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Decapod Crustacean Phylogenetics

edited by

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Contents

Decapod Phylogeny: What Can Protein-Coding Genes Tell Us?

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ABSTRACT

The high diversity of decapods has attracted the interest of many carcinologists, but there is no consensus on their phylogeny as yet. This is in spite of numerous endeavors using both morphological and molecular approaches. New sources of information are necessary to help elucidate the phylogenetic relationships among decapods. Here we demonstrate the applicability of nuclear protein-coding genes in the phylogenetic analysis of this group. Using only two protein-coding genes, we have successfully resolved most of the infraordinal relationships with good statistical support, indicating the superior efficiency of these markers compared to nuclear ribosomal RNA and mitochondrial genes now commonly used in phylogenetic reconstruction of decapods. Available evidence suggests that these two markers suffer from the problems of alignment ambiguities and rapid saturation, respectively. We have also applied nuclear protein-coding genes in revealing inter- and intrafamilial evolutionary history. Trees with robust support can be obtained using sequences of two to three genes for the infraorders and families tested, including the most species-rich group, the Brachyura. The new genes are also shown to be informative in elucidating interspecific phylogeny. Thus, these nuclear protein-coding genes are applicable at various taxonomic levels and will provide a valuable new source of information for reconstructing the tree of life of Decapoda.

1 INTRODUCTION

The Decapoda is one of the most diverse groups of Crustacea. The ecological and morphological diversity of decapods, together with their economic importance, makes them the most studied of all crustaceans (Martin & Davis 2001). A robust phylogeny is therefore crucial to understanding the evolution and diversification in this group of animals. The extraordinary morphological diversity, however, poses substantial challenges to their phylogenetic study. There have been many systematic schemes and phylogenetic hypotheses proposed for Decapoda (reviewed in Martin & Davis 2001; Schram 2001). Morphological cladistic analyses have provided some insights, but they leave many key disputes unsettled, especially concerning the relationship of deeper nodes (e.g., Scholtz & Richter 1995; Dixon et al. 2003; Schram & Dixon 2004). Thus, researchers have recently shifted their attention to new sources of information from the genome to resolve decapod phylogeny.

2 MOLECULAR PHYLOGENY OF THE DECAPODA

Mitochondrial genes have been the most commonly used markers in animal phylogenetic studies, including the decapod crustaceans, for many years (Schubart this volume). These markers benefit from the ease of amplification due to relatively higher copy numbers relative to nuclear genes and the availability of many universal primers (Simon et al. 1994). The haploid and non-recombinant nature of mtDNA also presents fewer problems in phylogenetic reconstruction. The rate of nucleotide substitutions among mitochondrial genes is generally more rapid than that among genes in the nuclear genome (Moore 1995). Accordingly, mitochondrial genes could more accurately reflect the relationships among recently diverged taxa. Most of the phylogenetic studies in lower taxonomic levels of decapods rely exclusively on mitochondrial DNA sequences, and these genes do provide us with some insights into the evolutionary history of the Decapoda (reviewed in Schubart et al. 2000; Schubart this volume).

Mitochondrial genes, however, are being criticized for several disadvantages. All of the mitochondrial genes are linked and inherited as a single molecule. Therefore, they share a common evolutionary history and cannot provide an independent phylogenetic inference. The high mutation rate of mitochondrial DNA also limits its utility in the phylogenetics of deep divergences. Furthermore, the highly A/T-biased mitochondrial DNA, especially at the third codon position of the protein-coding genes, suffers from high levels of homoplasy and thus exhibits strong negative effects in phylogenetic analyses. In this regard, decapod molecular systematists have tried to incorporate nuclear rRNA genes, which evolve at a much slower rate, in addition to mitochondrial DNA markers, for decapod phylogeny. Analyses of the 18S rRNA gene have resolved some familial relationships and laid the foundation for further taxonomic revision (e.g., Spears et al. 1992; Pérez-Losada et al. 2002; Ahyong et al. 2007). The nuclear rRNA genes, however, suffer from alignment ambiguities. This poses problems in phylogenetic inference, particularly in nodes with deep divergence (i.e., infraordinal relationships). The two recent studies on the phylogeny of decapod infraorders based primarily on 18S and 28S rRNA gene sequences (combined with morphological characters or the relatively much shorter fragments of mitochondrial 16S rRNA and histone 3) yield contrasting topologies (Ahyong & O'Meally 2004; Porter et al. 2005), suggesting the current markers are insufficient in reconstructing a robust high-level phylogeny of Decapoda.

