

**A REVISION OF THE *PORTUNUS PELAGICUS* (LINNAEUS, 1758)  
SPECIES COMPLEX (CRUSTACEA: BRACHYURA: PORTUNIDAE),  
WITH THE RECOGNITION OF FOUR SPECIES**

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**ABSTRACT.** – The systematics of the commercially important swimming crab, *Portunus pelagicus* (Linnaeus, 1758), is revised and four distinct species, *P. pelagicus* (Linnaeus, 1758), *P. segnis* (Forskål, 1775), *P. reticulatus* (Herbst, 1799) and *P. armatus* (A. Milne-Edwards, 1861), are recognised based on morphological and DNA characters as well as biogeographical considerations. A key to the species is provided. The species can be separated by a combination of characters of the carapace, pereopods, male abdomen, male first gonopod, and differing colour patterns. *Portunus pelagicus* sensu stricto is widespread across Southeast and East Asia and is sympatric with *P. armatus* in the Northern Territory, northern Australia. *Portunus armatus* is found around most of Australia and east to New Caledonia. *Portunus reticulatus* occurs in the eastern Indian Ocean and there is evidence that the Bay of Bengal may be a zone of hybridisation for *P. pelagicus* and *P. reticulatus*. *Portunus segnis* appears confined to the western Indian Ocean from Pakistan to South Africa, and is a Lessepsian migrant into the Mediterranean from the Red Sea.

**KEY WORDS.** – *Portunus pelagicus*, Crustacea, Brachyura, Portunidae, species-complex, taxonomy, molecular phylogenetics, spanning networks.

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## INTRODUCTION

Decapod crustaceans form a major component of commercial fisheries in the Indo-West Pacific region. The market demand for both the wild caught and aquaculture product is sustained and significant, with over 1.5 million tonnes landed each year (Otto et al., 2001). The crab fishery is dominated by a few members of a single family, the Portunidae. They include four species of mud crab (genus *Scylla* De Haan, 1833), the blue swimming crab [*Portunus pelagicus* (Linnaeus, 1758)] and the gazami crab [*P. trituberculatus* (Miers, 1876)] (also see Ng, 1998).

*Portunus trituberculatus* dominates the official global catch, with disclosed landings of 346,982 tonnes in 2004, compared with 199,731 and 19,344 tonnes, respectively, for *P. pelagicus* and the *Scylla* species [then combined under the

name *Scylla serrata* (Forskål, 1755)] in 2001 (FAO, 2007). The fishery for *P. trituberculatus*, however, is restricted to China, Japan and Korea, and the wider Indo-West Pacific distribution of the four *Scylla* species and *P. pelagicus* make them more valuable commodities across many more countries. In particular, the abundance of *P. pelagicus* and increasing demand for this species for the frozen and tinned crabmeat industry throughout the Indo-West Pacific makes it a particularly valuable target species.

In recent years, genetic analyses in combination with morphometric and morphological studies have shown that the mud crab *Scylla serrata* (Forskål, 1775) is a complex of four similar species (Keenan et al., 1998). Likewise, the commercially important shovel-nosed lobster *Thenus orientalis* (Lund, 1793) was found to be a species complex comprising five species (Burton & Davie, 2007). These

studies suggest that the evolutionary history of speciation across the Indo-West Pacific region is more complex than previously thought, and that other putative widespread species may also show similar patterns if carefully scrutinised. While *Portunus pelagicus* is reportedly widespread throughout the Indo-West Pacific region, there have been indications that it may be a species complex. Published descriptions and figures of *P. pelagicus* from Africa, Asia, India and Australia, when compared directly, show that several distinct colour morphs exist. Nonetheless, earlier taxonomic reviews regarded these differences as mere geographic variants (Stephenson, 1968b), although Stephenson (1972a) speculated that such regional variability was the result of speciation processes at work. Dissimilarity in larval morphology has also suggested that the Indian, Pacific and Australian populations of *P. pelagicus* may constitute different species (Prasad & Tampi, 1953; Shinkarenko, 1979; Yatsuzuka & Sakai, 1980). An allozyme study of various populations of northern Australian *P. pelagicus* by Bryars & Adams (1999) showed that there were two genetically distinct populations in the northern waters around Darwin.

The present study was therefore initiated to determine whether *Portunus pelagicus* is a species complex, and, if so, the number of species, and the genetic and morphological distinctions between them. To do this, we obtained specimens of *P. pelagicus* from throughout its known geographic range, and have used DNA, morphometric and morphological methods to examine them.

## MATERIALS AND METHODS

**Specimen collection.** – Specimens of *Portunus pelagicus* sensu lato were collected from 25 localities throughout its reported range. These included Japan, Indonesia, Australia, Singapore, Thailand, Sri Lanka, India, Madagascar, Israel and the United Arab Emirates. In particular, type specimens of all available names currently considered to be synonyms were examined, and fresh specimens from type localities were obtained whenever possible [e.g., from the Red Sea, the type locality of *P. segnis* (Forskål, 1775)]. Fresh specimens were collected by colleagues, ourselves, or obtained from markets at fishing ports. Samples were preserved in 95% ethanol.

**Morphological examination and taxonomy.** – Measurements were made to the nearest 0.1 mm using electronic vernier calipers, and drawings were made using a camera lucida attached to a stereomicroscope. Terms and definitions used in this study follow Wee & Ng (1995). Measurements provided, in millimeters, are of the carapace width (taken at the widest point) and length (taken from the median frontal teeth to the posterior border of the carapace) (Fig. 1), respectively. G1 and G2 refer to the male first and second gonopods, respectively.

In addition to freshly collected material, specimens were borrowed from museums, especially available type material. Where historically reported material could not be re-

examined, we have attempted to attribute literature records based on the descriptions and figures. Records without clear data were regarded as incertae sedis and are treated separately. Where a type specimen was lost or destroyed, a neotype was designated to stabilise the name and prevent subsequent confusion.

Material examined is deposited in the following institutions: MNHN - Muséum national d'Histoire naturelle, Paris, France; MPL - Mauritius Institute, Port Louis, Mauritius; MZUF - Museo Zoologico La Specola dell'Università di Firenze, Italy; NHM - Natural History Museum, London, United Kingdom; NHMW - Naturhistorisches Museum in Wien, Vienna, Austria; QM - Queensland Museum, Brisbane, Australia; RMNH - Naturalis (ex Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands; SAM - South Australian Museum, Adelaide, Australia; SMF - Senckenberg Museum Forschungsinstitut, Frankfurt am Main, Germany; WAM - Western Australia Museum, Perth, Western Australia; ZMB - Zoologisches Museum Berlin, Berlin, Germany; ZMUC - Zoological Museum, University of Copenhagen, Copenhagen, Denmark; ZRC - Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore.

**Morphometrics.** – Fourteen measurements were taken (Fig. 1; Table 1), and standardised using ratios. Statistical tests were undertaken using SPSS 11.5 (SPSS, Inc., Chicago, IL). Data were tested for normal distribution using the Kolmogorov-Smirnov-test. Morphometric ratio comparisons between individual males from different geographic regions were carried out with a one-way ANOVA and a post hoc Scheffe test for comparison between groups. Stepwise discriminant analyses (DA) were performed to determine groupings. Owing to sexual dimorphism, only males were used for this portion of the study. Missing values were substituted by group means. The default F-value of 3.0 was assigned as the minimum value for variables to enter the model.

**Genetic analyses.** – Localities and numbers of specimens sampled for DNA analyses are given in Table 5. Freshly collected specimens were preserved in 95% ethanol. Total DNA was isolated using Qiagen's DNeasy Tissue Kit following the manufacturer's protocol. DNA was eluted in between 50 to 100 µl of elution buffer AE and stored at -20°C. All buffers used in the procedure were supplied in the kit with the exception of 100% absolute ethanol.

