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Decapod Crustacean Phylogenetics

edited by

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Molecular Phylogeny of the Thalassinidea Based on Nuclear and Mitochondrial Genes

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ABSTRACT

We conducted a molecularly based phylogenetic analysis with representatives of the thalassinidean families Axianassidae, Axiidae, Callianassidae, Callianideidae, Calocarididae, Ctenochelidae, Laomediidae, Micheleidae, Strahlaxiidae, Thalassinidae, Thomassiniidae, and Upogebiidae, along with decapod outgroup taxa representing the infraorders Anomura, Astacidea, Brachyura, Caridea, and Achelata. Analyses were based on two datasets, one corresponding to a partial fragment of the 16S mitochondrial gene and a second to a partial fragment of the 18S nuclear gene, representing roughly 1,800 nuclear and 550 mitochondrial characters. We incorporated 34 genera and 50 species in the analysis upon which our molecular phylogenetic trees were based and compared outcomes to morphologically based phylogenies. Our analysis finds the infraorder Thalassinidea to be paraphyletic, as presently comprised. We also find no support for monophyly in either the superfamily Axioidea or the superfamily Callianassoidea. Two large clades into which the infraorder is divided instead recall arrangements that were based upon larvae by Gurney and subsequently supported in some early taxonomic revisions. We conclude that these clades deserve separate infraordinal status, and we draw upon the work of de Saint Laurent for the name of each. One we refer to the infraorder Gebiidea, encompassing representatives of Upogebiidae, Laomediidae, Thalassinidae, and Axianassidae. The other we refer to Axiidea, encompassing Callianassidae, Ctenochelidae, Strahlaxiidae, Micheleidae, Callianideidae, Thomassiniidae, Axiidae, and Calocaridae. We accept previous evidence merging Eiconaxiidae with the Axiidae, and we suggest the Calocarididae should be likewise merged. We also present evidence to support merging of Thomassiniidae back into Callianideidae.

1 INTRODUCTION

The infraorder Thalassinidea encompasses a group of burrowing decapods that is almost global in distribution, with the northernmost record at 71° N and the southernmost at 55° S. Resembling hermit crabs in some features and lobsters in others (Borradaile 1903), they are known to populate sediments in depths from 0 to >2000 m (Dworschak 2005). Thalassinidean genera are in varied ways adapted morphologically to a fossorial existence, and many show evidence of a functional *linea thalassinica*, a hinge-line that to various degrees allows flexure of the carapacial branchiostegites for gill ventilation or cleaning while within a burrow. This character was invoked by some early workers to define membership in this group, but others discounted its systematic importance, as noted by Barnard (1950).

Thalassinideans often play major roles in mechanical bioturbation of sediments and mobilization of nutrients entrained in sediments or sedimentary pore-waters, with impacts on water chemistries as well as associated marine microbial, plant, and animal assemblages (Bird 2000, 2004; Dworschak 2000; Felder 2001; Atkinson & Taylor 2004; Coelho 2004; Dworschak et al. 2006; Klerks et al. 2007; Pillay et al. 2007). Larval life histories vary greatly within the group (Felder et al. 1985; Nates et al. 1997; Strasser & Felder 2000, 2005), as do burrow shapes, physiology, and trophic dependencies, which can also be phylogenetically informative (Felder 2001; Coelho 2004; Dworschak & Ott 1993). While classification of the thalassinideans has focused primarily on adult morphology, characters ranging from larval setation to fecal pellets at one time or another have been suggested as evidence for group relationships (Gurney 1942).

Recent accounts of thalassinidean diversity have usually recognized 11 families, 94 genera, and 556 species (Dworschak 2000, 2005). However, newly recognized species and genera can be added to these counts (bringing the count of genera to 99 and species to 600), and recognition of the family Axianassidae now appears to be justifiable on the bases of molecular (Tudge & Cunningham 2002) and comparative larval studies (Strasser & Felder 2005). The subfamily Gourretiinae was also raised to family rank (Sakai 2004), but in this case without supporting analyses and in clear contradiction to the cladistic evidence of Tudge et al. (2000), wherein members of Gourretiinae were shown to belong to Ctenochelidae. Also, the monogeneric family Eiconaxiidae has been proposed (Sakai & Ohta 2005) for *Eiconaxius*, but we continue to regard this group as a member of the monophyletic Axiidae in the absence of convincing morphological evidence that it is not just a specialized member of this family.

Phylogeny of the order Decapoda overall has been extensively debated at both higher and lower levels of classification but remains largely unresolved after a century of study (see de Saint Laurent 1973, 1979a, b; Felgenhauer & Abele 1983; McLaughlin & Holthuis 1985; Abele & Felgenhauer 1986; Kim & Abele 1990; Poore 1994; Scholtz & Richter 1995; Martin & Davis 2001; Schram 2001; Morrison et al. 2002; Tudge & Cunningham 2002; Dixon et al. 2003; Porter et al. 2005). Thalassinidean decapods were originally brought together by Borradaile (1903) into four families: Axiidae Huxley, 1879, Laomediidae Borradaile, 1903, Thalassinidae Dana, 1852, and Callianassidae Dana, 1852, with the callianassids subdivided to accommodate the subfamilies Callianassinae and Upogebiinae. While widely applied (de Man 1928; Bouvier 1940; Zariquiey Alvarez 1968), this classification did not conform to relationships deduced from larval morphology by Gurney (1938) who, lacking comparative materials of the Axianassidae and Thalassinidae, found larval similarities to group at least Callianassidae with Axiidae, and Upogebidae with Laomediidae (see also Gurney 1942). This provided possible insight to phylogeny within the overall group, and suggested paraphyly within "Callianassidae" as it had been previously conceived, prompting at least some workers (Barnard 1950) to adopt Gurney's scheme. Following publication of a short paper in the early 1970s (de Saint Laurent 1973), which adopted Gurney's separation of the Upogebiidae and Callianassidae, there appeared several subsequent works applying revisions based upon adult morphology (Le Loeuff & Intès 1974; de Saint Laurent 1979a, b; de Saint Laurent & Le Loeuff 1979). In the following two decades, a host of morphologically based revisions impacted family and subfamily ranks among varied subgroups of the thalassinideans (Kensley 1989; Sakai & de Saint Laurent 1989; Manning & Felder 1991; Sakai 1992, 1999; Poore 1994).

