeidae. These phylogenies, which are based on partial sequences of the 16S and 12S rDNA, contain five of the 13 nominal species in *Hexapanopeus* and a single undescribed species that appears to be assignable to the genus. In addition, we have included representatives of 18 species of the family Panopeidae in order to better address both the monophyly of *Hexapanopeus* and the relationships of species currently assigned to *Hexapanopeus* to other panopeid taxa. Although only five species of *Hexapanopeus* are included in the dataset, these five species represent five of the six nominal species known from the western Atlantic. It is clear from our analyses that the genus *Hexapanopeus* is markedly polyphyletic and that further study of all its putative members is warranted, by both morphological and molecular methods.

4.1 *Hexapanopeus angustifrons* and *Hexapanopeus paulensis*

The phylogenies presented here lend support to a narrowed definition of *Hexapanopeus* that includes only the type-species of the genus *Hexapanopeus angustifrons* (Benedict & Rathbun, 1891) and *Hexapanopeus paulensis* Rathbun, 1930, pending results of morphological and molecular analyses for the remaining eight present congeners. It is interesting to note that in all analyses these taxa form a monophyletic clade and that within both species there is further evidence for genetic structure. It is unclear if the genetic divergence seen in these clades is the result of cryptic speciation or population differentiation, but the current analyses suggest some combination of the two might occur in each complex.

4.2 *Hexapanopeus nov. sp.*

In the analyses of the 16S dataset, the sister group to the *H. angustifrons/H. paulensis* clade is an undescribed species from intertidal waters of south Texas in the western Gulf of Mexico. This undescribed species resembles *H. paulensis* in general morphology, but it has a very distinctive gonopod, which most resembles that of *Acantholobulus schmitti* (Rathbun, 1930). In contrast to the results of the 16S dataset, the 12S dataset lends support to a clade that is composed of the undescribed species and *Glyptoplax smithii* A. Milne-Edwards, 1880, as the sister group to the *H. angustifrons/H. paulensis* clade. Unfortunately, suitable material of *Glyptoplax pugnax* Smith, 1870, the type species of the genus, has not to date been available for molecular analysis; therefore, it remains unclear whether this undescribed species is most appropriately treated as a member of the genus *Hexapanopeus*, the genus *Glyptoplax*, or a new monospecific genus.

4.3 *Hexapanopeus lobipes*

The species *Hexapanopeus lobipes* (A. Milne-Edwards, 1880) has had a very unsettled taxonomic history. After being described as a species of *Neopanope* A. Milne-Edwards, 1880, it was later transferred to the genus *Lophopanopeus* Rathbun, 1898, by Rathbun in 1898. In his 1948 revision of the genus *Lophopanopeus*, Menzies pointed out that *H. lobipes* does not fit the diagnosis of the genus *Lophopanopeus*. Upon transferring the species to the genus *Hexapanopeus*, he noted that "it seems to fit the diagnosis of that genus better than that of any other American genus." Only isolated records of *Hexapanopeus lobipes* have been reported since Menzies' 1948 work (Wicksten 2005, Felder et al. in press), and there has been no reassessment of its placement within the genus *Hexapanopeus*. The gonopod of *H. lobipes* is distinctive and has little resemblance to those in other members of the genus *Hexapanopeus*. Furthermore, unlike the carapaces of *H. angustifrons* and *H. paulensis*, which have five distinct anterolateral teeth, the 1st and 2nd antero-lateral teeth of

H. lobipes are generally fused, giving the appearance of four anterolateral teeth. On the basis of these and other morphological features, it is unclear whether *H. lobipes* is justifiably assignable to the genus *Hexapanopeus*. Whatever the case to be made on the basis of morphology alone, we cannot concur with Ng et al. (2008) in reassigning this species to *Lophopanopeus*.

Our analyses support removal of *H. lobipes* from the genus *Hexapanopeus* and appear to justify establishment of a new monospecific genus for *H. lobipes*. In both topologies, *H. lobipes* falls outside the clade formed by *H. angustifrons* and *H. paulensis*. In the phylogeny inferred from the 16S dataset, *H. lobipes* is the sister group to *Panopeus americanus* Saussure, 1857, with ML bootstrap and pP values of <50/90, respectively. The phylogeny inferred from the 12S dataset presents *H. lobipes* as a sister group to *Panopeus s.s.* H. Milne Edwards, 1834, with ML bootstrap and pP values of <50/51, respectively. Despite low support values, both topologies lend support to the removal of *H. lobipes* from the genus *Hexapanopeus* and the erection of a new genus for the species, as is currently in progress.