Consequently, nuclear protein-coding genes could serve as an excellent new source of information. These genes have the clear advantage of being easy to align. Moreover, many potential candidates are present in the genome with diverse evolutionary rates that are suitable to address phylogeny at different taxonomic levels. Despite the apparently high potential utility of protein-coding gene markers, several limitations have restricted the development and application of these markers. First, the protein-coding genes have a much lower number of copies in the genome, compared to highly abundant nuclear rRNA and mitochondrial genes, and therefore are more difficult to amplify through PCR. The degenerate third codon positions further challenge the design of PCR primers, and long stretches of introns might be present, making amplification difficult or even impossible. Furthermore, paralogs might be present, resulting in problems in phylogenetic analyses. Thus, though these genes appear to be informative, their application in decapod phylogenetics has been relatively limited to date (e.g., histone 3: Porter et al. 2005; glyceraldehyde-3-phosphate dehydrogenase: Buhay et al. 2007).

With the recent advances in molecular techniques (e.g., EST) and the accumulation of large amounts of genome sequence data, scientists can search for new molecular markers or apply the existing ones to their target organisms much more easily than before. Accordingly, the protein-coding genes play an increasingly dominant role in phylogenetic studies. This is especially true for the taxonomic groups with more comprehensive genomic information (e.g., vertebrates and insects). New protein-coding gene markers have also been successfully developed for other arthropods (e.g., spider, Ayoub et al. 2007; Mysida, Audzijonyte et al. 2008), and have proved to be informative or even superior to nuclear rRNA and mitochondrial genes in resolving power (Audzijonyte et al. 2008).

Thus, the development and application of these markers in Decapoda molecular systematic studies could be a new strategy in addressing the controversial issues in decapod phylogeny. In this paper, we report recent advances in our laboratory in applying nuclear protein-coding genes to decapod phylogenetics across different taxonomic levels. Their utility was examined by comparing the statistical support in topologies obtained in the present study with those from previous studies using nuclear rRNA and/or mitochondrial genes.

3 NEW INSIGHTS INTO THE INFRAORDINAL RELATIONSHIPS AMONG DECAPODA REVEALED BY PROTEIN-CODING GENES

We have employed partial segments of two nuclear protein-coding genes, phosphoenolpyruvate carboxykinase (PEPCK, 570 bp) and sodium-potassium ATPase α-subunit (NaK, 534 bp), to reconstruct the phylogeny among 69 decapod species (Tsang et al. 2008a). This analysis has now been extended to 135 species from 60 families (Fig. 6.1). The topology inferred from Bayesian inference reveals that the Reptantia and all but one of its infraorders are monophyletic. The nodal support for most of the infraordinal and inter-familial relationships is high (posterior probability ≥ 0.95), indicating the high resolving power of the protein-coding genes. Thalassinidea, however, is polyphyletic. This corroborates the results of a previous study based on mitochondrial gene rearrangements and sequences from both mitochondrial and nuclear rRNA genes (Morrison et al. 2002). We recover two distinct lineages in Thalassinidea that correspond to the two strongly supported clades obtained in the previous molecular studies (Tudge and Cunningham 2002; Ahyong and O'Meally 2004; Tsang et al. 2008b). The division of Thalassinidea into the two major groups is also supported by larval morphology, external somatic morphology, and foregut ossicles (Gurney 1938; de Saint Laurent 1973; Sakai 2005; Tsang et al. 2008b).