Among recent workers to address the thalassinideans overall, some have proposed the group to be monophyletic (Poore 1994; Scholtz & Richter 1995; Schram 2001; Dixon et al. 2003; Ahyong & O'Meally 2004; Tsang et al. 2008b) and others paraphyletic or polyphyletic (de Saint Laurent 1973; Tudge 1997; Tudge & Cunningham 2002; Morrison et al. 2002; Tsang et al. 2008a). The group was morphologically rediagnosed less than 15 years ago on the basis of a single synapomorphy, the presence of a dense row of evenly spaced long setae along inferior margins of pereopod 2 (Poore 1994, 1997); it was also therewith reestablished that the *linea thalassinica* was a likely homolog of the *linea anomurica*, and that varied permutations of this character were thus not diagnostic.

However, monophyly of the group remains uncertain (see discussion in Martin & Davis 2001), as do evolutionary relationships among families assigned to the infraorder Thalassinidea, which makes for a problematic classification.

Based on morphological cladistic analyses, Poore (1994) distributed families among three super-families: Thalassinoidea (one family), Axioidea (four families), and Callianassoidea (six families). In a subsequent morphological cladistic analysis of the order Decapoda (Dixon et al. 2003) seven families of Thalassinidea were included. While the intention of the latter authors was not specifi-cally to solve phylogenetic relationships within Thalassinidea, it is noteworthy that members of the superfamily Callianassoidea were found to be paraphyletic (Dixon et al. 2003: fig. 6), with *Jaxea* positioned basally instead of being clustered with *Callianassa, Upogebia*, and *Callianidea*. The latter grouping of three is also contrary to relationships suggested by larval evidence.

Some inconsistencies between views on the classification and systematics of Thalassinidea re-sult from limited taxonomic representation. For example, Poore (1994) did not include *Axianassa*, only *Laomedia* (Axianassidae effectively excluded). The family Ctenochelidae (represented by four genera) appeared to be paraphyletic with respect to Callinassidae (one genus) in Poore's (1994) treatment, but in a more robust cladistic analysis involving six ctenochelid genera and numerous callianassid genera (Tudge et al. 2000), support was found for family status of both Callianassidae and Ctenochelidae. The latter analysis did not support all subfamilies proposed for membership within Callianassidae or Ctenochelidae.

Molecular genetic approaches also have been applied to understand evolutionary relationships within Thalassinidea. Tudge & Cunningham (2002) analyzed nuclear 18S and mitochondrial (mt) 16S sequence data from fourteen species representing seven of the twelve families of Thalassinidea. They found low support for monophyly of Thalassinidea, discovering instead two clades, one in-cluding Strahlaxiidae and Callianassidae (seven species) and the other Upogebiidae (two species), Axianassidae, Laomediidae (two species), and Thalassinidae. Porter et al. (2005) probed evolution-ary relationships of the order Decapoda with the aid of four DNA fragments but included only members of Callianassidae in their analysis.

Our own molecular studies of Thalassinidea have been under way since 2002 (Felder et al. 2003; Felder & Robles 2004; Robles & Felder 2004). Recently, concurrent studies have come to our at-tention, bearing on many of the same questions we address (Tsang et al. 2008a, b). These studies differ from our own in terms of thalassinidean and outgroup taxa included and in outcomes. We take this opportunity to present our independent findings and compare them with those of other recent molecular phylogenetic studies. Principal objectives of our study are to resolve questions of mono-phyly of the Thalassinidea as a whole, but also to address monophyly and diagnostic characters of its constituent families and subfamilies. In a separate analysis (Felder & Robles this volume), other taxa are brought into an analysis of specifically the family Callianassidae.

2   MATERIALS AND METHODS

2.1   *Taxa included*

Our sample consisted of 55 organisms representing 12 currently accepted families of Thalassinidea (Table 1) and three commonly recognized superfamilies (*sensu* Martin & Davis 2001). To represent the superfamily Callianassoidea, we included representatives of Axianassidae, Callianassidae, Cal-lianideidae, Ctenocheleidae, Laomediidae, Thomassiniidae, and Upogebiidae. For the superfamily Axioidea we included representatives of Axiidae, Calocarididae, Micheleidae, and Strahlaxiidae. We were unable to include Eiconaxiidae, a monogeneric family proposed by Sakai & Ohta (2005), which we regard as a highly specialized axiid. To represent the superfamily Thalassinoidea, we included a species of the genus *Thalassina*, the only genus in the family Thalassinidae.

To serve as outgroups, we included sequence data for 20 species representing as many genera, from infraorders (and listed families) as follow: Anomura (Galatheidae, Hippidae, Lithodidae), Astacidea (Astacidae, Cambaridae, Enoplometopidae, Nephropidae, Parastacidae), Brachyura (Cancridae, Portunidae), Caridea (Atyidae, Hippolytidae, Palaemonidae, Pandalidae), and Achelata (Palinuridae, Scyllaridae), to test for monophyly of Thalassinidea.

2.2   *DNA extraction, PCR, and sequencing*

DNA was extracted from muscle tissues excised from the abdomen or pleopods following standard protocols (Robles et al. 2007). Standard PCR amplification and automated sequencing protocols were used to sequence a fragment of approximately 550 bp of the 16S rDNA and 1,800 bp of the 18S rDNA genes. Both strands were sequenced. Primers used for PCR were 16ar (5-CGC CTG TTT ATC AAA AAC AT-3), 16br (5-CCG GTC TGA ACT CAG ATC ACG T-3) (Palumbi et al. 1991), 1472 (5-AGA TAG AAA CCA ACC TGG-3) (Crandall & Fitzpatrick 1996), and 16L2 (5-TGC CTG TTT ATC AAA AAC AT-3) (Schubart et al. 2002). Primers used for the 18S fragment were 18S-A (5'-AAC CTG GTT GAT CCT GCC AGT-3'), 18S-B (5'-TGA TCC TTC CGC AGG TTC ACC T-3') (Medlin et al. 1988), 18S-L (5'-CCA ACT ACG AGC TTT TTA ACT G-3'), 18S-C (5'-CGG TAA TTC CAG CTC CAA TAG-3'), 18S-Y (5'-CAG ACA AAT CGC TCC ACC AAC-3'), 18S-O (5'-AAG GGC ACC ACC AGG AGT GGA G-3') (Apakupakul et al. 1999).