The COI gene was amplified using Polymerase Chain Reaction (PCR) with universal primers COIa (5'-AGTATAAGCGTCTGGGTAGTC-3') and COIf (5'-CCTGCAGGAGGAGGAGATCC-3') obtained from Kessing et al. (1989). This primer pair amplifies a COI fragment that corresponds to positions (5' to 3') 681-1294 of the mitochondrial genome. PCR were performed in a final volume of 50 µl containing 5 µl 10× Taq Polymerase Buffer, 5 µl (25 mM) MgCl<sub>2</sub>, 5 µl 0.5 mM dNTPs, 1 unit Taq polymerase (Perkin Elmer) and 0.5 µl each of 25 pmol/µl COIa and COIf.

An initial denaturation step of 94°C for 2 minutes was followed by 30 cycles of 1 minute at 94°C, 1 minute at 50°C and 1.5 minutes at 72°C. All PCR products were checked for positive amplification by visualising its presence compared with a 100 bp DNA ladder (Promega, Madison, USA) when electrophoresed in a 1% agarose gel stained with ethidium bromide. Positively amplified fragments were purified from excess dNTPs and primers using QIAquick PCR purification columns (Qiagen) following the manufacturer's protocol.

The purified PCR product was subject to cycle sequencing using the ABI PRISM® Dye terminator kit containing AmpliTaq and BigDye (ver. 3) dye terminator. Each sequencing reaction volume comprised of 5–8 ng of PCR product, 1 µl of BigDye, 0.5 µl of 5x BigDye sequencing buffer, 0.4 µl of sequencing primer (COIa or COIb, 2pmol/µl) and topped up to 5 µl with sterile Milli-Q water. The cycle sequencing profile comprised 30 cycles of 30 sec at 95°C, 15 sec at 50°C and 4 minutes at 60°C. All extension products

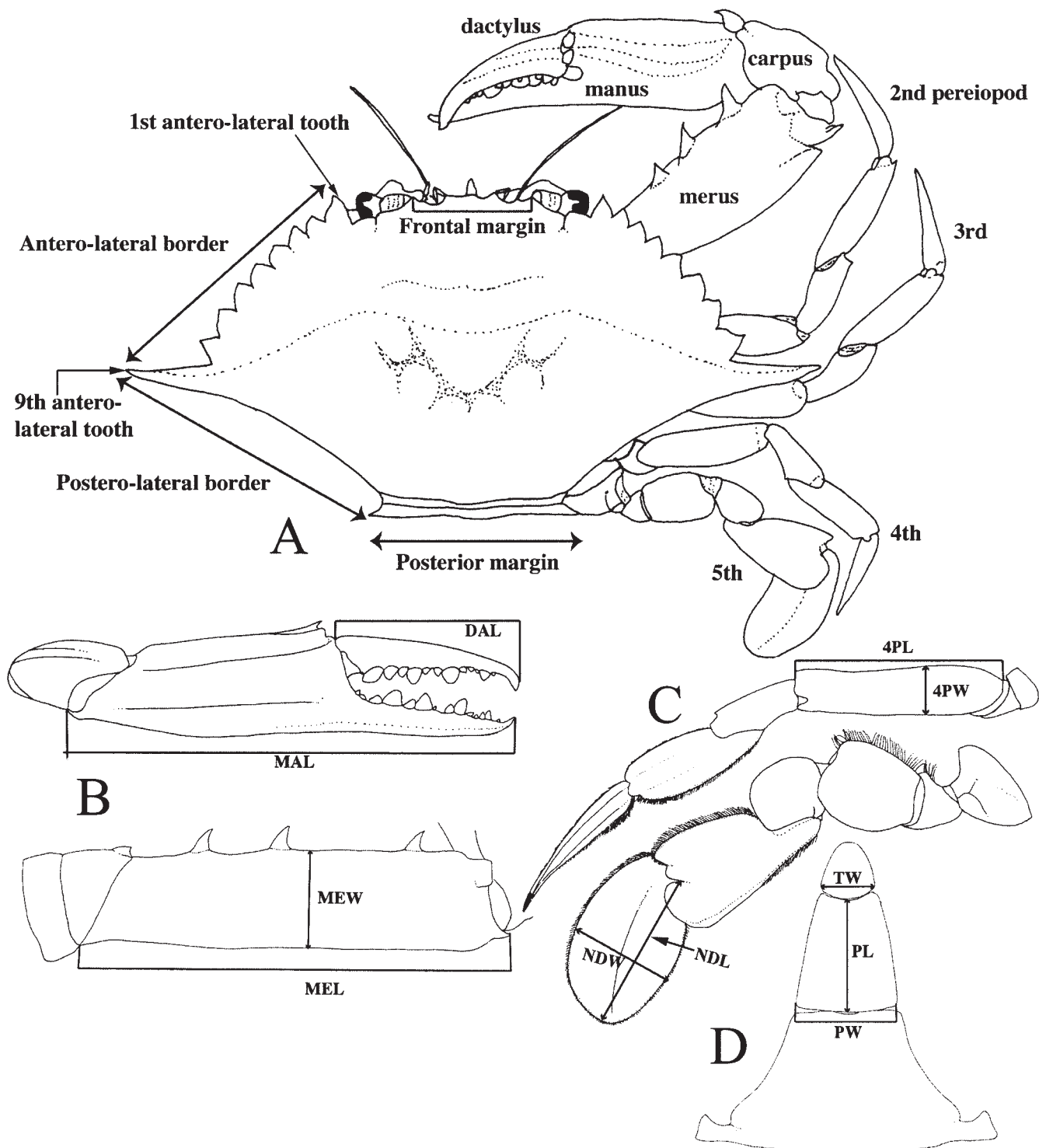


Fig. 1. Schematic drawings of a generalized *Portunus pelagicus* illustrating morphological terms and measurements used in the study. A, dorsal surface and appendages; B, cheliped; C, pereiopods; D, abdomen.

Table 1. List of dimensions measured and ratios used in morphometric analyses.

Character measured	Ratio derived
<b>Carapace</b>	
Carapace length (CL)	
Carapace width (excluding 9 <sup>th</sup> anterior-lateral tooth) (CW1)	CW1/CL
Carapace width (including 9 <sup>th</sup> anterior-lateral tooth) (CW2)	CW2/CL
<b>Appendage</b>	
Major cheliped merus length (MEL)	
Major cheliped merus width (MEW)	MEL/MEW
Major cheliped manus length (MAL)	
Major cheliped dactylus length (DAL)	MAL/DAL
4 <sup>th</sup> pereopod merus length (4PL)	
4 <sup>th</sup> pereopod merus width (4PW)	4PL/4PW
Natatory leg dactylus length (NDL)	
Natatory leg dactylus width (NDW)	NDL/NDW
<b>Abdomen</b>	
Penultimate segment length (PL)	
Penultimate segment width (PW)	PL/PW
Telson width (TW)	PL/TW

are purified using ethanol and sodium acetate precipitation. Sequences were read using the ABI 3100 automated capillary sequencer.

**Sequence analyses.** – To avoid pseudogenes (Bensasson et al., 2001; Gusmão et al., 2000; Mathews et al., 2002; Williams & Knowlton, 2001), sequences with ambiguous chromatograms were discarded and the remainder were translated to amino acids to check for stop codons. Sequence contigs were aligned by eye using the programme Sequencher version 4.0 (Genecodes, Ann Arbor) and subsequently aligned with ClustalX Multiple Sequence Alignment Program version 1.7 (Thompson et al., 1997) using preset settings and edited in MacClade v.4.08 (Maddison & Maddison, 2005) before being exported into MEGA (Kumar et al., 2004), Arlequin v.3.00 (Schneider et al., 2000), PAUP\* 4.0b10 (Swofford, 2002) and TCS (Clement et al., 2000) for further analyses.