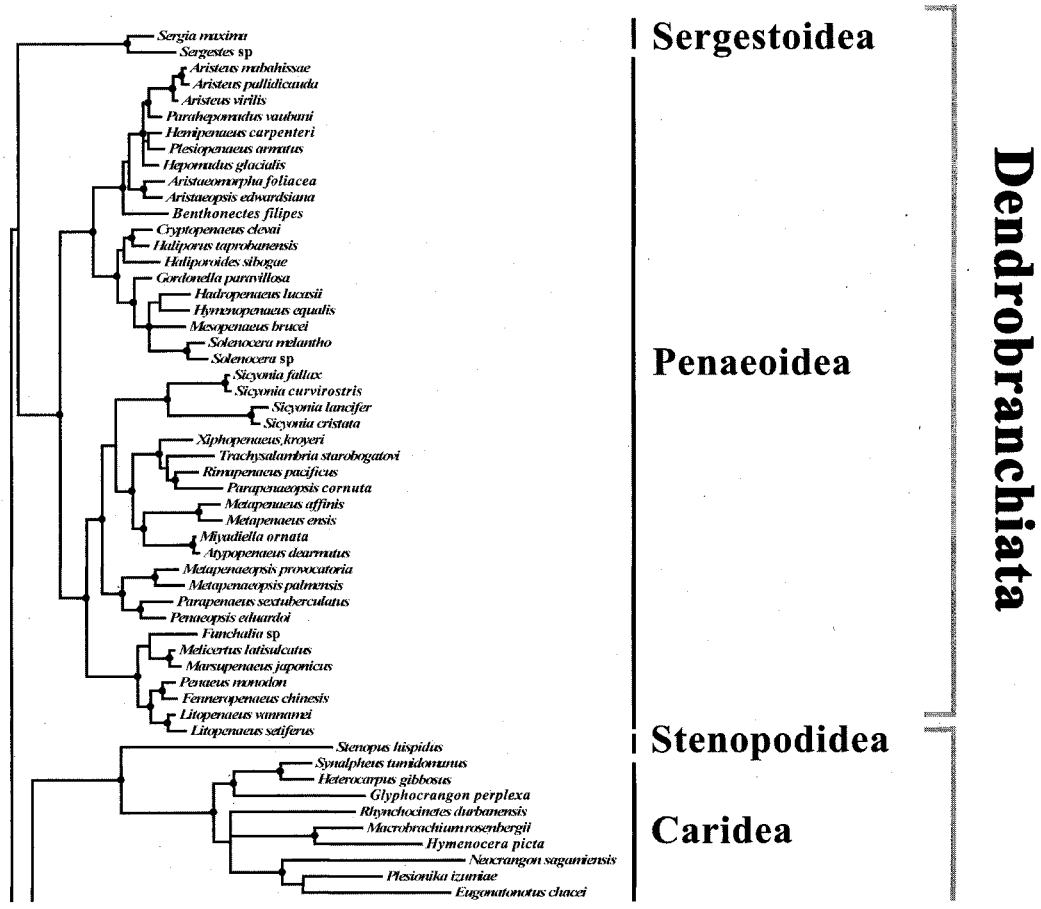
Within Pleocyemata, Stenopodidea and Caridea form a sister clade to Reptantia, supporting the view of Burkenroad (1981). Anomura and Brachyura show high affinity in concordance with the traditional grouping of Meiura. Enoplometopidae and Thaumastochelidae are found to be closely related to Nephropidae, justifying their placement in Astacidea. Yet Thaumastochelidae is nested within Nephropidae, making the latter paraphyletic, and thus future taxonomic re-evaluation is warranted. An interesting finding is that Polychelidae, long considered to be a basal reptant group, clusters with Achelata and Astacidea, and is therefore more derived than expected. Instead, thalassinidean-like creatures are the stem lineage of Reptantia based on our phylogeny.

All in all, the protein-coding genes apparently provide high resolving power in deeper branches within Decapoda. The phylogenetic positions of several 'problematic' taxa have been clarified and new insights into decapod evolution obtained. We advocate further development and application of these markers for the higher level phylogeny of decapods.