2.3   *Phylogenetic analyses*

Consensus of complementary sequences was obtained with the Sequencher software program (ver 4.7, Genecodes, Ann Arbor, MI). Multiple sequence aligning was performed with the aid of BioEdit v.7.08.0 (Hall 1999) with the following settings: 6-2/6-2 penalty (opening-gap extension, pairwise/multiple alignment, respectively) following a profile alignment strategy. Base composition, pattern of substitution for pairwise comparison, and analysis of variability along both fragments of the 16S mtDNA and the 18S nDNA were performed as implemented in PAUP 4.0 beta 10 (Swofford 1998). Homogeneity of nucleotide frequency among taxa was also assessed for each gene with a χ^2 test as implemented in PAUP. Previous to the analysis of the combined data, we performed an incongruence length difference (ILD) test or partition homogeneity test (Bull et al. 1993), as implemented in PAUP, to determine whether the 16S and 18S genes could be considered samples of the same underlying phylogeny.

Phylogenetic analyses were conducted using MRBAYES for Bayesian analysis (BAY) and PAUP 4.0 beta 10 for both maximum parsimony (MP) and neighbor joining (NJ) analyses; maximum likelihood (ML) analysis was conducted with RAxML v.7.0.4 (Stamatakis 2006) using the online version at the Cyber Infrastructure for Phylogenetic Research (CIPRES) website (Stamatakis et al. 2008). Prior to conducting the BAY and NJ analyses, the model of evolution that best fit the data was determined with the software MODELTEST (Posada & Crandall 1998). ML was performed with the default parameters for RAxML for the GTR model of evolution. BAY analysis was performed sampling one tree every 1,000 generations for 2,000,000 generations, starting with a random tree, thus obtaining 2,001 trees. A preliminary analysis showed that stasis was reached at approximately 30,000 generations. Thus, we discarded 51 trees corresponding to the first 50,000 generations and obtained a 50% majority rule consensus tree from the remaining 1,950 saved trees. NJ analysis was carried out with a distance correction set with the parameters obtained from MODELTEST (Posada & Crandall 1998). MP analysis was performed as a heuristic search with gaps treated as a fifth character, multistate characters interpreted as uncertain, and all characters considered as unordered. The search was conducted with a random sequence addition and 1,000 replicates, including tree bisection and reconnection (TBR) as a branch swapping option; branch swapping was performed on the best trees only.

To determine confidence values for the resulting trees, we ran 2,000 bootstrap pseudo-replicates for NJ and MP analysis, based on the same parameters as above. For ML analysis, we selected the option to automatically determine the number of bootstraps to be run in RAxML. Thus, 250 bootstrap pseudo-replicates were run. On the molecular trees, confidence values >50% were reported for ML, MP, and NJ analyses (bootstraps), while for the BAY analysis values were reported for posterior probabilities of the respective nodes among all the saved trees. Sequences as well as alignments have been submitted to GenBank as a Popset.

3 RESULTS

Unrooted trees (not shown here) yielded well-defined separations of Brachyura, Caridea, and Achelata, but not Thalassinidea. As Caridea was by this method shown to be the most distinct infraorder from all other infraorders, we used this clade thereafter to root our tree. Our final alignment included 2,094 bp, 1,729 for the 18S nuclear gene and 365 bp for the 16S mt gene (excluding primer regions, saturated and ambiguous fragments of both genes). Of these, 1,363 were invariable, 699 were variable but not parsimony informative, and 534 were parsimony informative characters. The ILD test showed no significant incongruence (P = 0.578). Thus we used the combined 16S and 18S fragments for our analysis. The nucleotide composition of this dataset can be considered homogeneous ($\chi^2 = 65.96$, df = 186, P = 1.00), with a slightly larger percentage of A-T (26.0%; 26.2 %).

The best-fitting model of substitution, selected with the Akaike information criterion (AIC, Akaike 1974) as implemented in MODELTEST (Posada & Crandall 1998), was the general time-reversible model, with invariable sites and a gamma distribution GTR+Γ+δ (Tavaré 1986) and with the following parameters: assumed nucleotide frequencies: A = 0.2677, C = 0.2066, G = 0.2592, T = 0.2665; substitution rates A-C = 1.6548, A-G = 5.2680, A-T = 2.7285, C-G = 1.1068, C-T = 6.5936, G-T = 1.0000; proportion of invariable sites Γ = 0.5407; variable sites followed a gamma distribution with shape parameter δ = 0.5144. These values were used to obtain both BAY and NJ trees. All four phylogenetic methods yielded almost identical tree topologies with high support values (Fig. 1). Differences found between the methods were limited primarily to a few of the internal/terminal clades.

3.1 *Testing for monophyly of the Thalassinidea*

Our analyses showed Thalassinidea to be a distinctly paraphyletic group (Fig. 1). Members of the infraorder were separated into two well-supported clades. "Clade-A" grouped representatives of the families Upogebiidae, Laomediidae, Thalassinidae, and Axianassidae, thus encompassing our sole representative of the superfamily Thalassinoidea together with several families that are typically included in the superfamily Callianassoidea. "Clade-B" grouped representatives of the families Axiidae, Callianassidae, Calocarididae, Ctenochelidae, Micheleidae, Strahlaxiidae, and Thomassiniidae, thus encompassing remaining members of the superfamily Callianassoidea along with all members of the Axioidea, but clearly showing the latter superfamily to be polyphyletic. As rooted, our analysis positions Clade-B (hereafter called Axiidea) as a sister taxon of the other decapod infraorders (outgroup Caridea excepted), not of Clade-A (hereafter called Gebiidea) (Fig. 1).