**Tree reconstruction.** – We used Modeltest ver. 3.7 (Posada & Crandall, 1998) to determine the substitution model for the dataset with the resultant best fit model using the Akaike Information Criterion (AIC) being Tamura-Nei (TrN) + invariable sites (I) + gamma distribution (G). Two tree search methods [Maximum Parsimony (MP) and Minimum Evolution (ME)] were used to infer relationships between putative species. A heuristic tree search was conducted using the MP algorithm with 100 random sequence additions and tree bisection-reconnection branch swapping. Three other portunid species were used as outgroups: *Charybdis lucifera* (Fabricius, 1798), *Portunus sanguinolentus* (Herbst, 1873) and *P. trituberculatus* (Miers, 1876). PAUP\* 4.0b10 (Swofford, 2002) and MEGA version 2.0 (Kumar et al., 2004) were used for MP and ME tree construction, respectively. Topological robustness was assessed with 1,000 bootstrap replicates for both methods.

**Haplotype parsimony network.** – Identical COI sequences were collapsed into distinct haplotypes and relationships between haplotypes were analysed in a parsimony network estimated with TCS version 1.21 (Clement et al., 2000) using the statistical parsimony procedure described in Crandall (1994) and Templeton et al. (1992). This method estimates the unrooted tree and provides a 95% plausible set for all sequence type linkages within the unrooted tree. Outgroup weights were calculated following Castelleo & Templeton (1994), which predicts the oldest haplotype based on neutral coalescent theory applied to intraspecific networks (Posada & Crandall, 2001).

**Species delimitation.** – The barcoding hypothesis of fixed inter- and intra-specific divergence thresholds at the COI locus (Hebert et al., 2003) was tested by plotting pair-wise percentage divergences within and between sequences for all four species. However for clarity, we specifically excluded the haplotypes of *P. reticulatus* that are the same as *P. pelagicus* (see Results).

## RESULTS

To prevent confusion, the term *Portunus pelagicus* sensu lato henceforth applies to the broad concept of the species as it has been considered to date. *Portunus pelagicus* sensu stricto refers to the revised and restricted concept of the species as defined by the present study.

In total, 468 specimens were examined. These include 127 individuals from the Pacific, 149 from the Western Indian Ocean and Persian Gulf region, 49 from east of the Indian subcontinent, Sri Lanka and Andaman sea, and 143 specimens from Australia and New Caledonia.

Table 2. List of nominal names associated with *Portunus pelagicus*, authority and type locality.

Name	Author	Type locality	Type material status
<i>Cancer pelagicus</i>	Linnaeus, 1758	Ambon, Moluccas	Lost; neotype designated
<i>Cancer segnis</i>	Forskål, 1775	Jeddah, Red Sea	Lost; neotype designated
<i>Cancer cedonulli</i>	Herbst, 1794	East Indian Sea	Lost; neotype designated
<i>Cancer reticulatus</i>	Herbst, 1799	East Indian Sea	Lectotype deposited at the Berlin Zoological Museum.
<i>Portunus denticulatus</i>	De Procé, 1822	Philippines	Lost; neotype designated
<i>Portunus armatus</i>	A. Milne-Edwards, 1861	Shark Bay, Western Australia	Lectotype deposited at Natural History Museum, London
<i>Portunus pelagicus</i> var. <i>sinensis</i>	Shen, 1932	China	Holotype deposited Zoological. Museum Fan Memorial Institute of Biology
<i>Portunus mauritianus</i>	Ward, 1942	Mauritius	Holotype deposited at Desjardins Museum, Mauritius.

Sixty-four specimens were measured for discriminant function analyses, and partial COI sequences were obtained from 300 individuals of *P. pelagicus* sensu lato collected from 25 localities (Table 5). A minimum of three individuals per population was sampled, although it was only possible to sample a single specimen from Pakistan as the specimens were severely decayed and damaged in transit.

**Morphology.** – Morphological character analysis initially suggested four natural groupings: — 1) a true *Portunus pelagicus* morphotype predominantly distributed in Southeast Asia; 2) a distinctive Australian morphotype; 3) another morphotype in the eastern Indian Ocean centred on the western Bay of Bengal through to the Andaman Sea; and a final morphotype in the western Indian Ocean. These groupings thus formed the species concepts that we tested using genetic and morphometric techniques. There are seven available names in the synonymy of *P. pelagicus* sensu lato that are potentially available to use for the four recognised morphotypes (Table 2). The full justification of our decisions regarding valid name allocation is given under the systematic accounts. However, to simplify discussion of the results of the morphometric and genetic analyses we here use the following names for the four species now recognised: *Portunus pelagicus* (Linnaeus, 1758), *P. segnis* (Forskål, 1775), *P. reticulatus* (Herbst, 1799) and *P. armatus* (A. Milne-Edwards, 1861) (see Table 3 for synonyms and distribution summaries).

**Morphometrics.** – Results of the canonical analysis of the output from the discriminant function analysis are given in the scatter plot (Fig. 2) with 80.6% of original grouped cases correctly classified. Of eight variables tested, only three were significantly different in single character ratios whilst no clear groupings (with a 95% confidence interval) could be elucidated with discriminant function analysis. One-way ANOVA analyses of ratios among males of different species revealed significant differences in: 1) carapace width to carapace length (CW2/CL) ( $df = 3, F = 4.153; P < 0.05$ ); 2) cheliped merus length to width (MEL/MEW) ( $df = 3, F =$

4.786;  $P < 0.05$ ); and 3) cheliped manus to dactylus (MAL/DAL) ( $df = 3, F = 9.549; P < 0.01$ ). The post hoc Scheffe's test also showed that CW2/CL is significantly different between *Portunus armatus* and *P. segnis* ( $P < 0.05$ ), MEL/MEW is significantly different between *P. armatus*, *P. reticulatus* and *P. pelagicus* ( $P < 0.05$ ), and MAL/DAL is significantly different between *P. pelagicus* and *P. reticulatus*, and *P. pelagicus* and *P. armatus* ( $P < 0.05$ ).

**Genetics.** – Three hundred individuals of *P. pelagicus* sensu lato were sampled from 25 populations across the Indo-West Pacific, and were found to consist of 128 specimens of *P. pelagicus* sensu stricto, 50 specimens of *P. armatus*, 77 specimens of *P. reticulatus*, and 45 specimens of *P. segnis*. For *P. reticulatus*, the sample size includes 21 specimens

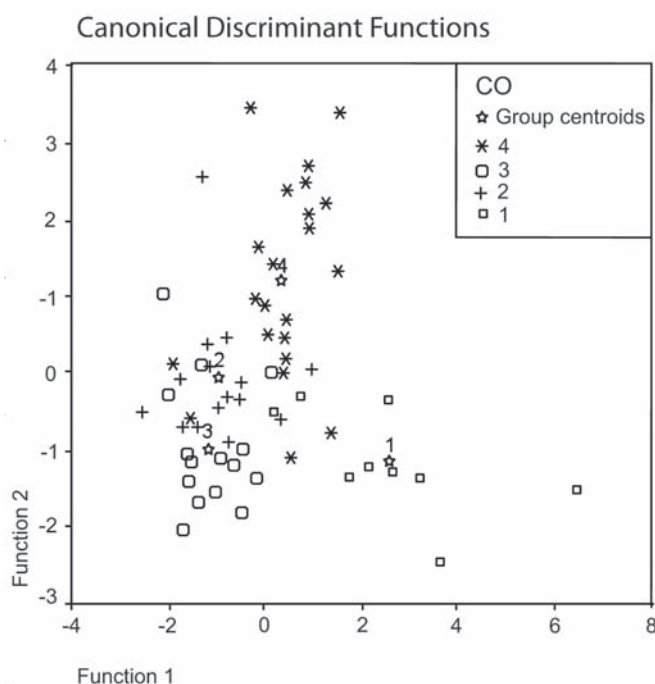


Fig. 2. Scatter plot of canonical scores from forward stepwise discriminant function analysis. Group 1, *Portunus armatus*; 2, *P. reticulatus*; 3, *P. segnis*; 4, *P. pelagicus*.