4 UTILITY OF PROTEIN-CODING GENES IN SUPERFAMILY/FAMILY LEVEL PHYLOGENETIC STUDIES

4.1 *Phylogeny of Penaeoidea*

The penaeoid shrimps constitute a diverse group of marine decapods. This superfamily contains most of the commercially important shrimps, constituting more than one third of the annual crustacean wild catch (FAO fisheries data). A robust phylogenetic tree is, therefore, crucial for creating a stable and natural classification, which would facilitate effective fisheries management and aquaculture. Previous phylogenetic hypotheses concerning Penaeoidea were derived mainly from morphological analyses (e.g., Kubo 1949; Burkenroad 1983; see also Tavares et al. this volume). Recent molecular studies based on mitochondrial markers, however, yielded highly conflicting conclusions. A close association among Aristeidae, Benthesicymidae, and Sicyoniidae was suggested, while Penaeidae was revealed to be paraphyletic due to the incursion of Solenoceridae



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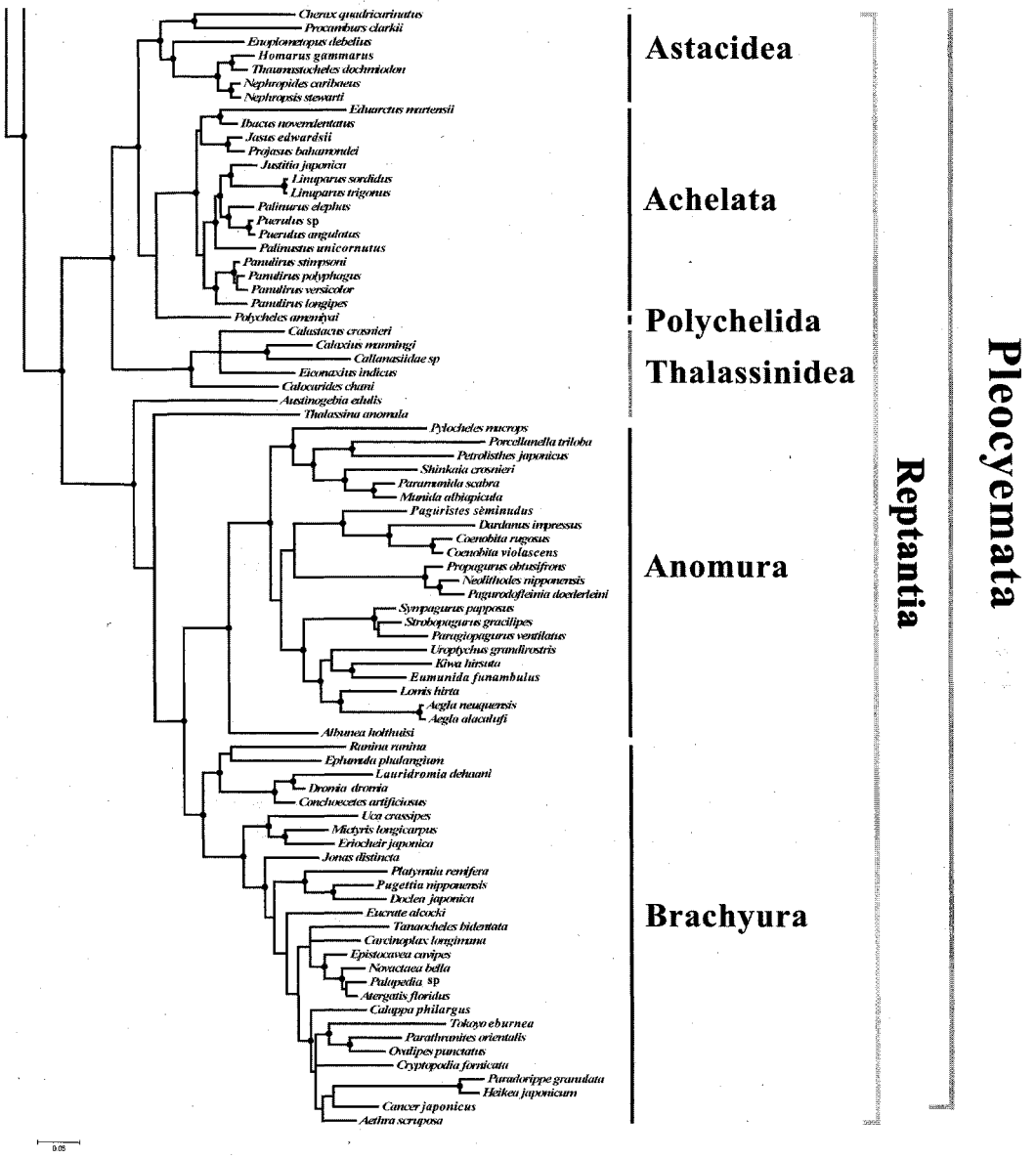

Figure 1. Phylogenetic tree of Decapoda (135 species from 60 families) constructed from combined PEPCK and NaK gene sequences (total 1104 bp). The analysis used Bayesian inference under the best-fitting model GTR+I+G. The analysis was run with 5 million generations consisting of four chains, sampled every 500 generations with the first 0.5 million generations discarded as burnin. Three independent runs were performed to confirm the topology. The nodes with posterior probabilities ≥ 0.95 are denoted by black dots. The infraorder classification of the species is indicated by the bars to the right.