3.2 *The families of "Gebiidea"*

One highly supported node shows a monophyletic family Upogebiidae while another well-supported node groups all representatives of Laomediidae, Thalassinidae, and Axianassidae. Structure within the Upogebiidae itself shows two sister clades, one of them moderately supported, that also suggest paraphyly in the genus *Upogebia* as presently applied. The companion clade includes Axianassidae positioned as a sister clade to a monophyletic Laomediidae, albeit at low support values.
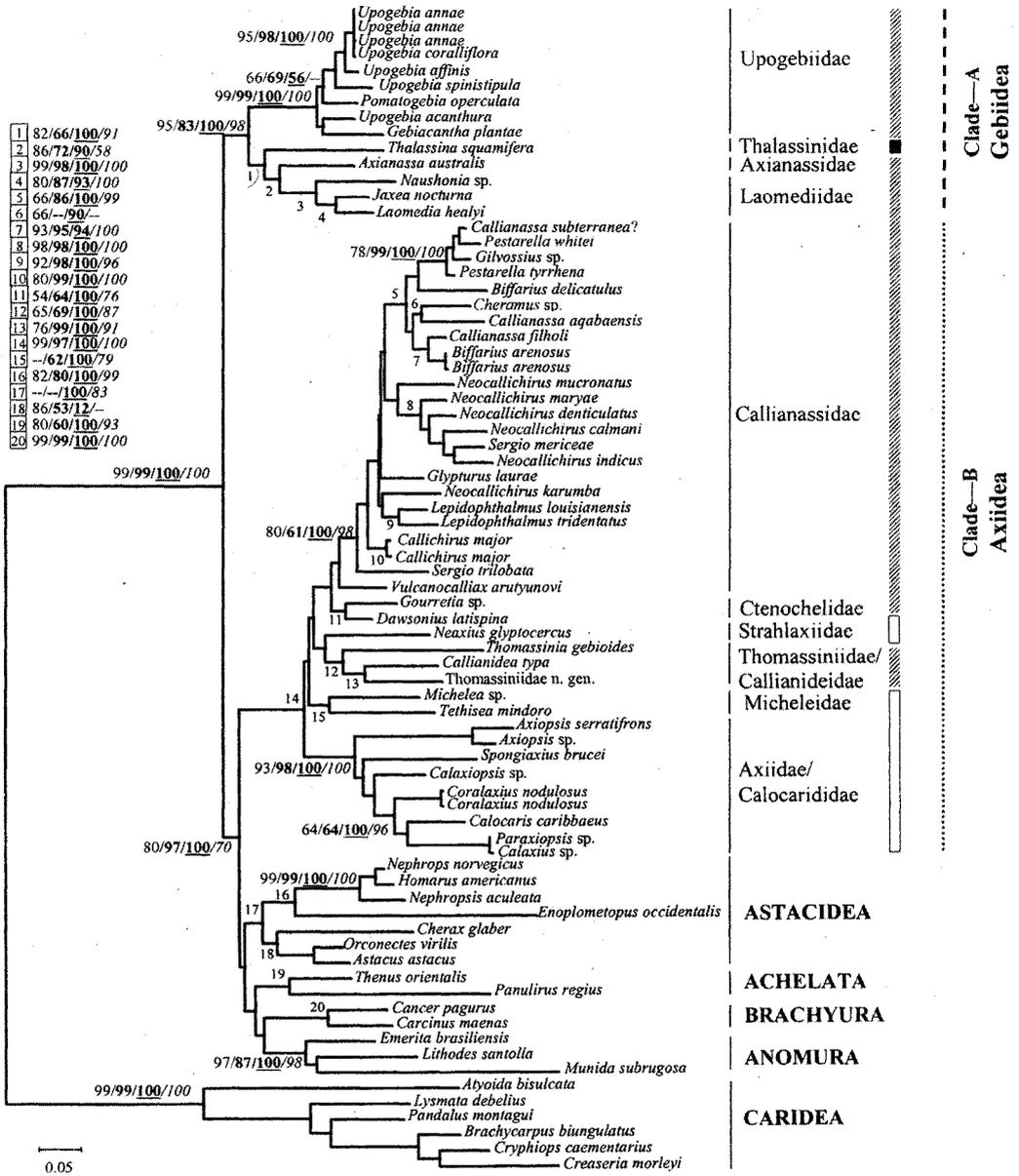
Figure 1. Evolutionary relationships among 12 families of Thalassinidea (*sensu* Martin & Davis 2001) inferred from a Bayesian analysis of 16S and 18S rDNA data. Support values shown from left to right are for NJ, MP, BAY, and ML respectively; "–" represents value equal to or lower than 50%; "?" indicates questioned identity of a sequence from GenBank. Vertical bar indicates assignments to herewith-rejected superfamilies Axioidea (open), Thalassinoidea (solid), and Callianassoidea (cross-hatched). We question identity of "*Callianassa subterranea*" in this tree, ostensibly representing the type species of that genus. It is included here on the basis of sequence data from GenBank (Table 1), originally used in Porter et al. (2005) and thereafter by Tsang et al. (2008b). Our own 16S sequence data for relatively topotypic specimens (morphologically confirmed as *C. subterranea*) do not match those in GenBank (DQ079706).

Table 1. List of specimens used for molecular analysis, as commonly classified (*sensu* Martin & Davis 2001). Letter abbreviations preceding catalog numbers indicate collections as follow: MV = Museum Victoria; NHMW = Naturhistorisches Museum, Wien; NMCR = National Museum of the Philippines, Manila; ULLZ = University of Louisiana—Lafayette Zoological Collection; USNM = National Museum of Natural History; ZRC = Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore; KC, MLP, and KAC = voucher IDs as reported in corresponding publication. Where two catalog numbers appear for the same sample, tissue was donated to the University of Louisiana at Lafayette and archived there under a ULLZ number, while original voucher retains number at the respective museum. Sequences obtained from GenBank are shown by accession number (Acc. No.) for the respective gene; the source where first published (S) is as follows: 1 = Porter et al. 2005; 2 = Bracken et al., this volume; 3 = Tudge & Cunningham 2002; 4 = Ahyong & O'Meally 2004; 5 = Pérez-Losada et al. 2002a; 6 = Pérez-Losada et al. 2002b; 7 = Pérez-Losada et al. 2004; 8 = Crandall et al. 2000; 9 = Giribet et al. 2001; 10 = Morrison et al. 2002. "?" following *Callianassa subterranea* indicates questionable identity of the sequence in GenBank.

