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RESEARCH ARTICLE

Integrative taxonomy of commercially important deep water penaeoid shrimps from India

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Abstract. The deep water penaeoid shrimp is an important commercial crustacean resource along the Indian coast. The molecular and morphological information of this group from the Indian coast is scarcely known. In this study, we investigated the identification and phylogenetic relationships of the deep water penaeoid shrimps using three mitochondrial (cytochrome oxidase subunit I (COI), cytochrome b, 16S rRNA) genes, which were compared with 54 morphological characters and further used to evaluate character evolution. Our study revealed remarkable molecular divergence (3.3–33.0%) in nine species from three genera of Solenoceridae, four species from three genera of Penaeidae and one species from Aristeidae using COI. Phylogenetic analysis using maximum-likelihood and Bayesian approaches revealed that all species from these families are monophyletic. The present analysis revealed the existence of subgroups in the genus *Solenocera* suggesting the slow reduction of postrostral carina which corresponds to the increase in distributional depth during the evolutionary process which further indicates the origin of the genus in the continental shelf and extending up to the continental slope. In addition, we generated the DNA barcode database involving these species which can help further to investigate the detailed evolution and biogeography of these valuable crustacean resources.

Keywords. character evolution; cytochrome oxidase subunit I; 16S rRNA; Bayesian.

Introduction

The deep water penaeoid shrimps are commercially valuable and constituted more than 40% of the total deep water shrimp landings during 2015 (CMFRI 2016) which includes families: Aristeidae, Solenoceridae and Penaeidae distributed at a depth range of 100–3200 m occupying the continental shelf and slope of the Indian coast (George 1979; Suseelan 1989; Suseelan *et al.* 1989; Gueguen 1998; Dineshbabu and Manissery 2009). Among these, *Aristeus alcocki*, *Metapenaeopsis andamanensis*, *M. coniger*, *Solencera hextii* and *Penaeopsis jerryi* form the targeted species of trawl fishery, in the southwest and southeast coasts of India (Radhakrishnan *et al.* 2012; James 2014). In recent years there was a decline in the stock of deep water penaeoid shrimps (CMFRI reports: 2014, 2015, 2016) due to the increased fishing effort over the years. Therefore, it becomes pertinent to review all the species of Indian deep waters. Moreover a few names that appear in the checklist (Radhakrishnan *et al.* 2012) were not recorded in the regular fishery.

Detailed species and larval level identification forms the prerequisite for the proper conservation and management of the declining deep water shrimp resource of the country. DNA barcoding has been successfully used for species identification and discovery of new species, utilizing 650 bp fragments of the mitochondrial gene, cytochrome oxidase subunit I (COI) (Hebert *et al.* 2003;

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Smith *et al.* 2006; Bucklin and Frost 2009; Asgharian *et al.* 2011; Baldwin *et al.* 2011; Zhang and Hanner 2011; Silva *et al.* 2013). COI was effectively used for the discrimination of closely related species (Hebert *et al.* 2003) and detection of cryptic species (Ni *et al.* 2012) as well as for the identification of fish products (Carvalho *et al.* 2011, 2014). Mitochondrial DNA (Mt-DNA) sequence information has been used as an accurate and automated species identification tool for carrying out studies in a wide range of animal taxa, due to the presence of a significant amount of information (Hebert *et al.* 2003). Phylogenetic relationship of selected penaeoids has been studied in detail, using partial Mt-DNA of 16 species by Vázquez-Bader *et al.* (2004), 11 species by Quan *et al.* (2004), 30 species by Chan *et al.* (2008) and 54 species by Voloch *et al.* (2009) from Indo-West Pacific and Atlantic waters. Additionally, the genus *Parapenaeopsis* from Chinese water (Li *et al.* 2014), *Metapenaeopsis* from Atlantic Ocean (Cheng *et al.* 2015) and *Parapenaeus* from Indo-West Pacific and Atlantic (Yang *et al.* 2015) were studied thoroughly. However, analysis of a combination of dataset (molecular and morphological) has been used effectively for phylogenetic relationships, origin, diversification of the taxa and biogeographic distributions of decapoda (Vereshchaka *et al.* 2015; Yang *et al.* 2015). The present study aims to demonstrate the identification and phylogenetic relationships of deep water penaeoid shrimps from the Indian coast using morphological characters and Mt-DNA sequence data. Also, it aims to identify the important morphological characters for differentiating the clades and dispersal pattern of these commercially important shrimps.

Materials and methods

Specimens of deep-sea penaeoid shrimps were collected (2013–2016) from commercial trawl landings along the Bay of Bengal and southeastern Arabian Sea. A total of 14 species were collected (Aristeidae: genus 1, species 1; Solenoceridae: genus 3, species 9; Penaeidae: genus 3, species 4) (table 1), preserved in 90–95% ethanol for molecular studies and deposited at Crustacean Fisheries Division, Central Marine Fisheries Research Institute, Cochin, India.

Molecular analysis

The total genomic DNA was extracted from the pleopod of the individual specimens using a DNeasy Blood & Tissue kit (Qiagen) according to the manufacturer's protocol. The cells were lysed by incubating at 56°C for 2 h and all other steps were followed as per the protocol. The universal primer for three mitochondrial genes: COI, 16S rRNA (16S) and cytochrome b (Cytb) partial sequences were amplified (Folmer *et al.* 1994; Palumbi 1996; Merritt *et al.* 1998). The reactions were performed in 25 μL reaction cocktails containing genomic DNA (0.5 μg/μL), *Taq* DNA polymerase (0.05 U/μL), 1× buffer, $MgCl_2$ (3 mM), 10 pM/μL of each primer and dNTPs (200 μM). The polymerase chain reaction (PCR) thermal profile used was 94°C for 5 min for initial denaturation, followed by 35 cycles of 94°C for 1 min, 52°C for 1 min, 72°C for 1.5 min and a final extension at 72°C for 5 min. Amplification of PCR products was confirmed by electrophoresis on a 1.5% agarose gel containing ethidium bromide and visualized under a UV transilluminator (Lark, India). Amplified PCR products were purified with the XcelGen DNA Gel/PCR Purification Mini kit (Xcelris Labs Limited, India) according to the manufacturer's protocol. The eluted PCR products were sequenced bidirectionally by the dideoxy chain termination method using the Big-Dye Ready-Reaction kit v 3.1 (Applied Biosystems) on an ABI prism 3770 automated sequencer at AgriGenome Labs, Scigenom, Cochin, India.