(Vázquez-Bader et al. 2004). Yet these inferred topologies were poorly supported. As a result, it remains unanswered whether the contrasting results represent actual discrepancies between character evolution and speciation or artifacts of gene tree reconstruction.

Using the two nuclear protein-coding genes, PEPCK and NaK, applied in the decapod infraordinal phylogenetic study, we reconstructed a largely resolved, well-supported phylogeny of Penaeoidea (Fig. 2). The monophyly of the superfamily and four out of its five families is evident. Yet the Penaeidae is clearly paraphyletic as Sicyoniidae is nested within it. Two major lineages are recovered in the superfamily, one consisting of Solenoceridae, Aristeidae, and Benthesicymiidae, with the latter two as sister taxa, and the other composed of Penaeidae and Sicyoniidae. This topology is largely congruent with the morphology-inferred phylogeny of the penaeoids. Members from

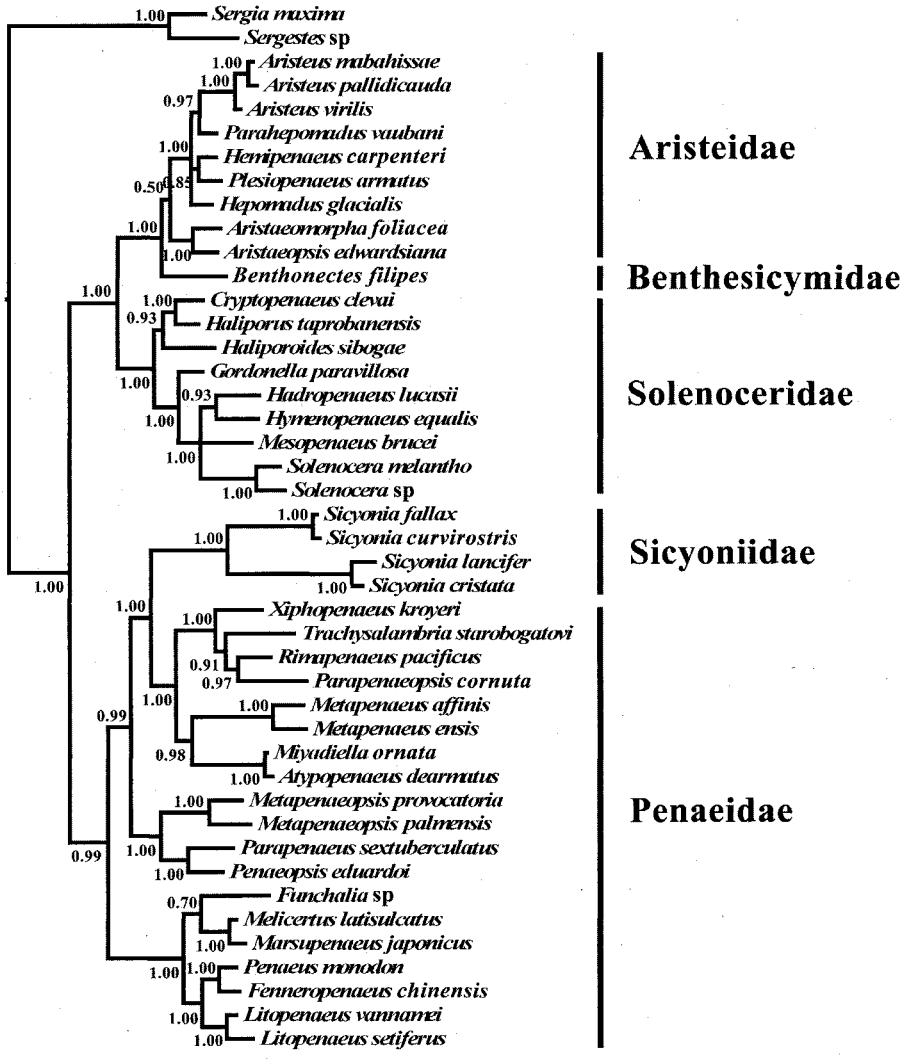

Figure 2. Phylogenetic tree of Penaeoidea (42 species + 2 outgroups from Sergestidae) constructed from combined PEPCK and NaK (total 1104 bp) analysis using Bayesian inference under the best-fitting model GTR+I+G. The analysis was run with 5 million generations consisting of four chains, sampled every 500 generations with the first 0.5 million generations discarded as burnin. Three independent runs were performed to confirm the topology. The posterior probability values are indicated on the branches. The bars to the right indicate the five families of Penaeoidea.

the families Penaeidae and Sicyoniidae are predominantly littoral water inhabitants, while those of the Aristeidae, Benthesicymidae, and Solenoceridae are mainly found in bathy- or mesopelagic environments. Our results thus suggest that habitat-associated radiation may play an important role in the diversification of penaeoid shrimps. Moreover, the three tribes of Penaeidae are shown to be monophyletic with strong nodal support, corroborating morphological evidence and the previous molecular study using mitochondrial 16S rDNA sequence data (Chan et al. 2008).

The concordance among sources of information (e.g., between independent genes and morphological characters) and topology with a high statistical support again indicate the superior and high resolving power of protein-coding genes over other markers currently used in decapod molecular systematics.

4.2 *Phylogeny of Brachyura*