Taxon Name	Catalog No.	Acc. No. 18S	Acc. No. 16S	S
OUTGROUP				
Anomura				
Galatheidae				
Munida subrugosa (White, 1847)	KACmusu	AF439382	AY050075	6/5
Hippidae				
Emerita brasiliensis Schmitt, 1935	KACembr	AF439384	DQ079712	6/1
Lithodidae				
Lithodes santolla (Molina, 1782)	LAClisa	AF439385	AY595927	6/7
Astacidea				
Astacidae				
Astacus astacus (Linnaeus, 1758)	JF134	AF235959	AF235983	8
Cambaridae				
Orconectes virilis (Hagen, 1870)	JC897	AF235965	AF235989	8
Enoplometopidae				
Enoplometopus occidentalis (Randall, 1840)		AY583966	AY583892	4
Nephropidae				
Homarus americanus H. Milne Edwards, 1837	KAChoam	AF235971	AF370876	8/9
Nephrops norvegicus (Linnaeus, 1758)	KC2163	DQ079762	DQ079726	1
Nephropsis aculeata Smith, 1881	KC2117	DQ079761	DQ079727	1
Parastacidae				
Cherax glaber Rieck, 1967	KACchgl	DQ079745	AF135978	1
Brachyura				
Cancridae				
Cancer pagurus Linnaeus, 1758	KC2158	DQ079743	DQ079708	1
Portunidae				
Carcinus maenas (Linnaeus, 1758)	KACcama	DQ079744	DQ079709	1
Caridea				
Atyidae				
Atyoida bisulcata (Randall, 1840)	KC2138	DQ079747	DQ079704	1
Hippolytidae				
Lysmata debelius Bruce, 1983	MLP121	DQ079752	DQ079718	1
Palaemonidae				
Creaseria morleyi (Creaser, 1936)	MLP102	DQ079746	DQ079710	1
Cryphiops caementarius (Molina, 1782)	JC1219	DQ079747	DQ079711	1
Brachycarpus biunguiculatus (Lucas, 1846)	ULLZ 7430	EU868779	EU868685	2

Table 1. continued.

Taxon Name	Catalog No.	Acc. No. 18S	Acc. No. 16S	S
Pandalidae				
Pandalus montagui Leach, 1814	ULLZ 6966	EU868792	EU868698	2
Achelata				
Palinuridae				
Panulirus regius De Brito Capello, 1846	KC2167	DQ079765	DQ079730	1
Scyllaridae				
Thenus orientalis (Lund, 1793)	NONE	EU875001	EU874951	3
INGROUP				
Thalassinidea				
Axioidea				
Axiidae				
Axiopsis	ULLZ 7750	EU874970	EU874920	
Axiopsis serratifrons (A. Milne-Edwards, 1873)	ULLZ 8996	EU874992	EU874942	
Calaxius sp.	ULLZ 7041	EU874960	EU874910	
Coralaxius nodulosus (Meinert, 1877)	ULLZ 7011	EU874959	EU874909	
Coralaxius nodulosus (Meinert, 1877)	ULLZ 7329	EU874963	EU874913	
Paraxiopsis sp.	ULLZ 7559	EU874967	EU874917	
Spongiaxius brucei (Sakai, 1986)	ULLZ 8937 MV J55585	EU874991	EU874941	
Calocarididae				
Calaxiopsis sp.	ULLZ 8918 MV J55576	EU874988	EU874938	
Calocaris ~caribbaeus Kensley, 1996	ULLZ 8285	EU874979	EU874929	
Micheleidae				
Michelea sp.	ULLZ 8920 MV J55702	EU874990	EU874940	
Tethisea mindoro Poore, 1997	ULLZ 8919 MV J55703	EU874989	EU874939	
Strahlaxiidae				
Neaxius glyptocercus von Martens, 1868	MV J39643	EU874994	EU874944	3
Callianassoidea				
Axianassidae				
Axianassa australis Rodrigues & Shimizu, 1992	MV J44613	EU874998	EU874948	3
Callianassidae				
Callianassinae				
Biffarius arenosus (Poore, 1975)	BaV3	DQ079739	DQ079705	1
Biffarius arenosus (Poore, 1975)	MV J40669	EU874995	EU874945	3
Biffarius delicatulus Rodrigues & Manning, 1992	USNM 309754	EU875003	EU874953	3
Callianassa aqabaensis Dworschak, 2003	ULLZ 7924	EU874975	EU874925	
Callianassa filholi A. Milne-Edwards, 1878	MV J44818	EU874999	EU874949	3
Callianassa subterranea? (Montagu, 1808)	KACcasu	DQ079740	DQ079706	1
Gilvossius sp.	ULLZ 7919	EU874974	EU874924	
Pestarella tyrrhena (Petagna, 1792)	ULLZ 7931	EU874977	EU874927	
Pestarella whitei (Sakai, 1999)	ULLZ 7932 NHMW 21948	EU874978	EU874928	

Table 1. continued.

Taxon Name	Catalog No.	Acc. No. 18S	Acc. No. 16S	S
Callichirinae				
Callichirus major (Say, 1818)	MV J39044	AF436002	AF436041	10
Callichirus major (Say, 1818)	KAC 1864	DQ079741	DQ079707	1
Glypturus laurae (de Saint Laurent, 1984)	ULLZ 8446 NHMW 21939	EU874985	EU874935	
Lepidophthalmus louisianensis (Schmitt, 1935)	ULLZ 7918	EU874973	EU874923	
Lepidophthalmus tridentatus (von Martens, 1868)	ULLZ 7928 NMCR 27007	EU874976	EU874926	
Neocallichirus calmani (Nobili, 1904)	ULLZ 8439 NHMW 21943	EU874982	EU874932	
Neocallichirus denticulatus Ngoc-Ho, 1994	ULLZ 8441 NHMW 21945	EU874984	EU874934	
Neocallichirus indicus (de Man, 1905)	ULLZ 8437 NHMW 21942	EU874981	EU874931	
Neocallichirus karumba (Poore & Griffin, 1979)	ULLZ 8435 ZRC 2002-0274	EU874980	EU874930	
Neocallichirus mucronatus (Strahl, 1861)	ULLZ 8440 NHMW 21944	EU874983	EU874933	
Neocallichirus maryae (Schmitt, 1935)	USNM 309751	EU875002	EU874952	3
Sergio mericae Manning & Felder, 1995	USNM 309755	EU875004	EU874954	3
Sergio trilobata (Biffar, 1970)	ULLZ 7916	EU874972	EU874922	
Cheraminae				
Cheramus sp.	ULLZ 7313	EU874962	EU874912	
Vulcanocalliacinae				
Vulcanocalliax arutyunovi Dworschak & Cunha, 2007	ULLZ 7620 NHMW 21927	EU874969	EU874919	
Callianideidae				
Callianidea typa H. Milne Edwards, 1837	ULLZ 9179	EU874993	EU874943	
Ctenochelidae				
Gourretia sp.	ULLZ 7370	EU874965	EU874915	
Dawsonius latispina (Dawson, 1967)	ULLZ 7306	EU874961	EU874911	
Laomediidae				
Jaxea nocturna Nardo, 1847	MV J39045	AF436006	AF436046	10
Laomedia healyi Yaldwyn & Wear, 1970	MV J40697	EU874996	EU874946	3
Naushonia sp.	ULLZ 8915	EU874987	EU874937	
Thomassiniidae				
Thomassinia gebioides de Saint Laurent, 1979	ULLZ 8903	EU874986	EU874936	
Thomassiniidae [unnamed genus]	ULLZ 7752	EU874971	EU874921	
Upogebiidae				
Gebiacantha plantae (Sakai, 1982)	MV J44914	EU875000	EU874950	3
Pomatogebia operculata (Schmitt, 1924)	ULLZ 6905	EU874957	EU874907	
Upogebia acanthura (Coelho, 1973)	ULLZ 7593	EU874968	EU874918	
Upogebia affinis (Say, 1818)	MV J40668	AF436007	AF436047	10
Upogebia annae Thistle, 1973	ULLZ 6757	EU874955	EU874905	
Upogebia annae Thistle, 1973	ULLZ 7009	EU874958	EU874908	