Data analysis

Molecular sequences were checked and confirmed using ABI SeqEditor v.1.0. Protein coding gene sequences (COI and Cytb) were translated into amino acids using Transeq (EMBOSS online tool) to avoid the inclusion of pseudogenes (Tsang *et al.* 2008). All the sequences were blasted to report GenBank data to verify the potential contamination and the nucleotide sequences were aligned using the Clustal W algorithm (Thompson *et al.* 1994). The aligned data were edited using bioedit V.7.0.5.2 (Hall 1999), gaps in sequences was treated as missing data. All the sequences were submitted to the GenBank (table 1). The pairwise genetic distance was calculated using MEGA 6.0 (Tamura *et al.* 2013).

For phylogenetic analysis, the maximum-likelihood (ML) method was used for individual gene sequences to compare the similarity between tree topology and MEGA 6.0 was used to select the best-fit model for individual and combined data. General time-reversible model with a gamma distribution and invariable sites (GTR+G+I) (COI and Cytb), and Tamura–Nei model with a gamma distribution and invariable sites (TrN+G+I) (16S) were selected and used to generate ML gene trees with 1000 bootstrap replicates (Nei and Kumar 2000; Tamura *et al.* 2013).

Two methods were followed to construct the phylogenetic tree from concatenated data: maximum parsimony (Mp) analysis was conducted using PAUP v.4.0 (Swofford 2002) with all the characters assigning equal weightage and branch support was assessed using 1000 bootstrap replicates. A Bayesian inference (BI) was conducted with MrBayes v. 3.2.1 (Ronquist and Hulsenbeck 2003) and Markov chain Monte Carlo algorithms were run for 5,00,000 generations, sampling one tree every 100 generations. All the parameter estimations were checked and observation of likelihood (L) scores allowed us to

Table 1. Sampling location, voucher number, collection depth and GenBank numbers of deep water penaeoid shrimps along Indian Coast.

Species	Collected location	Depth	Specimen ID	COI	16S	Cytb
Aristeus alcocki	SWCI (08°55′N, 76°32′E)	300–450	CMFRI:CFD:AA2	KM361437	KM819687	KX584726
	SWCI (08°55′N, 76°32′E)	300–450	CMFRI:CFD:AA7	KM378656	KM819690	
	SECI (08°47′N, 78°09′E)	300–450	CMFRI:CFD:At1	KY817931	KJ396316	
	SECI (10°45′N, 79°50′E)	300–450	CMFRI:CFD:An1	KY817932	KJ486492	KX584725
	SECI (10°45′N, 79°50′E)	300–450	CMFRI:CFD:An2	KY817933		
	SECI (13°07′N, 80°17′E)	300–450	CMFRI:CFD:Ac1	KY817934		
	SECI (13°07′N, 80°17′E)	300–450	CMFRI:CFD:Ac2	KY817935		
	SECI (08°47′N, 78°09′E)	300–450	CMFRI:CFD:At2	KY817936		
	SECI (08°47′N, 78°09′E)	300–450	CMFRI:CFD:At3	KY817937		
M. andamanensis	SECI (08°47′N, 78°09′E)	200–270	CMFRI:CFD:MA1	KR349302	KP721229	KR706194
	SECI (08°47′N, 78°09′E)	200–270	CMFRI:CFD:MA2	KR349303	KP721230	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:MA3	KP721232	KP721224	
	SECI (08°47′N, 78°09′E)	200–270	CMFRI:CFD:MA4	KR349301	KP721228	
	SECI (08°47′N, 78°09′E)	200–270	CMFRI:CFD:MA5	KR349305	KP721231	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:M11	KU237179	KU237192	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:M12	KU237181	KU237188	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:M13	KU237180	KU237190	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:M14	KU237177	KU237191	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:M15	KU237178	KU237189	
M. coniger	SECI (08°47′N, 78°09′E)	200–270	CMFRI:CFD:MC1	KP721234	KP721222	KR706193
	SECI (08°47′N, 78°09′E)	200–270	CMFRI:CFD:MC2	KP721235	KP721226	KR706192
	SECI (08°47′N, 78°09′E)	200–270	CMFRI:CFD:MC3	KR349304		
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:MC4	KP721233	KP721223	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:MC5	KR349300	KP721227	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:MC6	–	KP721225	
	SWCI (09°59′N, 76°14′E)	200–270	CMFRI:CFD:M1	KU237184	KU237193	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:M2	KU237185	KU237195	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:M3	KU237183	KU237196	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:M4	KU237182	KU237197	
	SWCI (09°59′N, 76°14′E)	200–270	CMFRI:CFD:M5	KU237186	KU237198	
	SWCI (09°59′N, 76°14′E)	200–270	CMFRI:CFD:M6	KU237187	KU237194	
P. investigatoris	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:Pi1	KX584730	KX584727	KX584732
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:Pi2	KX584731	KX584728	KX584733
	SWCI (09°59′N, 76°14′E)	200–270	CMFRI:CFD:Pi3	–	KX584729	
Penaeopsis jerryi	SWCI (09°59′N, 76°14′E)	200–270	CMFRI:CFD:PJ7	KU133279	KU133283	KU133282
	SWCI (09°59′N, 76°14′E)	200–270	CMFRI:CFD:PJ8	KU133280	KU133284	KU133281
Hadropenaeus lucasii	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:Ss6	KX574339	KX574329	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:sb1	KY419831	KY419832	
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:Ss66	KX574340	KX574330	
Hymenopenaeus equalis	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:HE7	KX530788	KX530792	KX530790
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:HE8	KX530789	KX530793	KX530791
	SWCI (08°55′N, 76°32′E)	200–270	CMFRI:CFD:HE2	KU133286	KU133288	
	SWCI (09°59′N, 76°14′E)	200–270	CMFRI:CFD:HE77	KU133285	KU133287	KU133289
Solenocera annectens	SECI (08°47′N, 78°09′E)	200–250	CMFRI:CFD:SSP1	KX550066	KX530803	KX550068
	SECI (08°47′N, 78°09′E)	200–250	CMFRI:CFD:SSP2	KX550067	KX530804	KX550069
S. choprai	SWCI (09°59′N, 76°14′E)	120	CMFRI:CFD:SSP3	KX574338	KY817938	KY817940
	SWCI (09°59′N, 76°14′E)	120	CMFRI:CFD:SSP4	KX574337	KY817939	KY817941
S. crassicornis	SECI (10°45′N, 79°50′E)	110	CMFRI:CFD:Scr1	KX584723	KX584719	KX584721
	SECI (10°45′N, 79°50′E)	110	CMFRI:CFD:Scr2	KX584724	KX584720	KX584722
S. hextii	SWCI (08°55′N, 76°32′E)	260–300	CMFRI:CFD:SH3	KU133271	KU133277	KU133275
	SWCI (08°55′N, 76°32′E)	260–300	CMFRI:CFD:SH4	KU133272	KU133278	KU133276
	SWCI (08°55′N, 76°32′E)	260–300	CMFRI:CFD:SH2	KU133270		
	SWCI (08°55′N, 76°32′E)	260–300	CMFRI:CFD:SH33	KX530795	KX530801	KX530797
	SWCI (09°59′N, 76°14′E)	260–300	CMFRI:CFD:SH44	KX530796	KX530802	KX530798
	SWCI (09°59′N, 76°14′E)	260–300	CMFRI:CFD:SH22	KX530794		
S. melantho	SECI (17°41′N, 83°18′E)	110	CMFRI:CFD:Sm1	KX584715	KX574331	KX584713
	SECI (17°41′N, 83°18′E)	110	CMFRI:CFD:Sm2	KX584716	KX574332	KX584714