4.4 *Hexapanopeus manningi*

Hexapanopeus manningi Sankarankutty and Ferreira, 2000, was described on the basis of material from Rio Grande do Norte, Brazil. This species was distinguished from *Hexapanopeus caribbaeus* (Stimpson, 1871) by characters of the frontal margin, the 3rd anterolateral tooth of the carapace, and the apical process of the gonopod; however, upon the basis of synoptic comparisons of the male paratype (USNM 260923) to material of *H. caribbaeus* from eastern Florida, it appears that there is considerable morphological overlap between these two taxa, raising the question as to whether *H. manningi* might be a junior synonym of *H. caribbaeus*. The topology inferred from the 16S dataset places *H. manningi* in very close proximity to *H. caribbaeus*; distance between these taxa is very short and comparable to that within other accepted single-species clades in our tree. The clade containing both *H. manningi* and *H. caribbaeus* has high support values, with ML bootstrap and pP values of 100/100, respectively. The strongest support for a synonymy of the two taxa comes from the topology inferred from the 12S dataset, with *H. manningi* positioned within the clade of *H. caribbaeus*. Our molecular phylogenies support synonymy of *H. manningi* with *H. caribbaeus*, and we herewith recommend that taxonomic revision, regardless of the eventual generic assignment to be accorded (see² below).

4.5 *Hexapanopeus caribbaeus*

Hexapanopeus caribbaeus was originally described as a representative of the genus *Micropanope*; however, upon erection of the genus *Hexapanopeus*, Rathbun (1898) transferred this species to the genus *Hexapanopeus* apparently on the basis of carapace shape. It wasn't until the 1997 work by Sankarankutty and Manning that distinct differences between the gonopod of *H. caribbaeus* and that of the type-species *H. angustifrons* were noted. In the present analysis, this species is clearly separated from *Hexapanopeus s.s.*, and shown to be more closely allied to the genus *Acantholobulus*.

4.6 Genus *Acantholobulus*

Felder and Martin (2003) erected the genus *Acantholobulus* to accommodate a number of species from the genera *Panopeus* and *Hexapanopeus*, which included: 1) the type-species *Acantholobulus bermudensis* (Benedict & Rathbun, 1898), formerly *Panopeus bermudensis*; 2) *Acantholobulus miraflorensis* (Abele & Kim, 1989), formerly *Panopeus miraflorensis*; 3) *Acantholobulus pacificus* (Edmondson, 1931), formerly *Panopeus pacificus*; and 4) *Acantholobulus schmitti* (Rathbun, 1930), formerly *Hexapanopeus schmitti*. Despite similarities between *H. caribbaeus* and *A. schmitti* in both carapace and gonopod morphology, the possible relationship between *H. caribbaeus* and newly assigned members of the genus *Acantholobulus* was not addressed. The phylogenies inferred

from both our datasets strongly support inclusion of *H. caribbaeus* within the genus *Acantholobulus*. While the phylogeny inferred from the 16S dataset shows *H. caribbaeus* nested with *Acantholobulus*, the topology inferred by analysis of the 12S datasets supports a sister group relationship between *H. caribbaeus* and both *A. bermudensis* and *A. schmitti*. Although both of these relationships are supported by $pP > 75$, the 16S dataset shows considerably higher pP (99/77 for 16S/12S, respectively). As additional species of *Acantholobulus* become available for inclusion in our analysis, the relationship between *Acantholobulus* and its closest relatives should be more definitively resolved. Even so, it is by present findings established that *H. caribbaeus* is well separated from *Hexapanopeus* s.s., and we apply the new combination *Acantholobulus caribbaeus* (Stimpson, 1871).

4.7 *Panopeus americanus*

In a study of mud crabs from the northwestern Atlantic, Schubart et al. (2000) clearly showed polyphyly in the genus *Panopeus*, with both *Acantholobulus bermudensis* (as *Panopeus bermudensis*, see discussion above) and *Panopeus americanus* falling well outside *Panopeus* s.s. (Schubart et al. 2000, Fig. 1). In the present study, we find additional support for these findings with the topologies inferred from both datasets positioning *P. americanus* outside *Panopeus* s.s.; however, the topologies differ in where *P. americanus* is placed relative to species of other genera. In the topology inferred from the 16S dataset, *P. americanus* is a sister group to *H. lobipes*, while in the topology inferred from the 12S dataset, *P. americanus* is the sister group to the clade containing *E. depressus*, *E. dissimilis*, *N. packardii*, *D. sayi*, and *R. harrisii*. However, this arrangement is poorly supported with ML bootstrap and pP values less than 50. Despite the differences in the topologies inferred from these two datasets, both provide evidence for the removal of *P. americanus* from *Panopeus*. Pending a thorough analysis of adult and larval morphology, data presented here support the establishment of a new genus for *P. americanus*.