Table 3. Names assigned to each morphotype group, synonymies if any, and geographic distribution.

Morphotype group	Synonyms	Distribution
<i>P. pelagicus</i> sensu stricto	<i>P. cedonulli</i> <i>P. denticulatus</i> <i>P. pelagicus</i> var. <i>sinensis</i>	West Pacific Ocean; Japan to Indonesian Archipelago, Straits of Malacca to Thailand. Northern Territory, Australia, Bay of Bengal (?)
<i>P. segnis</i>	<i>P. mauritanus</i>	West Indian Ocean; West of Indian sub-continent, Pakistan, Persian Gulf, Red Sea, Mediterranean Sea, East coast of Africa.
<i>P. reticulatus</i>	None	East Indian Ocean; East of Indian subcontinent, Sri Lanka, Bay of Bengal
<i>P. armatus</i>	None	Australia, New Caledonia

possessing haplotypes considered typically *P. pelagicus* (Figs. 3, 5). Furthermore, there is a clade comprising two individuals collected from Japan that may possibly represent a cryptic species. Due to sampling constraints and other circumstances, voucher specimens were not always kept. Of the 300 individuals, 109 unique COI haplotypes were obtained. All unique haplotype sequences have been deposited in Genbank (accession numbers EF661877–EF661976 and GQ272555–GQ272564). A total of 102 polymorphic sites and 113 substitutions (91 transitions, 22 transversions) out of 573 basepairs (i.e., 17.8% variable sites) were observed for all four species.

Haplotype and nucleotide diversities of individual populations ranged from 0 to 1 and 0 to 0.013 respectively. Tables 4 and 5 summarise various population parameters as calculated by Arlequin for each species, and by species populations respectively. *Portunus segnis* was collected from locality codes 1–5; *P. reticulatus*, 6–8; *P. pelagicus*, 9–18 and *P. armatus*, 19–25. Sample size is denoted by *n*, number of haplotypes (*N<sub>h</sub>*), number of polymorphic sites (*N<sub>p</sub>*), haplotype diversity (*h*) and nucleotide diversity ( $\pi$ ). In general, each species group displayed high haplotype diversity and low nucleotide diversity.

**Phylogenetics.** – Phylogenetic analyses were carried out using the entire data set of 109 unique haplotypes. Both analyses reproduced trees of the similar topology as that shown in Fig. 3. Out of 573 characters used in the analysis, 106 were parsimony informative, and the MP tree recovered had a length of 275 steps (CI = 0.771 and RI = 0.757). While it is clear that the species complex is closely related and that each terminal clade (with the exception of the *P. armatus* clade) shows high bootstrap support (>80), it was not possible to infer which of the four species is basal to the rest as they were polarized into two distinct dichotomies. Average inter-specific percentage divergences for the four species are reported in Table 6 and the frequency histograms of both inter and intra-specific divergence is illustrated in Fig. 4.

Owing to more intensive sampling effort for *P. pelagicus*, a higher degree of polymorphism was observed. Interestingly, 21 out of 77 specimens of *P. reticulatus* (27%) collected from India, Sri Lanka and Phuket shared the same or similar haplotypes common to *P. pelagicus* (annotated by "\*" in

Fig. 3, haplotype 32 in Fig. 5A, C). The sister species to *P. pelagicus* is *P. segnis*, collected from the Western border of the Indian Ocean and the Red Sea with relatively high ME bootstrap support (98%). Two specimens of "*P. pelagicus*" collected from the northwestern Pacific in Kyushu, Japan, possessed two unique haplotypes which were not only significantly divergent from the rest, but also make up a sister clade with *P. reticulatus* and *P. armatus* ("\*\*" in Fig. 3). Unfortunately, due to administrative and legal constraints beyond our control, only tissue samples were kept from these two specimens and we were unable to further assess them morphologically. Thus, they are not further considered in the following taxonomic account but nevertheless possibly represent a fifth cryptic species.

The next well-supported clade with a bootstrap value of 99% comprises haplotypes obtained from individuals of *P. reticulatus* and *P. armatus*, collected from two distant geographic regions, India/Sri Lanka, and Australia/New Caledonia. Owing to low percentage divergence between them, their relationships could not be resolved with a high degree of confidence (i.e., moderate to insignificant bootstrap value for *P. reticulatus* and *P. armatus* clades respectively) even though haplotypes obtained from these two species are distinctly unique with no overlap (note, however, the overlap of haplotypes between *P. pelagicus* and *P. reticulatus* as discussed above).

**Species delimitation.** – Maximum and minimum inter-specific divergence between these four species ranged between 8.8% and 1.2% while intra-specific divergence ranged from between 0% to a maximum of 2% (Fig. 4). The overlap between inter and intra-specific divergence (Fig. 4A) is singularly attributed to low genetic differentiation between *P. reticulatus* and *P. armatus*; haplotypes of these two species were connected together when a parsimony network was constructed using TCS.

Despite this low divergence, no common haplotypes are shared between these two species. Although they can be considered as a single molecular taxonomic unit because of this, morphological differences between these two species suggest otherwise (see Systematic account for detailed discussion). Inter-specific divergence between *P. segnis* and *P. pelagicus* ranged from 3.2–4.8% accounting for the peak in frequency denoted by "B" in Fig. 4, whilst the range shown