Table 1 (*contd*)

Species	Collected location	Depth	Specimen ID	COI	16S	Cytb
	SECI (17°41′N, 83°18′E)	110	Sm11	KX584717		
	SECI (17°41′N, 83°18′E)	110	Sm12	KX584718		
S. pectinata	SWCI (08°55′N, 76°32′E)	150–200	Spc1	KX550071	KX550074	KX550072
	SWCI (08°55′N, 76°32′E)	150–200	Spc2	KX550070	KX550075	KX550073
S. rathbuni	SWCI (08°55′N, 76°32′E)	150–200	Ss4	KX574327	KX574335	KX574333
	SWCI (08°55′N, 76°32′E)	150–200	Ss44	KX574328	KX574336	KX574334
Oplophorus gracilirostris	SWCI (08°56′N, 76°32′E)		CMFRI:CFD:OT	KJ472213	KJ819551	KJ819552
Palinustus waguensis	SWCI (08°56′N, 76°32′E)		CMFRI:CFD:PW1	KF959668	KJ363167	–

determine the burn-in and stable distributions of the data. A 50% majority rule consensus tree was constructed from the remaining saved trees and was printed by Fig Tree v. 1.4.3 (Rambaut 2016) with all relevant support values.

Morphological character evolution

Ancestral state reconstruction was used to evaluate character evolutions (Pagel 1999). Fifty-two morphological characters (24 binary, 27 multistate and one noninformative) were chosen and considered for phylogenetic analysis based on the original taxonomic work of Ramadan (1938), Crosnier (1978, 1985), Pérez Farfante and Kensley (1997) and Dall (1999). All these major characters were reexamined carefully, listed in table 2. The data matrix in table 3 was analysed with Mp using combinations of programs: Mesquite v.3.01 (Maddison and Maddison 2015) and PAUP v.4.0 (Swofford 2002). These characters were given equal weightage and unordered, the code given for each state (i.e. 0, 1, 2, 3 and 4). Branch support was assessed using 1000 bootstrap replicates without any out-groups.

Results

The molecular data used in the present analysis constitutes 27 individuals belonging to nine species from three genera of Solenoceridae, 27 individuals belonging to four species from three genera of Penaeidae and 13 individuals from *Aristeus alcocki* of Aristeidae. The out-group for these analyses represents the individuals from *Oplophorus gracilirostris* and *Palinustus waguensis*. Among them, two sequences of *A. alcocki*, three sequences of *O. gracilirostris* and two sequences of *P. waguensis* from our earlier studies were used for analysis (table 1). No insertion, deletion or stop codons were observed and missing sequences were denoted with '–' in the final alignment. A total of 63 COI sequences (665 bp including gaps), 55 16S sequences (540 bp including gaps) and 29 Cytb sequences (341 bp including gaps) were obtained from deep water penaeoid shrimps. We followed the taxonomic identification keys of penaeoid shrimps by Crosnier (1978, 1985, 1987), Pérez Farfante and Kensley (1997) and Dall (1999).

Replicates of all taxa formed a monophyletic and sister clade in the COI Bayesian tree (figure 1). The mean value of K_2P distances was recorded for all the taxa (table 4) which indicated 0.0–3.0% divergence between the individuals and 16.5–20.5% between the genus in the family Penaeidae, while divergence was found to be slightly higher (19.1–24.5%) in between the genus of family Solenoceridae. However, *A. alcocki* (family Aristeidae) formed a few sister clades with <2.0% divergence (ranges: 0.0–1.7%). *M. andamanesis* and *M. coniger* (between 3.3%) both were closer and appeared to exhibit a significant relationship with the genus *Solenocera* and sister clade of genus *Parapenaeus* and *Penaeopsis*. The genetic distances ranged from 7.1 to 21.8% in genus *Solenocera* showing three major clades.

Phylogenetic relationships

The tree topologies using Mp and BI approaches reported similarities with strong support in most of the nodes. Three of the families, Aristeidae (1.0, 100), Penaeidae (1.0, 63) and Solenoceridae (0.79) are found to be monophyletic forming the superfamily Penaeoidea which exhibited strong support (0.98, 100). In the family Penaeidae, the genus *Metapenaeopsis* was separated with high support (1.0, but 68) in comparison with the two genera namely, *Parapenaeus* and *Penaeopsis* (0.68, 68). In Solenoceridae family, genus *Hymenopenaeus* and *Hadropenaeus* were found to be distantly related to the genus *Solenocera* (0.79). *S. hextii* showed early divergence from this group (1.0, 100) while the remaining species clustered to give rise to two subgroups with strong support (0.80, 81). The first subgroup included *S. rathbuni*, *S. pectinata* and *S. annectens* while the second subgroup represented *S. melantho*, *S. choprai* and *S. crassicornis* (figure 2). In addition, COI gene sequences from the NCBI GenBank were retrieved for each genus separately except for *Penaeopsis* and combined with our sequences to understand the phylogenetic position of our species (figures 1–5 in electronic supplementary material at http://www.ias.ac.in/jgenet/).