Table 1. continued.

Taxon Name	Catalog No.	Acc. No. 18S	Acc. No. 16S	S
Upogebia annae Thistle, 1973	ULLZ 7522	EU874966	EU874916	
Upogebia coralliflora Williams & Scott, 1989	ULLZ 6765	EU874956	EU874906	
Upogebia spinistipula Williams & Heard, 1991	ULLZ 7360	EU874964	EU874914	
Thalassinoidea				
Thalassinidae				
Thalassina squamifera de Man, 1915	MV J41662	EU874997	EU874947	3

Naushonia is not isolated from the other two laomediid genera at high support values, while Axianassidae + Laomediidae form a sister group to Thalassinidae.

3.3 *The families of "Axiidea"*

Within this large clade, there is high support for grouping together members of Axiidae and Calocarididae into an internal clade, separated from representatives of all other axioid families as well as from Callianassidae and Ctenochelidae. Branch lengths are short for some of these separations, but support values are generally high. The two calocaridid genera included in this study, *Calaxiopsis* (already listed by Sakai & Ohta 2005 as an axiid) and *Calocaris*, were placed separately within Axiidae, casting doubt on the monophyly of Calocarididae (although it must be remembered that only two of six calocaridid genera and five of 21 axiid genera were included).

  While clearly separated from the axiid and calocaridid genera, other axioid families were positioned immediately basal to the callianassids and ctenochelids, but without majority rule support. Although represented by only two species each, there is no evidence to contradict monophyly of either the Micheleidae or the Ctenochelidae (noting that we treat both *Dawsonius* and *Gourretia* within the Ctenochelidae, rather than in the Gourretiidae of Sakai 1999). Sister-group positioning of the Strahlaxiidae to a clade encompassing representatives of the Callianideidae and Thomassiniidae appears atypical at first glance, but Poore (1994) found *Strahlaxius* closer to Micheleidae than to Axiidae. Incorporation of *Callianidea* in a clade including *Thomassinia* and a thomassiniid-like species raises questions about the distinctiveness of these families. Within Callianassidae, there is some evidence to support current subfamilial groupings as well as some evidence of polyphyly among representative taxa, especially of the genera *Biffarius* and *Sergio*. These and other generic level issues are independently addressed in an expanded analysis of the Callianassidae (Felder & Robles, this volume).

4   DISCUSSION

4.1 *Monophyly or paraphyly*

While current schemes of classification treat Thalassinidea as an infraorder, issues such as its monophyly and its phylogenetic position, as well as the phylogenetic relationships among its constituent families, remain under debate. We have presented here a combined analysis based on two molecular datasets, one mitochondrial and one nuclear, and it does not support a monophyletic Thalassinidea.

  When de Saint Laurent (1973) raised the subfamily Upogebiinae to family rank, she did so after concluding that its morphological differences were too striking to maintain the group within Callianassidae. In doing so, she commented on the family's affinities and suggested Upogebiidae was more closely related to Laomediidae and Thalassinidae than to Callianassidae and Axiidae. She relied on differences in larval morphology as justification, citing by footnote "Gurney . . . 1940," in obvious reference to Gurney (1942).

Later, de Saint Laurent (1979a) cited differences in the union between the epistome and the carapace, in the number and kind of chelate legs, in larval development, in the appendix interna and in other undefined features, while discussing the difficulty in precisely defining what she called "Thalassinacea." Larval morphology had long suggested that Thalassinidea was composed of two distinct groups (Gurney 1938). One, the Callianassidae and Axiidae, was concluded to have a "homarine" zoea somewhat resembling that of Nephropidae, and the other, Upogebiidae and Laomediidae, an "anomuran" zoea (see also Gurney 1942; Felder et al. 1985). On the basis of this evidence, de Saint Laurent (1979a) suggested two groups, which she termed "sections": "Gebiidea" (Upogebiidae, Laomediidae s. l., and Thalassinidae) and "Axiidea" (Axiidae and Callianassidae). She illustrated these as two of ten distinct lines in a "radiation Triasique" of Reptantia (de Saint Laurent 1979a: Fig, 1). Nevertheless, she described tentative links between Gebiidea and "Dromi-acea," "Anomala" and Brachyura as "sans doute articifielle." Subsequently, de Saint Laurent (1979b) followed this with more detailed diagnoses of the superfamily Axioidea and its families, Axiidae, Callianideidae, and Callianassidae, though it is unclear whether she believed the group to be other than monophyletic.