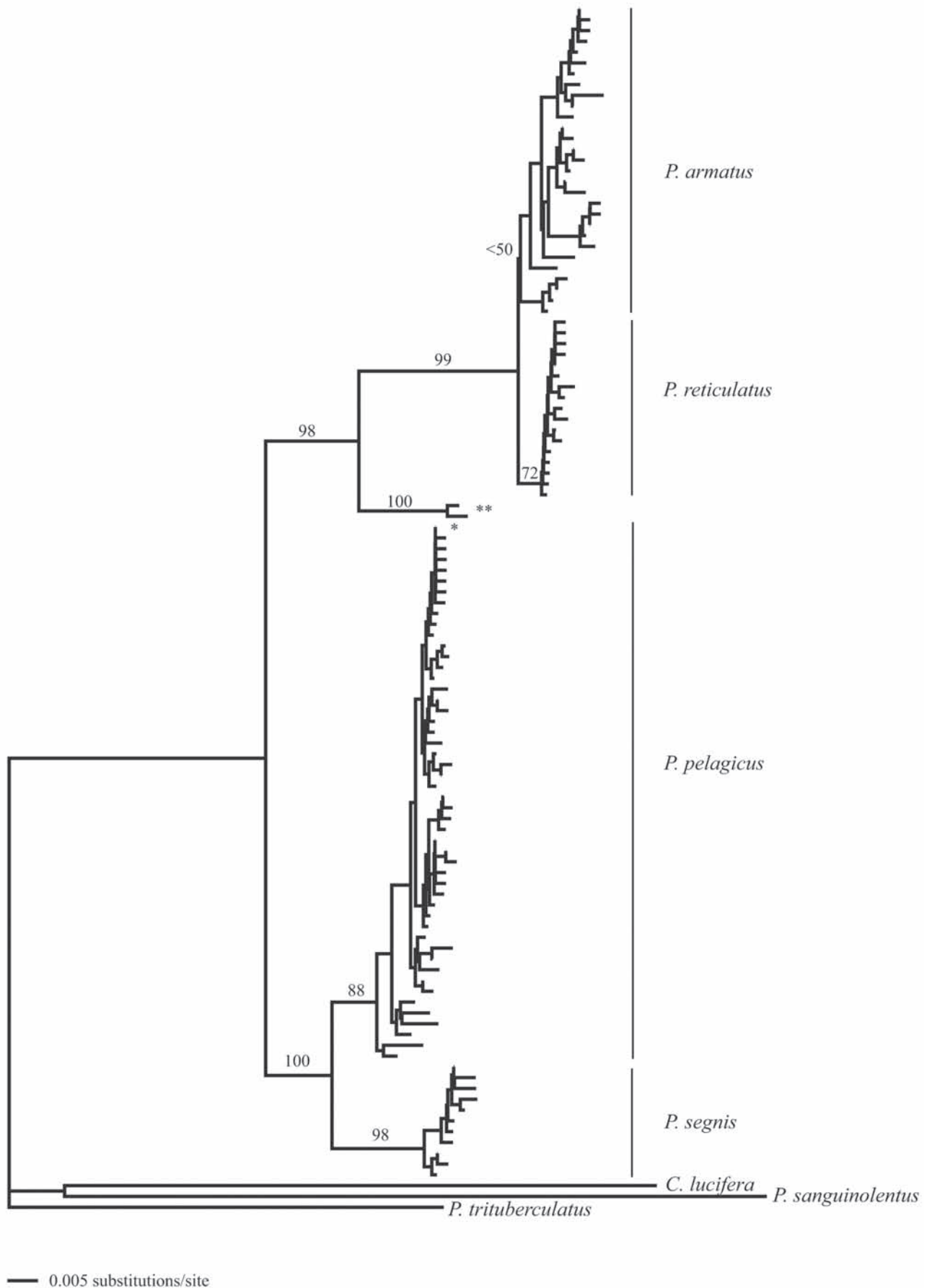


Fig. 3. Minimum Evolution bootstrap tree incorporating all unique COI haplotypes. Haplotypes of specimens obtained from *Portunus pelagicus*, *P. segnis*, *P. reticulatus* and *P. armatus* with *P. trituberculatus*, *P. sanguinolentus* and *Charydis lucifera* as outgroups. ‘\*’ Indicates the dominant haplotype found in *P. pelagicus* shared with eight *P. reticulatus* individuals. ‘\*\*’ Denotes two individuals collected from Japan that may constitute a possible cryptic species.

Table 4. Species population parameters. Sample size is denoted by (*n*), number of haplotypes (Nh), number of polymorphic sites (Np), haplotype diversity (*h*, to 3 decimal places) and nucleotide diversity ( $\pi$ , up to four decimal places). Superscript <sup>1</sup> and <sup>2</sup> refer to analysis of *P. reticulatus* haplotypes excluding those shared with *P. pelagicus* and analysis of *P. pelagicus* haplotypes excluding two haplotypes found from Japan that may constitute a possible cryptic species respectively.

Species	<i>N</i>	Nh	Np	<i>h</i>	$\pi$
<i>Portunus armatus</i>	50	29	38	0.950 ± 0.017	0.0189 ± 0.0097
<i>Portunus reticulatus</i>	77	22	52	0.776 ± 0.040	0.0570 ± 0.0279
<i>Portunus reticulatus</i> <sup>1</sup>	54	17	17	0.649 ± 0.076	0.0018 ± 0.0014
<i>Portunus segnis</i>	45	11	15	0.753 ± 0.045	0.0076 ± 0.0042
<i>Portunus pelagicus</i>	128	49	58	0.925 ± 0.013	0.0138 ± 0.0071
<i>Portunus pelagicus</i> <sup>2</sup>	126	44	39	0.891 ± 0.020	0.0056 ± 0.0032

in “C” accounts for all divergences between *P. armatus*/*P. reticulatus* and *P. pelagicus*/*P. segnis*.

**Intraspecific haplotype relationships.** – Four haplotype statistical parsimony networks generated by TCS were obtained from sequence data of all four species and they are presented in Fig. 5.

The relationships between haplotypes of *Portunus pelagicus*, *P. segnis*, *P. reticulatus* and *P. armatus* are illustrated (Fig. 5A, B, C, D, respectively). One network we have not shown consists of two haplotypes from the three northern Pacific specimens (marked \*\* in Fig. 3). These are separated from each other by a single mutational step, but differ from other *P. pelagicus* haplotypes by at least 25 mutational steps, and may represent a cryptic fifth species. Each circle represents a unique COI haplotype; the size of the circle reflects haplotype frequency and small unshaded circles represent a putative single mutation that was not sampled in the study, but would join all haplotypes within a 95% statistical confident parsimony network if present.

Based on the parsimony network, most haplotypes are species specific and geographically restricted with no single haplotype

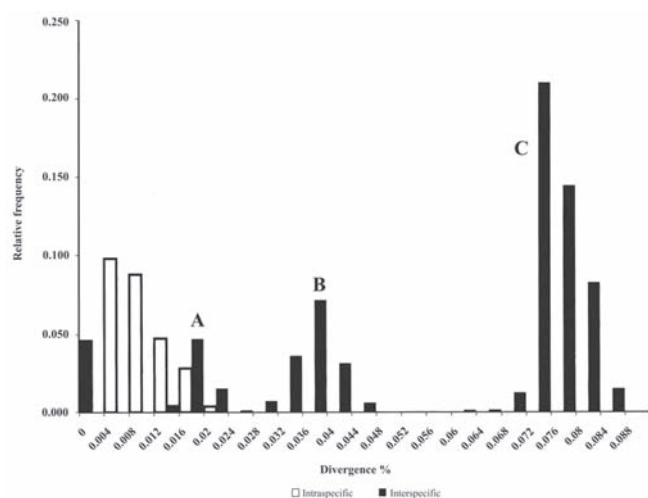


Fig. 4. Frequency histogram of intra and inter-specific divergence for COI locus for the four species excluding outlier haplotypes for clarity. A, Divergence between *Portunus armatus* and *P. reticulatus*; B, divergence between *P. pelagicus* and *P. segnis*; C, divergence between *P. armatus*/*P. reticulatus* and *P. segnis*/*P. pelagicus*.

dominating across the entire region, in consensus with the ME tree (Fig. 3). The exceptions are haplotypes 32 and 58, which occur in both *P. reticulatus* and *P. pelagicus*.

Haplotype network for *P. pelagicus*: *Portunus pelagicus* sensu stricto (Fig. 5A) shows high degrees of haplotype diversity. There are at least three widespread haplotypes with Haplotype 32 occurring with the highest frequency (*n* = 25) and in the most localities (6). Haplotype 32 is also common in *P. reticulatus* (*n* = 18). The remaining 25 individuals of *P. pelagicus* possessing Haplotype 32 make up 19.4% of the total number of individuals collected from the Pacific (*n* = 129). The next most common haplotype, Haplotype 58 (*n* = 17) differs from Haplotype 32 by a single mutation step. The third most common haplotype (Haplotype 51) comprised 16 individuals. Together, these three haplotypes account for 45% of the individuals sequenced. Thirty-seven haplotypes were singletons, appearing only in a particular individual while five haplotypes, Haplotype 57, 76, 79, 97, 98 were private, i.e., it occurred in more than one individual, but were restricted to a single locality. There are weak star-like phylogenies radiating from haplotypes 32, 51 and 58 but a high number of uncommon haplotypes spread out throughout the network for *P. pelagicus* were noted.