Table 2. List morphological characters and their states.

.	Character	Morphological description and coding	State no.
Carapace			
1	Rostrum structure	Straight	0
		Not straight	1
2	Rostrum length	Short	0
		Long or medium	1
3	Rostrum: dorsal teeth	3	0
		5–13+1 epigastric	1
4	Carapace general: 1	Pubescent	0
		Glabrous	1
5	Carapace general: 2	Glabrous with pubescent in base of the rostrum	0
		Not glabrous with pubescent in base of the rostrum	1
6	Prosartema	Present	0
		Absent	1
7	Postrostral carina	Extending beyond the gastric region or cervical sulcus	0
		Extending near to posterior end of carapace	1
8	Cervical sulcus	Present	0
		Absent	1
9	Ocular angle	Present	0
		Absent	1
10	Orbital spine	Present	0
		Absent	1
11	Postorbital spine	Present	0
		Absent	1
12	Antennal spine	Present	0
		Absent	1
13	Branchiostegal spine	Present	0
		Absent	1
14	Hepatic spine	Present	0
		Absent	1
15	Hepatic carina	Present	0
		Absent	1
16	Post-antennal spine	Present	0
		Absent	1
17	Ptergostamine spine	Present	0
		Absent	
18	Ptergostamine region	Not specific	0
		Recurved and forming blunt projection	1
		Distinctly formed, not rounded	2
19	Longitudinal sutures	Started from antennal spine to posterior end with same level	0
		Absent	1
20	Branchiocardic carina or sulcus	Strongly formed	0
		Inverted L shaped	1
		Faintly formed	2
		Absent	3
Thoracic appendages			
21	Stylocerite	Upwardly curved, reaching to distal end of eye	0
		Long and broad	1
		Short	2
		Joined with 1st antennular segment	3
22	Antennular flagella: upper	Long and tapering gradually	0
		Long, flat and tubular	1
		Short, flat and tubular	2
		Short, sub fallacious	3
		Sub equal to lower one	4
23	Antennular flagella: lower	Long, cylindrical	0
		With blunt tooth	1
		57–68 segments	2
24	Longest flagella/antennular peduncle length	FM: 1.1–1.32 M: 1.06–1.18	0
		FM: 1.0–1. 06 M: 1.0–1.15	1
		Nil	2

Table 2 (*contd*)

.	Character	Morphological description and coding	State no.
25	Third maxilliped	With base spine, reaching to the end of antennal scale	0
		Reaching to the end of 2nd or 3rd antennular peduncle	1
26	Pereopod I	Basal and ischial spines, reaching end of eye	0
		Basal, ischial and merus spines, reaching end of eye	1
		With meral spine, minute pleurobranch without pinnules, chela versus carpus length=1.14–1.35 times	2
		Reaches to middle of 2nd antennular peduncle	3
27	Pereopod II	With base spine, reaches to end of 2nd or 3rd antennular peduncle	0
		Reaches to end of 2nd antennular peduncle	1
		Small meral spine, minute pleurobranch without pinnules, chela versus carpus length=0.95–1.07 times	2
28	Pereopod III	Reaches to beyond the antennal scale	0
		With base spine, reaches to end of 2nd or 3rd antennular peduncle	1
		Reaches to end of 2nd or 3rd antennular peduncle	2
		Minute pleurobranch without pinnules, chela versus carpus length=0.95–1.07 times	3
29	Pereopod IV	Reaching middle of eye	0
		Minute pleurobranch without pinnules	1
		Slender, reaching end of 1st or 2nd antennular peduncle	2
		Thick and reaches little beyond of antennular peduncle	3
30	Pereopod V	Reaching middle of 2nd antennular peduncle	0
		Slender and reachesor extended the end of 3rd antennular peduncle	1
		Little thick, reaching to end of antennular flagella	2
Abdomen segments			
31	Abdomen I	Not carinated	0
		Faintly carinated	1
32	Abdomen II	Carinated	0
		Faintly carinated	1
		Not carinated	2
33	Abdomen III	Rounded	0
		Carinated	1
		Not carinated	2
34	Abdomen sub-carinae	4th–6th segment carinated	0
		Not subcarinated	1
35	VI abdomen longer than V ratio	1.98–2.07 time	0
		No	1
36	Appendix masculina	Carpal bone shape	0
		Subrectangular, convex	1
		Broader, oval shape	2
		Narrow, protuberance	3
		Petal shaped	4
37	Telson	Three pairs of movable spines	0
		Four pairs of movable spines	1
		With a pair of lateral spines	2
		Spines absent	3
Reproductive organs			
38	Thelycum: posterior plate is broad	Yes, depressed with side margin angled and bilobed	0
		Yes with trapezoid shape	1
		Yes with producing hallow	2
		Yes with rounded	3
		No	4
39	Thelycum: posterior lateral plate	Small with setae	0
		Strong, extending in both side	1
		Two conical processes with tubercle	2
		With two set of boss	3
		Not specific	4
40	Thelycum: anterior plate with boss	Two pair of small boss	0
		One pair of small boss	1
		No	2

Table 2 (*contd*)