Poore (1994) conducted a morphologically based analysis of 22 genera of Thalassinidea, con-cluding that monophyly of the infraorder Thalassinidea was supported by the presence of a marginal setal fringe on pereopod 2 of all members. The monophyly view has been supported by some re-cent morphological and molecular studies. Morphological analyses of Dixon et al. (2003) found Thalassinidea to be monophyletic, with three characters to support that view: the curved articula-tion between the ischium and merus in pereopod 1; the presence of a row of setae on pereopod 2 (same as Poore 1994); and an enlarged and lobate seventh thoracic sternite (observed first by Scholtz & Richter 1995). A more recent analysis of Decapoda, based on a combination of morphological and molecular data, also supported monophyly of Thalassinidea (Ayhong & O'Meally 2004). Their study included sequences of the 16S, 18S, and 28S genes as well as morphological characters in what was called a "total evidence" analysis. These authors found the five families of Thalassinidea included in their parsimony analysis to be monophyletic. In a molecular analysis of 16S and 18S data for 13 thalassinidean genera, Tudge & Cunningham (2002) previously had shown only weak support for monophyly of Thalassinidea on the basis of 18S sequences, and no support for mono-phyly on the basis of 16S sequences. Interestingly, their composite tree showed the clade including Upogebiidae, Axianassidae, Thalassinidae, and Laomediidae positioned as a sister clade to five de-capod outgroups, though at low support values. The molecular analysis of Porter et al. (2005) also infers thalassinideans to be monophyletic, but this analysis included representatives of only one family (Callianassidae), which we also find to be monophyletic, so no conclusion can be drawn for thalassinideans overall.

On the other hand, the molecular phylogenetic analyses of Morrison et al. (2002) presented ev-idence for polyphyly of Thalassinidea. Their analyses, based on sequences of the 16S, 18S, COII, and 28S genes, showed *Jaxea* and *Upogebia* (representing the families Laomediidae and Upogebi-idae, respectively) allied with *Panulirus* (infraorder Palinura or Achelata) in a separate clade from *Neotrypaea* and *Callichirus* (representing the family Callianassidae). These results were used to show that Thalassinidea does not belong among the true Anomura, but explanation for the two separated clades of Thalassinidea was appropriately not addressed, given the few constituent taxa represented. It is noteworthy that Morrison et al. (2002), using 16S, 18S, 28S, and one additional gene, found thalassinideans to be paraphyletic. This different result from that of Ayhong & O'Meally (2004) could have resulted from inclusion of the COII gene by Morrison et al. and/or inclusion of the morphological database by Ahyong & O'Meally.

This debate continues, published results being difficult to compare between analyses because of differences in taxa chosen, data used, and phylogenetic methods. Sakai (2005) and Sakai & Sawada (2006) found thalassinideans to be "diphyletic" on the basis of pyloric ossicle structure, and they proposed superfamily or infraordinal separations on this basis, though without discussing

group relationships. Very recent work on the basis of protein-coding genes (Tsang et al. 2008a) has shown evidence for at least paraphyly among the six included representatives of thalassindeans, the evidence for polyphyly having only weak support. The four axiids and calocaridids representing the Axiidea at the very least form a monophyletic clade. Their single thalassinid and single upogebiid did not group together as representatives of Gebiidea, but poor internodal support makes their positioning questionable.

Our molecular analysis argues against monophyly of the infraorder Thalassinidea, thus supporting conclusions of de Saint Laurent (1979a, b), Tudge et al. (2002), and Sakai & Sawada (2006), though not for the same reasons. Rooted to the Caridea, we find that the thalassinideans are distributed among two clades for which the rank of infraorder is more appropriate than superfamily, as the latter could imply membership in the same infraorder. One of these clades, first referred to as Gebiidea by de Saint Laurent (1979a), includes Upogebiidae, Thalassinidae, Axianassidae, and Laomediidae (Fig. 1: Clade-A). We reject the unnecessary replacement of this name by a restricted Thalassinidea (*sensu* Sakai & Sawada 2006) or redefined superfamily Thalassinoidea (*sensu* Sakai 2005; Tsang et al. 2008b).

The second clade we refer to as infraorder Axiidea, again using the term that de Saint Laurent (1979b) originally applied (Fig. 1: Clade-B). This is a monophyletic grouping of Axiidae, Calocarididae, Micheleidae, Thomassiniidae, Callianideidae, Strahlaxiidae, Ctenochelidae, and Callianassidae that is with strong support allied more closely to other decapod infraorders (outgroup taxa) than to the Gebiidea (Clade-A). We prefer Axiidea over the synonymous infraorder Callianassidea (*sensu* Sakai & Sawada 2006) or superfamily Callianassoidea (*sensu* Sakai 2005; Tsang et al. 2008b).

Our results differed somewhat from those of Tsang et al. (2008b: Fig. 1), even though we used the same 16S and 18S genetic markers. Among possible explanations are the following: 1) Our set of thalassinidean taxa was significantly different (55 thalassinidean specimens representing an additional family, more genera, and more species than in their sample of 27); 2) the two efforts may have differed slightly in parameters used to obtain alignments and in the way saturated fragments of genes were discarded (though unlikely as the efforts defined similar large clades); and 3) their selection of outgroups and of analyses was admittedly not designed to address the issue of thalassinidean monophyly. In addition, one could question our rooting of the tree to the Caridea even though, as noted in Results above, we selected this group in a preliminary unrooted analysis. To ascertain the impact of this selection on our analysis, we conducted an independent phylogenetic analysis excluding the Caridea but including all other outgroups otherwise used in Figure 1. That tree (not shown) showed no support for a monophyletic Thalassinidea and produced the same general groupings as in Figure 1.

Regardless of the rank ultimately assigned to our Clade-A and Clade-B, morphological characters summarized by other authors can be applied to diagnoses. The separation is supported by consistent group differences in larval morphology (Gurney 1938, 1942), possibly gastric mill morphology (Sakai 2005; Sakai & Sawada 2006), and the degree of chela development on the second pereopod (de Saint Laurent 1979a, b), even though questions remain as to whether all these shared character states represent synapomorphies. For example, while the second pereopod is never fully chelate in our Clade-B, as opposed to Clade-A, Poore (1994) has argued that this feature may have arisen multiple times among Decapoda. Our Clade-A is additionally supported by its members all lacking appendices internae on the pleopods, while they are present (with few exceptions among the axiids) in Clade-B.

4.2 *Previously applied superfamilies*

The most widely used current classification of the present infraorder Thalassinidea distributes all of its member families into three superfamilies, Axioidea, Thalassinoidea, and Callianassoidea (see Poore 1994; Martin & Davis 2001). Neither our analyses nor those of Tsang et al. (2008b), Sakai (2005), or Sakai & Sawada (2006) supported the monophyly of these superfamilies. One of our two

major clades, Gebiidea, clustered representatives of the families Upogebiidae, Laomediidae, Axianassidae, and Thalassinidae. Poore's (1994) scheme would have the first three of these members of Callianassoidea and the last one a member of the Thalassinoidea (Fig. 1: Clade-A). Our second major clade, Axiidea, mixes members of Axioidea and Callianassoidea (Fig. 1: Clade-B).