Haplotype network for *P. segnis*: haplotypes obtained for *P. segnis* (Fig. 5B) show two co-dominant haplotypes separated from each other by two mutational steps. Haplotype 102 (*n* = 16) is obtained from individuals collected from Mozambique and Madagascar while Haplotype 99 (*n* = 16) is restricted to the Red and Mediterranean Seas. Of the remaining nine haplotypes, six are singletons, one is shared between two individuals and the other is shared amongst three.

Haplotype network for *P. reticulatus* and *P. armatus*: due to low genetic divergence, COI haplotypes from individuals of *P. armatus* and *P. reticulatus* were joined together within the same parsimony network, but separated by a small but discrete break of five mutation steps at the 95% confidence interval (figure not shown). However, the two gene networks separate at a 99% confidence limit (Fig. 5C, D). At this level, the four haplotypes obtained from *P. armatus* collected from New Caledonia separate from the main network as well.

Despite this low divergence, the patterns of relationships between haplotypes found within these two species differ.



Table 5: List of localities and number of specimens used for each species. Sample size is denoted by (*n*), number of haplotypes (Nh), number of polymorphic sites (Np), haplotype diversity (*h*, to 3 decimal places) and nucleotide diversity ( $\pi$ , to 4 decimal places).

Code	Species/Locality	<i>n</i>	Nh	Np	<i>h</i>	$\pi$
<i>Portunus segnis</i>						
1	Israel: off Ashjod	18	6	8	0.562 ± 0.134	0.0038 ± 0.0022
2	United Arab Emirates: Abu Dhabi	5	2	1	0.400 ± 0.237	0.0014 ± 0.0014
3	Pakistan	1	1	0	0.000	0.000
4	Madagascar: Tulear	18	18	2	0.4640 ± 0.125	0.0009 ± 0.0009
5	Mozambique: Maputo Bay	3	1	0	0.000	0.000
<i>Portunus reticulatus</i>						
6	India: Chennai	14	11	46	0.956 ± 0.045	0.0239 ± 0.0128
7	Sri Lanka	49	14	46	0.631 ± 0.074	0.0379 ± 0.0188
8	Thailand: Phuket	14	4	4	0.495 ± 0.151	0.0038 ± 0.0025
<i>Portunus pelagicus</i>						
9	Singapore	7	5	10	0.857 ± 0.137	0.0060 ± 0.0040
10	Indonesia: Sumatra, Padang	6	4	7	0.867 ± 0.129	0.0044 ± 0.0032
11	Indonesia: Lombok	10	7	9	0.867 ± 0.107	0.0058 ± 0.0037
12	East Malaysia: Sarawak	4	4	8	1.000 ± 0.177	0.0070 ± 0.0053
13	Indonesia: Sulawesi, Manado	3	3	5	1.000 ± 0.272	0.0058 ± 0.0051
14	Philippines: Visayas, Samar and Negros Islands	37	14	10	0.824 ± 0.051	0.0039 ± 0.0024
15	Taiwan	8	2	1	0.250 ± 0.180	0.0044 ± 0.0006
16	Japan: Okinawa, Naha	14	3	2	0.385 ± 0.149	0.0007 ± 0.0008
17	Japan: Kyushu, Amakusa	26	14	41	0.905 ± 0.037	0.0138 ± 0.0074
18	China: Xiamen	14	5	5	0.725 ± 0.104	0.0053 ± 0.0033
<i>Portunus armatus</i>						
19	Australia: Northern Territory, Darwin (Ludmilla Creek)	4	4	8	1.000 ± 0.177	0.0076 ± 0.0056
20	Australia: Western Australia	5	4	11	0.900 ± 0.161	0.0094 ± 0.0064
21	Australia: South Australia, Spencer Gulf vicinity	6	3	11	0.600 ± 0.215	0.0075 ± 0.0050
22	Australia: South Australia, Gulf St Vincent, Brighton Beach	4	3	2	0.833 ± 0.222	0.0018 ± 0.0017
23	Australia: New South Wales	10	8	13	0.956 ± 0.059	0.0095 ± 0.0057
24	Australia: Queensland, Moreton Bay	16	10	16	0.917 ± 0.049	0.0073 ± 0.0043
25	New Caledonia	5	4	3	0.723 ± 0.222	0.0024 ± 0.0021

The network of haplotypes for *P. reticulatus* collected from Sri Lanka and Chennai, India, resemble a star phylogeny, with Haplotype 31 common to approximately 41% (32 out of 77 individuals) of the sample size and 17 other haplotypes differing from it by 1 to 3 mutational steps. The second most common haplotype ( $n = 18$ ) obtained from *P. reticulatus* specimens collected from the Bay of Bengal is Haplotype 32. This is the most common haplotype found in *P. pelagicus*. Haplotype 32 is separated from 31 by a sharp genetic break of at least 38 mutational steps (6.6% uncorrected differences). Haplotype 51, the third most dominant haplotype found in *P. pelagicus* occurred in two *P. reticulatus* individuals collected from Phuket. Haplotype 51 differed from 32 by three mutational steps.

In contrast, haplotypes unique to *P. armatus* show no distinct pattern, possibly due to low sample size. Of 50 individuals sampled, no significantly dominant haplotype was observed although eight individuals collected from South Australia and New South Wales share Haplotype 15 (16%). The second most common haplotype in the *P. armatus* network is Haplotype 1, comprising six individuals collected from New South Wales and Moreton Bay. Haplotypes were also not observed to be region specific, but heterogeneously distributed throughout the network. While singleton haplotypes were observed, two private haplotypes noted in this network are Haplotypes 24 and 27, collected from two individuals from Western Australia and New Caledonia respectively. The four haplotypes from five specimens of *P. armatus* collected in New Caledonia are also distant from the main Australian network, separated by five mutational steps.