.	Character	Morphological description and coding	State no.
41	Thelycum: anterior hallow plate	One pair of narrow vertical plates	0
		Square-like structure	1
		Not hallowed	2
42	Thelycum: anterior plate with rounded	Yes	0
		Sub-semicircular, tri-lobed	1
		No	2
43	Thelycum: anterior plate	Triangle or dimensional shape	0
		Subtriangular shape, apex rounded with setae	1
		Broad median plate with shallow transverse groove	2
		T shape grooved longitude median plate	3
		With a pair prominent spine	4
44	Thelycum: 3rd pereopods	A pair of symmetrical circular boss	0
		Sub-elliptical or triangle, corner arched with setae	1
		Not specific	2
45	Thelycum: 2nd pereopods	Well-developed sterna spine with triangle base	0
		Not specific	1
46	Petasma general	Asymmetrical and complex	0
		Symmetrical	1
47	Petasma structure	Sub-triangular or Triangular shape	0
		Coiled	1
		Sub-rectangular shape	2
		Simple, membranous, halves are united with midline	3
48	Petasma: dorsomedian	Broad with projection	0
		Narrow with projection	1
		Smooth, distal end with small spines	2
		With thickened	3
		Flat and fringed with spines	4
49	Petasma lateral lobules	With a tooth on either side	0
		Lateral lobule with 10–12 spines	1
		Lateral lobes with numerous setae	2
		Lateral accessory lobule with 8 spines	3
		Not specific	4
50	Petasma distoventral projection	Petaloid shape, crenulated and coiled	0
		Not petaloid shape, crenulated and coiled	1
51	Petasma distal end	Distally 18–20 small spines	0
		Pectinated distally with minute bristles	1
		Distal end with three lobules and armed with minute spines	2
		Carry a comb-like strong bristles tightly	3
		Not	4
52	CL length/petasma length	>2.1	0
		<2.0	1
		Not	2

Morphological character evolution

Fifty-four morphological characters representing the carapace (20), thoracic appendages (10), abdominal segments (7) and reproductive organs (15) were used to derive the character matrix (table 2). The characters on the carapace were generated based on the present (0), and absent (1) state except for the 18th and 20th characters. The remaining characters represented the thoracic appendages, abdominal segments and reproductive organs were separated/sorted as with multistate. The reproductive characters were strongly taxa-specific, thelycum demonstrated various shapes at the anterior (squares like hallow, narrow vertical, rounded, triangle, subtriangular shape, shallow transverse and T shape) and posterior (broad: bilobed, trapezoid shape, hallow, rounded boss numbers) regions. While in petasma, it was demonstrated based on the symmetrical and asymmetrical structure (like petaloid, broad, subrectangular, triangular and coiled) and the number of spines or setae.

Based on parsimony analysis, 10 characters were noninformative, 41 (78%) were informative while one character was constant and the strict consensus tree (consistency index = 0.67, retention index = 0.57, rescaled consistency index = 0.37) is represented in figure 3.

Table 3. The data matrix of morphological characters of deep water penaeoid shrimps along the Indian coast.

Taxa	Matrix
A. alcocki	11001101111011010010130212231102001114022212113141 42
M. andamanensis	01111001011010110012000100000010101000422220001140 41
M. coniger	01111001011010110012000000000000010100042223000140 40
P. investigatoris	10101011001000111003240210122002210323422110112101 42
P. jerryi	11101001111010010010300213122102211203422111110041 42
H. equalis	00101000111000001010300213102102221123422001110241 42
H. lucasii	00100000111000001013300210002102111421322202010321 22
S. annectens	00100000010010011110310210100102111421322202110421 12
S. choprai	00100010010010011010310210003101111421410202110341 22
S. crassicornis	00100010010010010010310210003111111434222200112321 42
S. hextii	00100010010010011011320210003202111422402202112311 02
S. melantho	00100010010010011011310210003102111422111222112211 42
S. pectinata	00100000010010011112311210002101111424322242110431 12
S. rathbuni	00100000010010011212310210002102111421222202110211 32

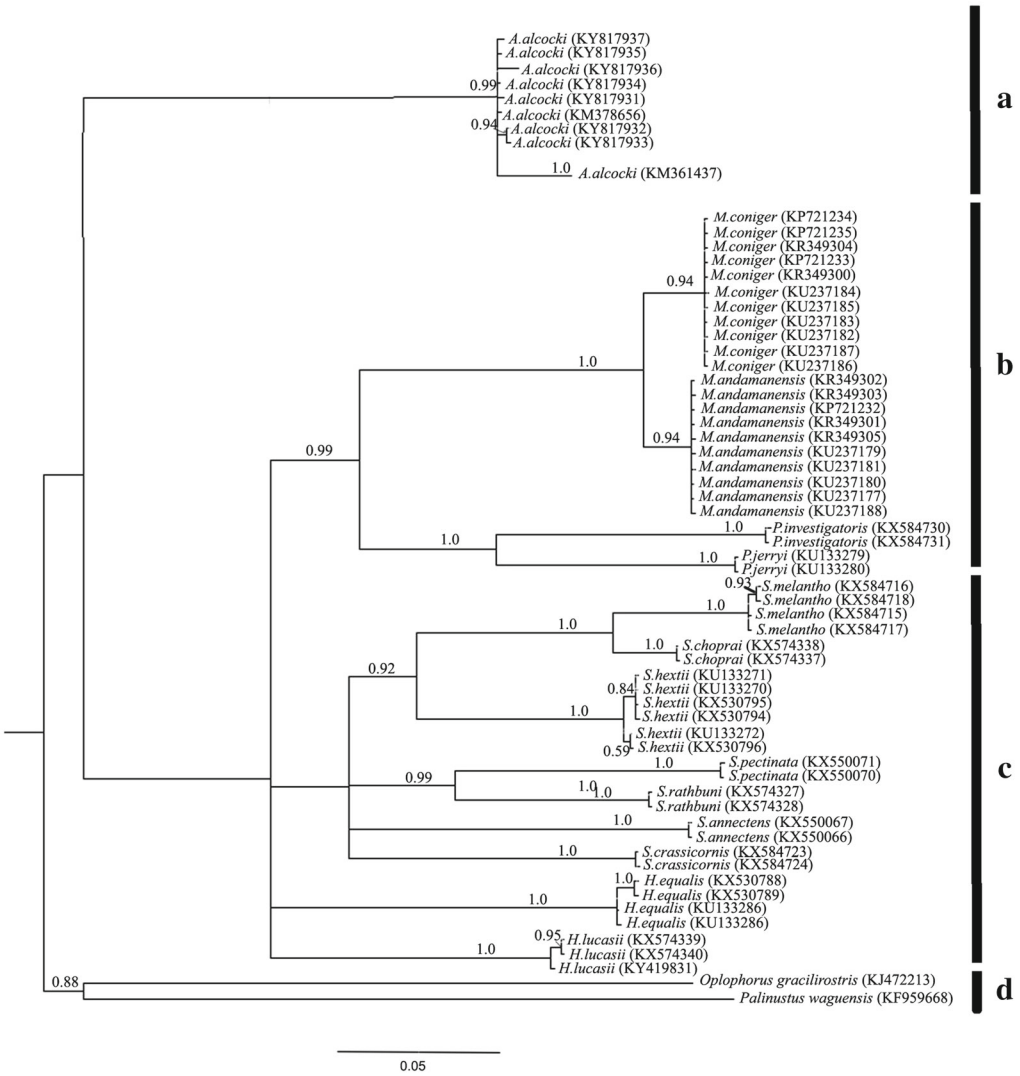

Figure 1. Phylogenetic tree recovered by Bayesian analysis from the COI gene data with nodal support values represent posterior probabilities: (a) Aristeidae, (b) Penaeidae, (c) Solenoceridae, and (d) out-group.