With more than 6,500 species, the Brachyura is the most species-rich infraorder of Decapoda (Ng et al. 2008). The large number of species and morphological diversity have led to a large number of phylogenetic hypotheses proposed (reviewed in Martin & Davis 2001). Investigating the phylogeny of Brachyura using nuclear 18S rRNA sequences, Ahyong et al. (2007) found that section Podotremata is paraphyletic, with the Raninidae being more closely related to Eubrachyura than other podotreme crabs. However, the relationships among the families in Eubrachyura are poorly resolved, although the monophyly of the group is strongly supported. These authors attributed the lack of resolution to the insufficient variability in the 18S rRNA sequences in these more recently diverged taxa. More comprehensive taxon sampling and use of more rapidly evolving genetic markers have been advocated (Ahyong et al. 2007).

We tried to reconstruct the phylogeny of Brachyura using three protein-coding genes, NaK, glyceraldehyde-3-phosphate dehydrogenase (GAPDH, 540 bp), and enolase (345 bp), making up a data set of 1419 bp. The topology recovered from Bayesian inference analysis of the combined data set supports the result of Ahyong et al. (2007) that the Podotremata is paraphyletic (Fig. 3), indicating that the gene trees constructed using the two types of markers (nuclear rRNA and protein-coding genes) are congruent. On the other hand, the protein-coding gene tree provides significantly better resolution within the Eubrachyura. The subsections Heterotremata and Thoracotremata are strongly supported to be reciprocally monophyletic, whilst the 18S rRNA gene tree gives little resolution here. Moreover, the close affinities of some of the families are revealed (e.g., Homolidae + Latreilliidae; Xanthidae + Trapeziidae + Goneplacidae; Matutidae + Calapidae + Euryplacidae). The results corroborate the new classification proposed by Ng et al. (2008) to a certain extent (such as most superfamily groupings), suggesting that the protein-coding gene tree is consistent with the morphological patterns observed.

Admittedly, quite a number of internal nodes remain poorly resolved in the present protein-coding gene tree. Yet the number of taxa analyzed here is relatively limited, as many families have not been included and many highly diverse families are only represented by one or two species. This obviously affects the resolution in such a species-rich group. It is worth noting that our data set consists of only 1419 characters, compared to 1830 used by Ahyong et al. (2007). Thus the nuclear protein-coding genes are more efficient in achieving a higher resolving power in comparison with the equivalent length of nuclear rRNA genes. We are confident that a more robust phylogeny of Brachyura could be obtained in future studies with more thorough taxon sampling and additional nuclear protein-coding genes. This study is now ongoing.