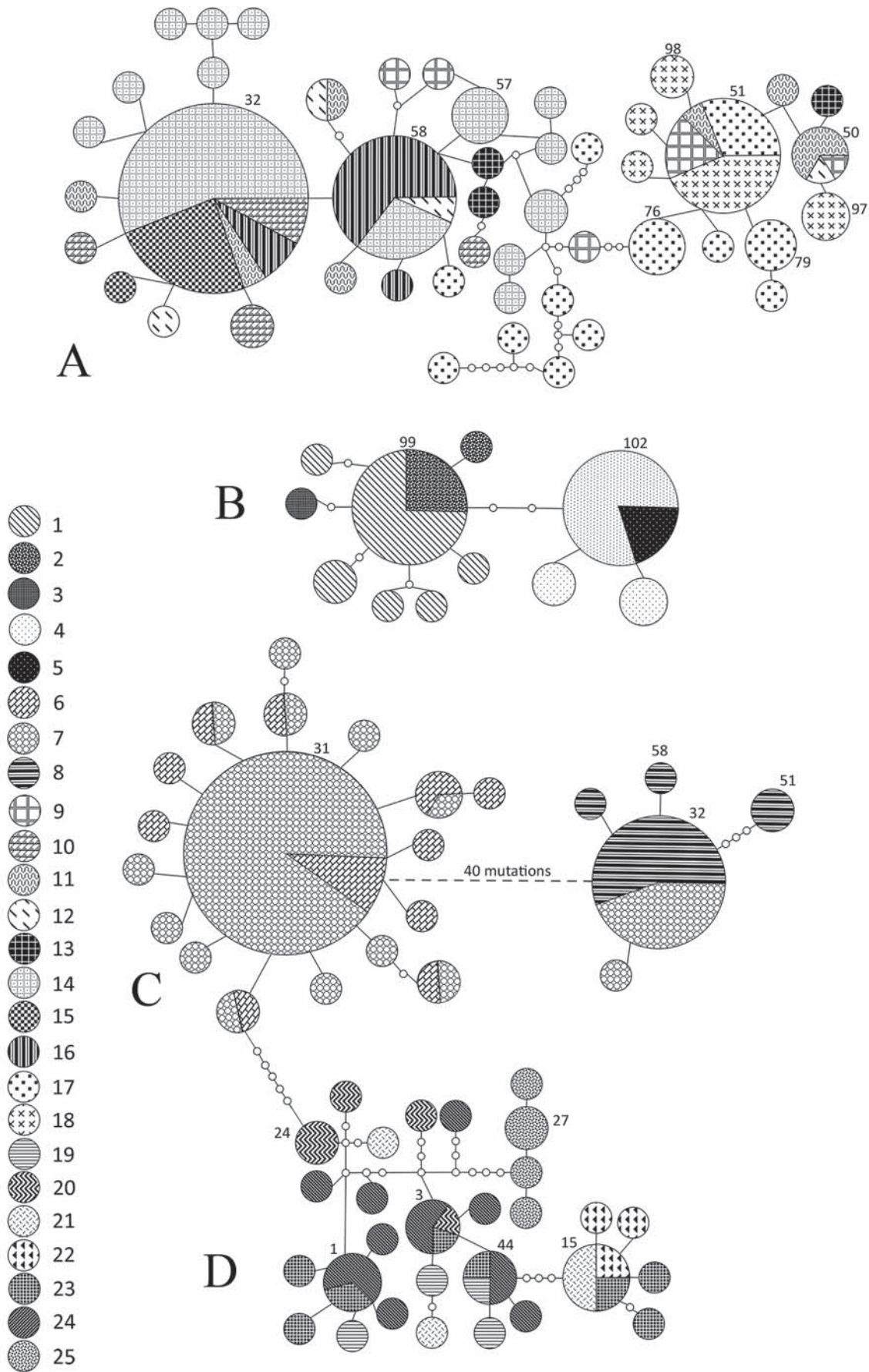


Fig. 5. Minimum parsimony spanning network constructed with TCS of *Portunus pelagicus* complex using a 573-basepair fragment from the COI gene. Each line represents one substitution; small unshaded circles indicate additional substitutions separating two haplotypes. The size of the circle is representative for the frequency of the haplotypes. Filled patterns correspond to geographic affinity of haplotypes. Network for: A, *P. pelagicus*; B, *P. segnis*; C, *P. reticulatus*; D, *P. armatus*. For key to localities, see Table 6.

Table 6: Average Mitochondrial CO1 divergences (Tamura-Nei substitution model) and estimates of time since divergence for the four species of the *Portunus pelagicus* complex based on a divergence rate of 2.3% Myr<sup>-1</sup>. Period since divergence above diagonal; % divergence (average) below diagonal. Divergence with three outgroup species used in the present study is also listed. MYA = millions of years ago.

Species	<i>Portunus pelagicus</i>	<i>Portunus reticulatus</i>	<i>Portunus segnis</i>	<i>Portunus armatus</i>
<i>Portunus pelagicus</i>	–	3–5 MYA	1.5–2.5 MYA	3.3–5.4 MYA
<i>Portunus reticulatus</i>	7.0%	–	3.3–5.4 MYA	0.78–2.5 MYA
<i>Portunus segnis</i>	3.5%	7.6%	–	3.08–5.07 MYA
<i>Portunus armatus</i>	7.6%	1.8%	7.1%	–
<i>Portunus trituberculatus</i>	11.6%	14.6%	12.1%	14.7%
<i>Portunus sanguinolentus</i>	16.4%	18.0%	16.9%	18.0%
<i>Charybdis lucifera</i>	17.8%	18.5%	18.0%	18.3%

The Australian and New Caledonian specimens, however, are morphologically identical.

**Network summary.** – In total, 80 out of 109 haplotypes (73%) of haplotypes obtained for the four species occurred as singletons and remaining haplotypes were mostly private or shared between individuals from similar geographic regions. The exceptions to this were haplotypes 32 and 51, which were shared by *P. pelagicus* and *P. reticulatus*.

Outgroup weight calculations derived from TCS suggest that Haplotype 102 (outgroup weight 0.462), Haplotype 32 (outgroup weight 0.167) and Haplotype 31 (outgroup weight 0.19) are the most ancestral haplotypes for *P. segnis*, *P. pelagicus* and *P. reticulatus* respectively. The most ancestral haplotype for *P. armatus* could not be determined due to its close relationship with *P. reticulatus*. The minimum spanning network for these two species shows that whilst close, phylogenetic relationships between haplotypes within these two species are dissimilar, suggesting different demographic histories.

## SYSTEMATIC ACCOUNT

The four recognised species are similar in morphology, so only diagnostic characters will be given to avoid repetition. Evaluating the hundreds of literature records of “*Portunus pelagicus*” has been challenging. Some of the old records do not specifically state where their material originated, and most do not provide figures. In some cases, original specimens have been re-examined, and when figures were provided, it was possible to determine species identity. Also, as the distributions of the four species are usually quite discrete with the exception of putative hybridisation zones in the Andaman Sea and northern Australia, we have used this to cross-refer each of the old records to one or more of the species as far as possible. Where a collection locality was not sufficiently precise, or where specimens came from a region where there was a risk of sympatry with another species, we listed the records as *incertae sedis*. Such records will need future verification.

### *Portunus (Portunus) pelagicus* (Linnaeus, 1758) (Figs. 6A, 7A, 8, 9, 10, 20A, 21A, 22A, 23A, 23E, 24A)

- Pagurus Reidjungan Rumphius, 1741: 11, Pl. 7, Fig. R.  
*Cancer pelagicus* Linnaeus, 1758: 626; Linnaeus, 1767: 1042.  
*Cancer pelagicus* – Forskål, 1775: 89.  
*Portunus denticulatus* Marion de Procé, 1822: 133.  
*Cancer cedonulli* Herbst, 1794: 2(5): 157, Pl. 39.  
*Lupa pelagica* – H. Milne Edwards, 1834: 450; Dana, 1852: 271; Stimpson, 1907: 76.  
*Neptunus pelagicus* – Heller, 1865: 27 (part); Miers, 1884: 229 (part); De Man, 1886–1887: 69; Kemp, 1918: 250.  
*Neptunus (Neptunus) pelagicus* – Miers, 1886: 173 (part); Alcock, 1899: 31 (key), 34, 35 (part); Parisi, 1916: 171 (part); Balss, 1922: 107; Yokoya, 1933: 177; Sakai, 1934: 303; Sakai, 1935: 128, Pl. 38; Sakai, 1939: 387–388, Pl. 49.  
*Neptunus peiagicus* [sic]: Estampador, 1959: 71.  
*Portunus (Portunus) pelagicus* var. *sinensis* Shen, 1932: 70, Pl. 3 Fig. 6, Pl. 4 Fig. 2.  
*Portunus (Portunus) pelagicus* – Serène, 1968: 68 (list); Utinomi, 1969: 87, Pl. 44; Sakai, 1976: 339, Pl. 118; Ng et al., 2008: 152.  
*Portunus pelagicus* – Fabricius, 1798: 367; Rathbun, 1902: 26; Rathbun, 1910a: 313; Rathbun, 1910b: 360, 361; Stephenson & Rees, 1967b: 34–35 (part), Figs. 12c, d, 17b; Stephenson, 1967: 17; 1968a: 386 (part), Fig. 2 C, D; 1972a: 15 key, 41 (checklist); 1972b: 137 (part); Kim, 1973: 355; Takeda, 1982: 148; Miyake, 1983: 84, Pl. 28; Ng, 1998: 1124 (part); Chen, 1989: 353, 355; Dai & Yang, 1991: 212–213, Fig. 112, Pl. 25(7); Gosliner et al., 1996: 237, colour photograph; Poupin, 1996: 32; Naiyanetr, 1998: 14 (photo), 73 (list); Minemizu, 2000: 234; Ng et al., 2001: 17. For other Taiwanese records, see Ng et al., 2001: 17).