Table 4. Average K2P distances of COI sequences between Taxa.

	AA	MA	MC	PI	PJ	HL	HQ	SA	SC	SCR	SH	SM	SP	SR
AA	0.03													
MA	0.280	0.001												
MC	0.293	0.033	0.00											
PI	0.282	0.174	0.194	0.00										
PJ	0.271	0.19	0.205	0.165	0.00									
HL	0.299	0.203	0.207	0.205	0.192	0.001								
HQ	0.266	0.225	0.219	0.256	0.216	0.200	0.00							
SA	0.330	0.237	0.246	0.260	0.205	0.192	0.206	0.00						
SC	0.253	0.227	0.218	0.242	0.204	0.206	0.219	0.184	0.00					
SCR	0.245	0.240	0.258	0.204	0.227	0.211	0.221	0.188	0.187	0.006				
SH	0.230	0.234	0.239	0.218	0.215	0.191	0.221	0.187	0.151	0.165	0.00			
SM	0.298	0.262	0.259	0.254	0.207	0.221	0.245	0.218	0.071	0.198	0.155	0.003		
SP	0.271	0.211	0.202	0.248	0.200	0.239	0.206	0.215	0.200	0.203	0.203	0.209	0.00	
SR	0.256	0.232	0226	0.240	0.199	0.216	0.211	0.183	0.155	0.180	0.156	0.175	0.152	0.00

AA, *Aristeus alcocki*; MA, *Metapenaeopsis andamanensis*; MC, *Metapenaeopsis coniger*; PI, *Parapenaeus investigatoris*; PJ, *Penaeopsis jerryi*; HL, *Hydropenaeus lucasii*; HQ, *Hymenopenus equalis*; SA, *Solenocera annectens*; SCR, *Solenocera crassicornis*; SC, *Solenocera choprai*; SH, *Solenocera hextii*; SM, *Solenocera melantho*; SP, *Solenocera pectinata*; SR, *Solenocera rathbuni*.

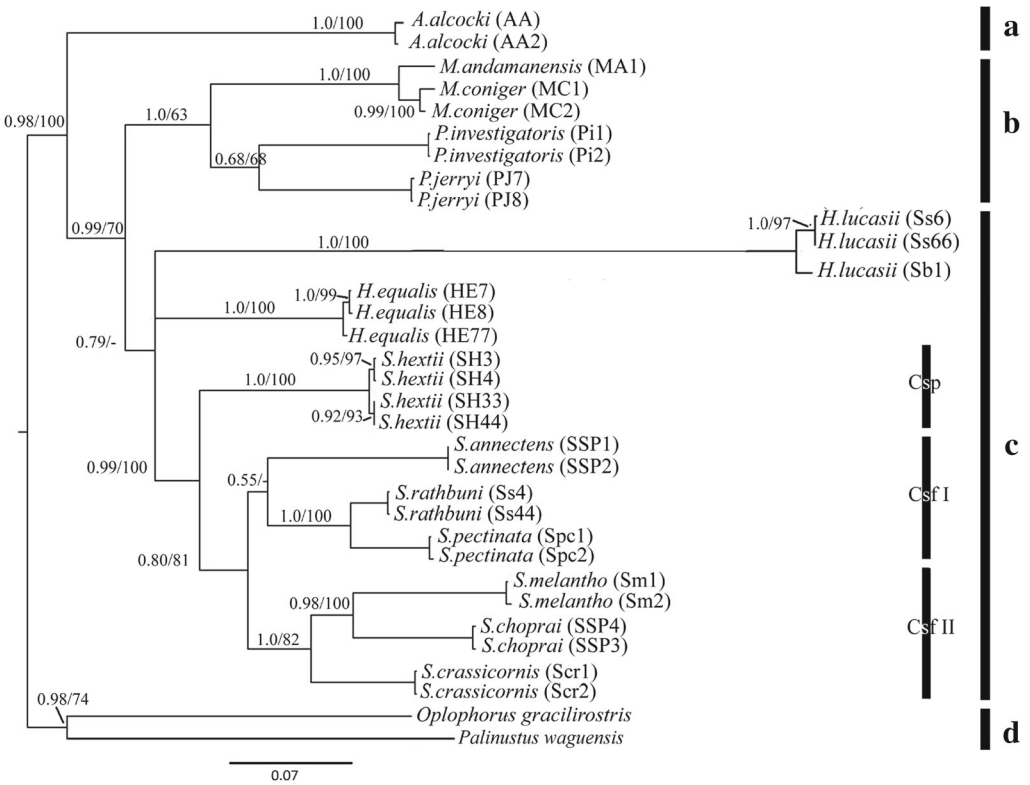

Figure 2. Phylogenetic tree recovered by Bayesian analysis based on the combined sequences of COI, Cytb and 16S genes. Nodal support values represent BI/Mp bootstrap, continental slope—Csp, continental shelf I—Csf I, continental shelf II—Csf II, (a) Aristeidae, (b) Penaeidae, (c) Solenoceridae, and (d) out-group.