In a morphologically based analysis, Dixon et al. (2003) supported Poore's (1994) superfamilies, but with some hesitation. Their only representative of Laomediidae (*Jaxea*) was positioned at the base of the clade for Thalassinidea instead of being clustered with Callianassidae, Callianideidae, and Upogebiidae (Dixon et al. 2003: Fig. 6). However, their goal was not to resolve internal relationships within Thalassinidea (their Thalassinida) but to suggest a new classification for the order Decapoda. We conclude that their support for the current superfamilies was overstated, since they included only one representative from each of five families of Thalassinidea and two specimens for another two families. In their analysis of the Decapoda, Ahyong & O'Meally (2004) also included five families of Thalassinidea. While having already noted our disagreement with their finding of monophyly for the group overall, we do agree to large extent with the interfamilial relationships they reported. They grouped *Upogebia*, *Jaxea*, and *Thalassina* in a single clade similar to our Clade-A. They also found *Biffarius*, *Callichirus*, and *Neaxius* in a second clade that resembles our Clade-B.

Sakai (2005) compared gastric mills among representatives of some thalassinidean families. He concluded that Thalassinidea should be divided into two superfamilies, Callianassoidea and Thalassinoidea, very similar to the clades we distinguish molecularly, acknowledging that his revision was being suggested on the basis of a single character and without comprehensive study of group representatives. In a second paper Sakai & Sawada (2006) elaborated on these observations and elevated the superfamilies to the infraorders Thalassinidea and the new name Callianassidea, effectively replacing de Saint Laurent's names, Gebiidea and Axiidea. They diagnosed their infraorders only in terms of pyloric ossicle shape and sought no supportive evidence from any other characters.

4.3 *Infraorder composition and internal family relationships*

Within our Clade-A, Gebiidea, family proximities are very similar to those reported in the recent molecular studies of Tsang et al. (2008b). As in Tudge & Cunningham (2002), members of the family Upogebiidae are grouped independently from the other three families, Thalassinidae, Axianassidae, and Laomediidae. Our support for separation of the family Axianassidae is weaker than that of Tudge & Cunningham (2002), but we judge neither our analysis nor that of Tsang et al. (2008b) to justify abandonment of this family. Topological placement appears to be external to the monophyletic Laomediidae, and a more robust coverage of axianassid species should be undertaken in subsequent analyses.

Recent work by Batang & Suzuki (2003) has examined the potential phylogenetic significance of gill-cleaning adaptations, as reviewed by Tsang et al. (2008b), calling attention to the striking dissimilarity of those in Upogebiibae from arrangements in the other three families that we place into the Gebiidea. Under our scenario, reported similarities of these structures in the Upogebiidae to those in the Callianassidae and Ctenochelidae must be regarded as convergent character states, likely in adaptation to similar sedimentary environments.

Within our Clade-B, Axiidea, we observe short branch lengths separating several of the primary clades, much as found by Tsang et al. (2008b). Separation of the Axiidae as the most basally positioned family is moderately to well supported, even at such short branch lengths. We also found that our molecular data did not support separation of monophyletic Calocarididae from a monophyletic Axiidae. Our calocaridid examples were unambiguously embedded in two separate subclades of the Axiidae. While our analysis did not include a representative of Eiconaxiidae, one was included in the analysis by Tsang et al. (2008b) and was clearly positioned among other clades of Axiidae and Calocarididae. Their evidence argues against retaining Eiconaxiidae as a separate family.

In as far as our two representatives tell us, Micheleidae are monophyletic and basal to the non-axiid lineage of Axiidea. Callianideidae (one species) appears embedded within Thomassiniidae

(*Thomassinia gebioides* plus a yet-to-be-named genus of thomassiniid). Tsang et al. (2008b) found a highly supported sister relationship between Micheleidae and Callianideidae but included no examples of Thomassiniidae.

Strahlaxiidae is in turn positioned topologically as a sister group to Callianideidae + Thomassiniidae, but without support, and the branch separating this entire group from the Callianassidae + Ctenochelidae clade lacks support. Given these poor resolutions, we must forego further interpretations.

Our analysis supports a monophyletic family Callianassidae but offers only modest support for positioning of the family Ctenochelidae as its sister group, a placement suggested on the basis of morphology (Poore 1994; Tudge et al. 2000). Without support, it was similarly positioned in the analyses of Tsang et al. (2008b), where the family was represented by the genus *Ctenocheles*. At moderate levels of support, the family Ctenochelidae appears to be monophyletic on the basis of the genera *Gourretia* and *Dawsonius* in our analyses. While our topology reflects some expected group relationships within the family Callianassidae, that issue is addressed more comprehensively in separate coverage of callianassid taxa (Felder & Robles this volume).

5   CONCLUSIONS

Our analysis shows paraphyly for what is presently referred to as the infraorder Thalassinidea and does not support its presently assigned taxa being redistributed among two constituent superfamilies or other subdivisons. There is no support for the superfamilies Axioidea, Thalassinoidea, and Callianassoidea (Poore 1994; Martin & Davis 2001). Rather, we support establishment of two separate infraorders that we label in accord with names introduced by de Saint Laurent (1979a): infraorder Gebiidea, composed of families Upogebiidae, Thalassinidae, Axianassidae, and Laomediidae; and infraoder Axiidea, composed of Axiidae, Calocarididae, Micheleidae, Thomassiniidae, Callianideidae, Strahlaxiidae, Ctenochelidae, and Callianassidae.

Our analysis supports family status for Axianassidae, Axiidae, Callianassidae, Ctenochelidae, Micheleidae, and Upogebiidae. While the limited support and sampling in our present analysis cannot confirm validity of the family Strahlaxiidae, there is no basis upon which to merge it with another family. On the other hand, its close relatives, Thomassiniidae and Callianideidae, appear to not represent distinct families. Similarly, highly supported clades in our own work and that of Tsang et al. (2008) show the families Eiconaxiidae and Calocaridiidae to be embedded within the Axiidae, rather than deserving independent family rank.

We do not suggest that our present analysis closes this debate, as sampling of genetic diversity in this group remains low. Rather, our continuing efforts are focused on adding representative taxa for molecular analyses, accumulating sequence data for additional genes, and preparing of a more thorough reappraisal of morphological characters. Our hope is that a reconciliation of molecular and morphological analyses will lead to a more stable classification.

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