5 UTILITY OF PROTEIN-CODING GENES IN PHYLOGENETIC RECONSTRUCTION AMONG GENERA/SPECIES: PHYLOGENY OF PALINURIDAE

Spiny lobsters of the family Palinuridae include many economically important species with a high potential in aquaculture. Accordingly, they receive considerable attention in attempts to investigate

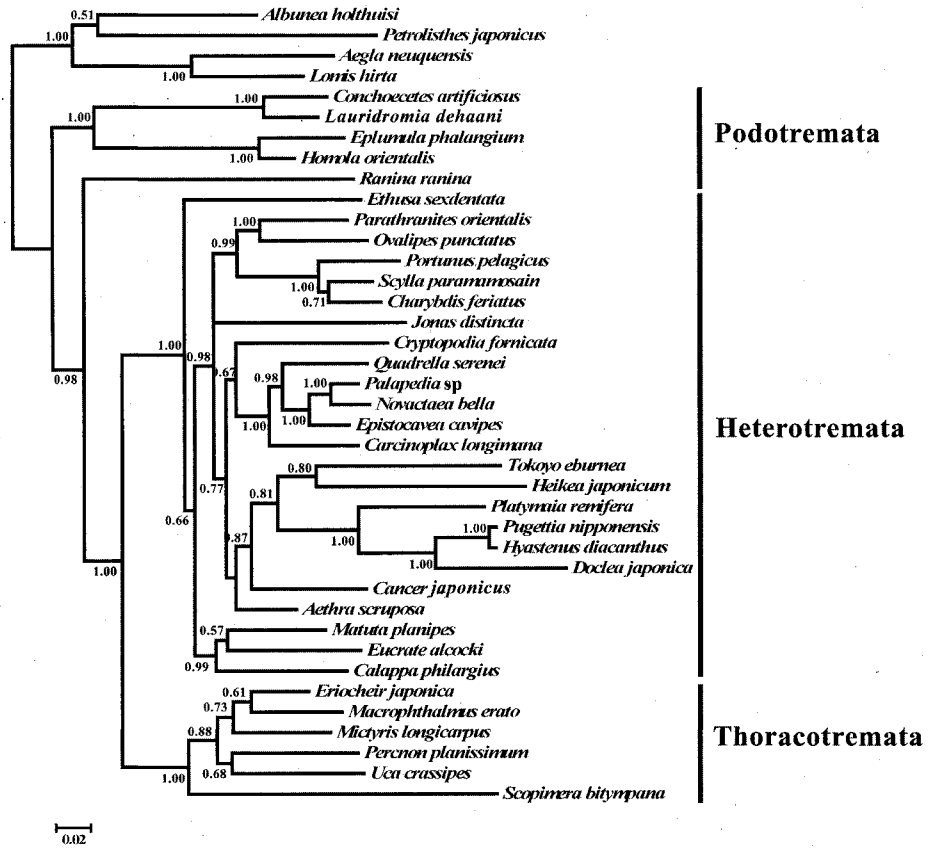

Figure 3. Phylogenetic tree of Brachyura (35 species + 4 outgroups from the infraorder Anomura) constructed from combined NaK, GAPDH, and enolase gene sequences (total 1419 bp). The analysis used Bayesian inference under the best-fitting model GTR+I+G. The analysis was run with 2 million generations consisting of four chains, sampled every 100 generations with the first 200,000 generations discarded as burnin. Three independent runs were performed to confirm the topology. The posterior probability values are indicated on the branches. The bars to the right indicate the three sections of Brachyura.

their genetic population structure and phylogeny for fishery management purposes. Morphological analyses recognize two major lineages in the Palinuridae, namely the Silentes and Stridentes, based on whether the lobsters have a stridulating sound-producing organ (George & Main 1967). The evolution of genera within these two groups was proposed to be associated with the invasion of shallow water habitats, formed by past tectonic movement, by ancestral deeper-water inhabitants (Pollock 1995; George 2005, 2006). Modifications in life-history traits are believed to be adaptations for the shallower water habitat (George 2005). Patek and Oakley (2003) investigated the phylogeny of the spiny lobsters using mitochondrial 16S and nuclear 18S and 28S rRNA gene sequences. They found some evidence for the division of Stridentes and Silentes, but most of the internal branches in the rRNA gene tree were poorly resolved, and the reciprocal monophyly of the two groups received very weak support. Moreover, the topologies derived from different gene segments and analytical methods showed conflicts. Thus, the phylogenetic hypotheses proposed could neither be accepted nor rejected confidently.