4.8 Genus *Eurypanopeus*

Schubart et al. (2000, Fig. 1) also provided evidence for polyphyly among species presently assigned to the genus *Eurypanopeus* A. Milne-Edwards, 1880, with species of *Eurypanopeus* falling into three separate clades. In the present study, topologies inferred from both datasets support the polyphyletic nature of *Eurypanopeus*, with representatives found in three clades for 16S (Fig. 1) and two clades for 12S (Fig. 2). It is unclear what effect the addition of sequence data from other species of *Eurypanopeus* would have on the analyses; however, on the basis of evidence presented here and by Schubart et al. (2000), comprehensive study and taxonomic revision of the genus are needed.

4.9 *Panoplax depressa*

Despite a gonopod that shares little in common with that of the typical panopeid, *Panoplax depressa* Stimpson, 1871, has long been considered a member of the subfamily Eucratopsinae within the family Panopeidae (Martin & Abele 1986, McLaughlin et al. 2005, Ng et al. 2008). The analyses presented here provide no support for the inclusion of *Panoplax* within the family Panopeidae. In topologies inferred from both datasets, *Panoplax depressa* is well separated from remaining representatives of the family Panopeidae. In the phylogeny inferred from the 16S dataset, *Panoplax depressa* is found nested within a poorly supported clade containing representatives of the families Xanthidae and Pseudorhombilidae (ML/ $pP < 50/99$). In the phylogeny inferred from the 12S dataset, *Panoplax depressa* is also excluded from the remaining representatives of the family Panopeidae, nested within a poorly supported clade containing representatives of the family Xanthidae (ML/ $pP < 50/90$). Despite the low support values for the clades currently containing *Panoplax depressa*, there is little evidence to support the inclusion of *Panoplax* within the family Panopeidae.

4.10 *Garthiope barbadensis*

The genus *Garthiope* Guinot, 1990, was described to accommodate three small species formerly attributed to the genus *Micropanope*. Upon its erection, similarities between *Garthiope* and the family Trapeziidae were noted; however, in their recent review Ng et al. (2008) considered the genus to be a part of the family Xanthidae. In the present analyses the complex relationship of *Garthiope* to the remaining taxa of the Xanthoidea *sensu* Martin & Davis (2001) is shown in the conflict between the 16S dataset and 12S dataset in regards to the placement of *Garthiope*. In the phylogeny inferred from the 16S dataset, *Garthiope barbadensis* (Rathbun, 1921) is found within the family Panopeidae, where it is located within a clade containing representatives of the subfamily Eucratopsinae. However, this clade has support values with ML and pP values of <50/98. To further confound our understanding, in the analyses of the 12S dataset, *Garthiope barbadensis* falls well outside the family Panopeidae in a clade containing representatives of the Eriphioidea, Carpilioidea, Goneplacoidea, and Portunoidea. As this arrangement also has poor support values (<50), the relationship of *Garthiope* to these groups remains unclear. The type-species of the genus *Garthiope spinipes* (A. Milne-Edwards, 1880) was not included in these analyses; as a result, it is unclear what effect its inclusion may have on the analyses. Further study of the group is needed to clarify how this genus is related to other representatives of the Xanthoidea *sensu* Martin & Davis (2001).

4.11 *Outgroup taxa*

Composition of the superfamily Xanthoidea *sensu* Martin & Davis (2001) is a subject of ongoing debate (Guinot 1978; Jamieson 1993; Coelho & Coelho Filho 1993; Schubart et al. 2000; Wetzer et al. 2003; Karasawa & Schweitzer 2006; Ng et al. 2008). In all of our analyses, the family Xanthidae is clearly shown to be polyphyletic. Analysis of the 16S dataset reveals a single clade containing representatives of Panopeidae, Pseudorhombilidae, and three subfamilies of Xanthidae; however, this clade is poorly supported with ML bootstrap values and pP of <50/99 (Fig. 1). Furthermore, a second clade contains a single representative of the family Xanthidae as well as representatives of Eriphioidea, Pilumnoidea, Carpilioidea, Goneplacoidea, and Portunoidea. This clade is well supported with ML bootstrap values and pP of 97/100. Within this clade we also find representatives of three families of Goneplacoidea, with two species of *Chasmocarcinus* representing Chasmocarcinidae, *Frevillea barbata* and *Sotoplax robertsi* representing Euryplacidae, and *Bathypylax typhlus* representing Goneplacidae. While Chasmocarcinidae and Euryplacidae form a poorly supported monophyletic clade, Goneplacidae is found in another clade with representatives of Portunoidea and Carpilioidea. Although neither of these clades is well supported (ML/pP <50/58 & <50/98), they provide evidence for a polyphyletic Goneplacoidea. While the topology inferred from the 12S dataset (Fig. 2) still presents evidence for a polyphyletic Xanthidae and Goneplacoidea, the evidence differs from that inferred by the 16S dataset (Fig. 1). However, support values for the outgroup topology inferred by the 12S dataset are very low, making any conclusions drawn from this topology questionable. Regardless of differences between these two topologies, it is apparent that both Goneplacoidea and Xanthidae are polyphyletic and in need of revision.

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