Discussion

The standardized usage of mitochondrial COI gene sequences as DNA barcodes has emerged as an accurate tool for rapid identification of various animal species providing high species resolution (e.g. Costa *et al.* 2007; Burns *et al.* 2008) and is increasingly used for crustacean identification (Goldstein and DeSalle 2011; Hultgren *et al.* 2014). In our study, 14 taxa of the seven genera from the penaeoid group have been incorporated in the barcoding gene (COI) analysis. The strong (>3.0%) genetic distance between the taxa in the COI gene, showed the identification

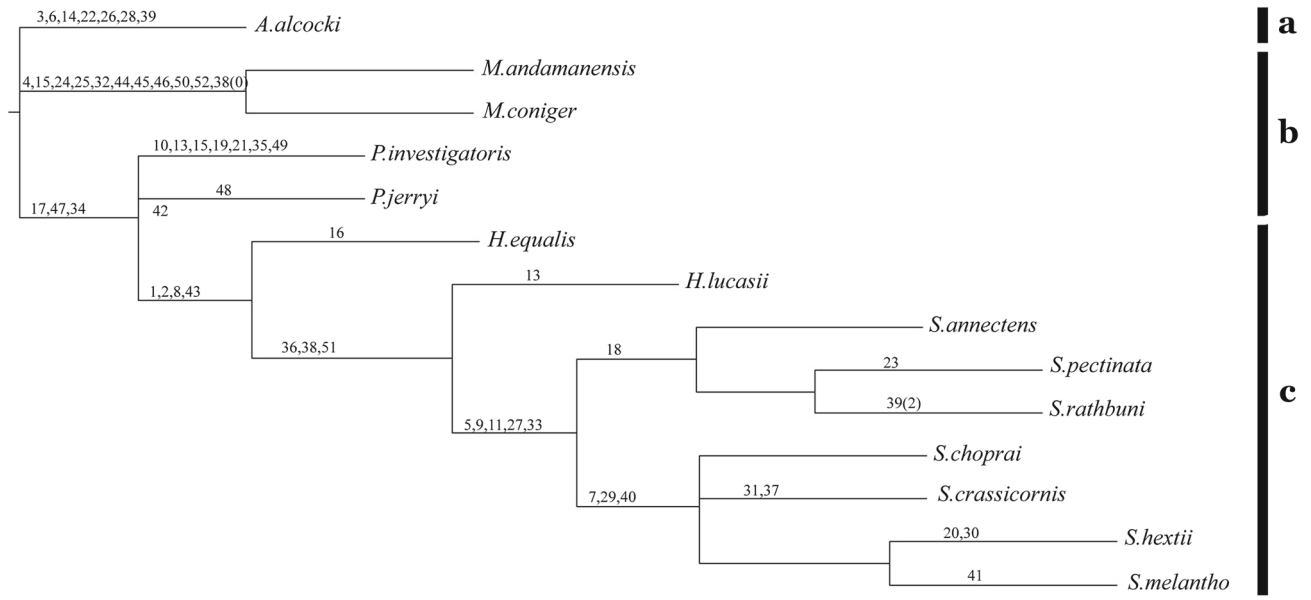

Figure 3. Strict consensus tree recovered by parsimony analysis using morphological characters: (a) Aristeidae, (b) Penaeidae, (c) Solenoceridae.

of the species in accordance with Crosnier (1978, 1984, 1985), Pérez Farfante and Kensley (1997) morphological classification scheme. The intraspecific distance of all taxa was in agreement with the Hebert *et al.* (2003) hypothesis except for *A. alcocki* (>3.0%), however this goes in concordance with Chan *et al.* (2017) where intraspecific distances were 3.8% indicating a very conservative genetic divergence.

The observation made by Cheng *et al.* (2015) states the existence of larger genetic distance (15.4%) between the species of the genus *Metapenaeopsis* which are mostly distributed in shallow water and 0.3% in *M. provocatoria longirostris* and *M. velutina* which inhabit deeper waters. Comparative results of the present study indicated less genetic distance (3.3%) between *M. andamanensis* and *M. coniger* due to the major differences in the thelycum (Crosnier 1987) being distributed in deeper waters (>200 m). According to Cheng *et al.* (2015) and the results of the present analysis a negative correlation is suggested between the depth and genetic distances.

Yang *et al.* (2015) worked on the genus *Parapenaeus* and the results of his study revealed less intraspecific distance (0.7%) in the species inhabiting shallow water and which takes up subsequent migration to the deeper water. Similar results (0.1% genetic distances) were observed in our study with *P. investigatoris*. These are widely distributed throughout the Indian Ocean and fairly abundant in south western coast of India at a depth of 160–300 m where the biological signatures of upwelling process is characterized by vertical mixing phenomena and cascading flows of denser upper layers enriching the deeper waters with organic nutrients (phytoplankton and zooplankton swarms) which would help crustacean development (Madhupratap and Haridas 1990). The study conducted by Chan *et al.* (2008) on the genus *Penaeopsis* revealed 1.9% genetic distance at the species level. Similarly, in this study, *P. jerryi* showed 0.0% distance between the individuals of the same species. This low rate of divergence might be due to the stabilizing selection on morphological or ecological characters.

Quan *et al.* (2004) observed higher genetic distance in genus *Solenocera* (22.8%) which is much smaller than the largest distance between genera in Penaeidae (25.39%) by COI analysis which indicates the presence of a greater amount of barcode gap between the members of these families. Similarly, results of the present study revealed higher genetic distance within and between the genera of Solenoceridae (15.1–24.5%) except between *S. melantho* and *S. crassicornis* (7.1%) while a slightly lesser distance in Penaeidae (16.5–20.5%).

Phylogenetic relationship

The results of the present study included mitochondrial genes (COI, Cytb and 16S) using Mp. BI and distance methods revealed two major clades with an out-group, which is in consensus with the reports of Crosnier (1978) and Burkenroad (1983) where taxonomical characters namely, gills formulas, prosartema, postorbital spines and antennular segments were used. Clade A consists of Aristeidae while clade B included the members of Penaeidae and clade C formed Solenoceridae. Each of the family exhibited monophyletic nature having strong support and large genetic distance. Compared with Aristeidae, Penaeidae and Solenoceridae showed close evolutionary relationship which can be further compared with the other published literature using mitochondrial markers

(Quan *et al.* 2004; Voloch *et al.* 2005; Cheng *et al.* 2015) and nuclear protein-coding genes (Ma *et al.* 2009).