Using sequences of three nuclear protein-coding genes, PEPCK, NaK, and histone 3, we generated a gene tree of the Palinuridae, with high statistical support for most of the nodes (Fig. 4), which allows us to reconstruct the evolutionary pathway within the family. The reciprocal monophyly of

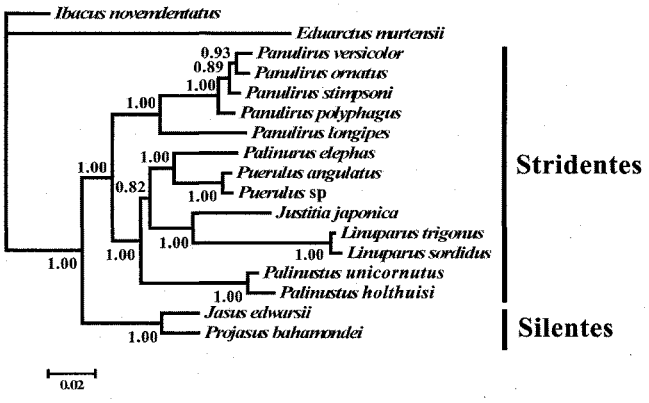

Figure 4. Phylogenetic tree of Palinuridae (15 species + 2 outgroups from the family Scyllaridae) constructed from combined PEPCK, NaK, and histone 3 gene sequence (total 1416 bp) analysis using Bayesian inference under the best-fitting model GTR+I+G. The analysis was run with 1 million generations consisting of four chains, sampled every 100 generations with the first 200,000 generations discarded as burnin. Three independent runs were performed to confirm the topology. The posterior probability values are indicated on the branches.

Stridentes and Silentes is strongly supported. Interestingly, the deep-water inhabiting genera of Stridentes (e.g., *Puerulus* and *Linuparus*), which are considered to be primitive (Pollock 1995; George 2006), are revealed to be derived in our tree. *Palinurus* is the basal lineage of the family, supporting the view of Davie (1990). Our present finding based on relatively limited taxa remains preliminary but clearly demonstrates the utility of protein-coding genes in elucidating the phylogeny of Palinuridae, by providing significantly better resolution as compared to previous studies based on similar taxon sampling and sequence data.

Apart from being informative in generic relationships, the protein-coding genes appear to be useful in resolving species level phylogeny as well. The histone 3 gene has already been employed in phylogenetic studies in a number of genera (e.g., Buhay et al. 2007; Page et al. 2008), while the present study represents the first application of the other two genes at this taxonomic level. We found that the five spiny species of *Panulirus* analyzed exhibit up to 6% and 3.5% sequence divergence in PEPCK and NaK, respectively. Moreover, our gene tree indicates the close affinity of *P. ornatus*, *P. versicolor*, *P. stimpsoni*, and *P. polyphagus*, whilst *P. longipes* is more distantly related. This is congruent with the phylogeny inferred from mitochondrial DNA analyses (Ptacek et al. 2001), suggesting the potential of the nuclear protein-coding genes in resolving interspecific relationships.

6 CONCLUSIONS

Our analyses using nuclear protein-coding genes indicate that they are highly informative for phylogeny estimation across all taxonomic levels of Decapoda, from infraordinal to interspecific relationships. Some new insights into the higher classifications of decapods are disclosed for the first time (e.g., polyphyly of Thalassinidea), and the phylogenetic positions of selected controversial taxa (e.g., Polychelidae, Enoplometopidae) are also resolved in our gene trees. Thus, these new gene markers are promising for future multi-loci studies on phylogenetic reconstruction of decapods. Our results also demonstrate that a large number of potential candidate genes in the genome remain unexplored for evolutionary studies. It is anticipated that our study will trigger the discovery and application of more protein-coding genes for phylogenetic analysis. The use of these genes as the basic repertoire in the phylogenetic toolkit in analyzing decapod relationships represents a major step towards our goal in assembling the tree of life for Decapoda.

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