In the present study, clade C included three genera (*Hadropenaeus*, *Hymenopenaeus* and *Solenocera*) of family Solenoceridae with high support. These three genera characterized by the presence or absence of respiratory tubes like antennular flagella and external ramus of uropod spines. These species occupy the benthic regions and mostly preferred soft substrates, where they bury deeply in soft sediments and stayed keeping their respiratory tubes upwards (Dineshbabu and Manissery 2009). These are divided into three subclades showing a strong support in a phylogenetic relationship. Dall (1999) described the species of the genus (*Solenocera*) which are inhabitants of the continental shelf and slope, from about 15 m down to several hundred metres distributed in the Indo-West Pacific. Based on the depth-wise distribution in Indian waters, this genus can be classified into three groups, namely upper continental slope (>250 m) (Csp), the continental shelf I (150–250 m) (Csf I) and continental shelf II (<150 m) (Csf II). Continental slope included only one species (*S. hextii*) which differed from other continental shelf species by the presence of distinct and inverted 'L' shaped branchiocardiac crest (FAO 1983). Continental shelf I included three species (*S. pectinata*, *S. rathbuni* and *S. annectens*) and could be differentiated from continental shelf II (*S. melantho*, *S. crassicornis* and *S. choprai)* by the presence of postrostral carina extending little or beyond the cervical sulcus but it was reaching or almost reaching the end of carapace in *S. melantho*, *S. crassicornis* and *S. choprai*. The molecular results of the present study were in accordance with the classification of Crosnier (1978).

Clade B included three genera (*Metapenaeopsis*, *Penaeopsis* and *Parapenaeus*) falling under the family Penaeidae exhibiting monophyletic (1.0, 68) characters as proposed by Burkenroad (1983). *Penaeopsis* and *Parapenaeus* align as a sister clade to the genus *Metapenaeopsis. Penaeopsis and Parapenaeus* possessed symmetrical petasma and maxilliped III without basal spine and where it was asymmetrical petasma and maxilliped III with basal spine in *Metapenaeopsis* as described by Burukovsky (1983). Similarly, Parapenaeini aligns as a sister clade to Penaeini as it was confirmed to be older from an evolutionary point of view in comparison with other penaeid group (Chan *et al.* 2008; Voloch *et al.* 2009).

Quan *et al.* (2004) examined 11 species of Penaeidae and *S. crassicornis* using a combined sequence (COI and 16S) resulted in the clustering of *S. crassicornis* within Parapenaeini cluster with a greater genetic distance. A similar observation was made by Voloch *et al.* (2005) in the phylogenetic classification of 39 species of Penaeidae and *S. koelbeli.* However, the results of the present study revealed that *S. crassicornis* clustered in the Solenoceridae with strong support (1.0, 82) instead of Parapenaeini indicating that *S. crassicornis* is monophyletic not paraphyletic. These results need to be studied in detail in future.

A. alcocki specimens belonging to the family Aristeidae clustered in clade A which appeared to be the earliest divergence in the penaeid group with strong support. This family differs from other penaeoid by not having prosartema on the eye and our result is fairly similar to Burkenroad (1983) classifications. However, Aristeidae is closely related to Penaeidae and Solenoceridae using nuclear protein-coding genes (Ma *et al.* 2009; Fernández *et al.* 2013).

Morphological character evolution

The studies based on morphological characters using parsimony analysis revealed that most of the synapomorphies are in the carapace and reproductive organs, which are frequently shared with other taxa in the family. The presence of three rostral teeth (03) and the absence of prosartema (06) and antennular flagella (22) forms the synapomorphic characters for the Aristeidae, showing that the *A. alcocki* species have diverged in the early phylogenetic evolution. Similarly, petasma and thelycum morphology separates *Metapenaeopsis* and *Parapenaeus* with a deep node (Crosnier 1985, 1987, 1991) particularly, process *a* in the petasma, the presence or absence of anterolateral protuberance in the thelycum, length of the rostrum, branchiostegal spine with or without carina are some of the important synapomorphies for *Parapenaeus* (Yang *et al.* 2015). In the present study, characters 13, 15, 21, 42, 48 and 49 for *Parapenaeus* and 43, 44, 45, 46, and 52 for *Metapenaeopsis* were observed to be synapomorphic. However, the members of the family Solenoceridae diverge from others with respect to postorbital spine (11), cervical sulcus (8) and rostral length (2) observed by Burukovsky (1983). Characters state 22 (1, 2) corresponding to antennular flagella modified as tube-like structure helpful in respiration along with ocular angle (9), and pereopod (27) were suggested to be synapomorphic for the genus *Solenocera* (Dall 1999). While the species in this genus are getting diverged by the presence of two synapomorphic characters like postrostral carina extending or not-extending to the end of the carapace (7) and thickness of pereopod IV (29). Thus, the development of the postrostral carina on the dorsal side of the carapace is found to have evolutionary importance to the genus *Solenocera*. Characters state 18 (1) corresponds to the pterygostomain region in *S. pectinata* and *S. rathbuni* re-curved while distinctly forming (18–2) in *S. annectens.* In a few other species, namely *S. melantho*, *S. crassicornis*, *S. choprai* and *S. hextii* thelycum characters were found to be important, but by molecular analysis, *S. hextii* was found to diverge from this group. So thelycal characters cannot be considered as synapomorphic for this species.

In conclusion, in the present study, we identified nine species which include three genera under Solenoceridae, four species from three genera of Penaeidae and one species

in the family Aristeidae with a higher molecular divergence (COI: 3.3–33.0%) obtained along the Indian coast. Further, we generated the DNA barcode database using these species which can help in further investigations concerning the detailed evolution and biogeography of these valuable crustacean resources. Results derived from the integration of molecular and morphological characters can contribute to the elaboration of phylogenetic hypotheses. Both data helped to understand species circumscriptions within this group and it clearly showed that all species from these families are monophyletic. A comparison of these data would be best to generate a robust phylogenetic hypothesis, instead of using only taxonomical or a single DNA region. Moreover, concatenation of sequences from three genes (COI, Cytb, 16S) would be best to generate robust phylogenetic hypothesis which strongly supports the monophyly in Penaeidae, Aristeidae and Solenoceridae. However, a few authors find Solenoceridae nested within Penaeidae, making this family paraphyletic. Nevertheless, large and accurate species data collections from Indian waters are the pre-requisite to understand and to explain the stage of evolutionary relationships in these families.

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