**Material examined.** – Neotype of *Cancer pelagicus* Linnaeus, 1758 (designated here), 1 male (142.0 × 67.1 mm) (ZRC 2007.0235), Pulau Tekong, Singapore, coll. H. H. Tan, Nov.2004 (simultaneous neotype of *Cancer cedonulli* Herbst, 1794). Others – AUSTRALIA: 1 male (SAM C15784), 1 male (SAM C15779), 1 male (SAM C15781), 1 male (122.1 × 53.9 mm) (SAM C15780), 1 male (SAM C15783), 1 male (SAM C 15785), Darwin, Northern Territory, coll. R. Buckworth, 22 Aug.1993; 1 male (120.6 × 52.7 mm) (SAM C15782), Darwin, Northern Territory, coll. Northern Territories Fisheries Department, 2 Dec.1993. CHINA: 1 male (113.5 × 64.0 mm) (NHM 62.95), Shanghai, coll. Jamiachi; 10 male (largest 152.8 × 70.8 mm), 10 females (largest 144.3 × 65.3 mm) (ZRC), Ying Ping Market, Xiamen, Fujian Province, coll. Z. Jaafar & N. K. Ng, 12 Nov.2005. INDONESIA: 4 males (largest 125.5 × 72.0 mm), 2 females (larger 124.7 × 70.3 mm), 1 ovi. female (115.0 ×

64.8 mm) (ZRC 2007.0216), fish market, Padang, West Sumatra, coll. J. C. Y. Lai & N. K. Ng, 6–8 Jul.2003; 1 female (129.3 × 58.2 mm) (ZRC 2003.0583), 3 males (largest 118.0 × 53.7 mm), 11 females (largest 125.5 × 56.7 mm) (ZRC 2007.0221) (Geropok, Lombok) coll. J. C. Y. Lai, 11–12 Feb.2003; 1 male (135.1 × 63.0 mm), 1 female (RMNH LOLNR 16221), Ambon, Molukken, coll. D. J. Hoedt, 1864; 1 male (110.7 × 48.8 mm) (RMNH D384), Ambon, Moluccas, Indonesia, coll. Schorel, 1879; 1 male (115.6 × 53.8mm), 4 females (largest 137.3 × 61.8 mm) (ZRC), Manado fish market, Sulawesi, coll. T. H. T. Tan & H. H. Tan, Jun.2003; JAPAN: 12 males (largest 157.1 × 70.4 mm), 3 females (largest 146.4 × 65.0 mm) (ZRC 2007.0233) Naha Fish Port, Okinawa Island, Ryukyus, coll. T. Naruse, Nov.2003. MALAYSIA: 1 female (ZRC 2001.0999), Parit Jawa, Muar Johore, coll. B. Jayne et al. 11 Apr.2001; 1 male (damaged), 3 females (ZRC 1987.646–649), Pulau Tiga, Sabah, coll. Lee Nyanti no.110, 27 Apr.1987. PHILIPPINES: 1 male (119.7 × 54.0mm) (ZRC 2002.302) (neotype of *Portunus denticulatus* Marion de Procé, 1822), Philippines: Bohol, Tagbilaran market, coll. J. C. Y. Lai et al., Nov.2001; 1 male (119.7 × 54.0 mm) (ZRC 2002.302), Tagbilaran market, Bohol, coll. J. C. Y. Lai et al., Nov.2001; 1 female (117.9 × 49.9 mm) (ZRC), fish market, Cebu City, coll. P. K. L. Ng, 21 Nov.2001. SINGAPORE: 5 males (largest 97.3 × 43.4 mm), 4 females (ZRC 2002.380), Changi Beach, coll. J. C. Y. Lai, 26 Jun.2003; 5 males (largest 155.7 × 73.4 mm), 2 females (larger 160.7 × 74.6 mm) (ZRC 2007.0235), Pulau Tekong South, coll. H. H. Tan, Nov.2004; 1 male (150.5 × 72.4 mm) ZRC 1981.8.14.102, Jurong Fish Market, coll. H. K. Voris, 11 Mar.1981; 5 males (largest 145.0 × 69.4mm) (ZRC 1990.615–619), Tuas, no other details; 2 males (larger 125.0 × 70.5 mm), 1 female (87.5 × 49.9 mm) (ZRC 1981.7.24.18), Tuas, coll. Mr Lee, 19 Feb.1981;

1 male (151.6 × 70.5 mm), 1 female (107.3 × 49.9 mm) (ZRC 2000.1334) Bedok Market, no other details; 2 males (larger 118.4 × 67.0 mm) (ZRC 2007.217), Beting Bronok, coll. P. K. L. Ng, 27 Oct.2003; 1 male (130.4 × 57.9 mm), 1 female (127.5 × 56.8 mm) (ZRC 2007.215), Pulau Hantu lagoon, coll. P. K. L. Ng, 13 Jul.2003. TAIWAN: 1 male (144.2 × 64.8 mm), 1 female (78.9 × 37.3 mm) (ZRC 2007.214), Hsin-Chu Fish Market, coll. J. C. Y. Lai, Dec.2003; 2 male (larger 143.3 × 66.2 mm), 3 females (152.0 × 66.2 mm) (ZRC 2007.218), exact locality unknown, coll. H. C. Liu, Jun.2004. VIETNAM: 1 male (145.4 × 66.2 mm), 1 female (133.8 × 62.0 mm) (ZRC 2007.211), fish market, Cat Ba Island, Hai Phong, coll. A. D. Tran, 22 Jun.2003; 1 male (127.2 × 60.5 mm), 1 female (135.6 × 60.7 mm) (ZRC 2007.0219), fish market, Nha Trang, coll. A. D. Tran, May/Jun.2003. "HAWAII": 1 male (43.0 × 24.5 mm) (NHM 80.35), from the "Challenger" collection, off Honolulu coral reefs, dredged from 40 to 10 fathoms or less, coll. H. M. S Challenger, 31 Jul.1875. "TAHITI": 2 males (photographs examined) (NHMW 2860), coll. "Novara" Expedition (1857–1859), reported by Heller (1865).

**Type material.** – The lectotype specimen of *Cancer pelagicus* Linnaeus, 1758, designated by Holthuis (2004: 1268) is no longer extant (see **Remarks**). Owing to the strong potential for confusion, and the commercial importance of the species, it is necessary to designate a neotype to ensure nomenclatural stability. We here designate a male (142.0 × 67.1 mm) (ZRC 2007.0235) collected from Singapore as the neotype for the species. This specimen was freshly collected for the present study, has been photographed in colour, and both fixed and preserved in 100% ethanol for DNA extraction.



Fig. 6. Live colours of males. A, *Portunus pelagicus* (Linnaeus, 1758) (142.7 × 67.1mm) (ZRC 2007.0235), Pulau Tekong, Singapore; B, *Portunus segnis* (Forskål, 1775) (140.1 × 62.3mm) (ZRC 2007.0220), Tulear, Madagascar (photograph: H. H. Tan); C, *Portunus reticulatus* (Herbst, 1799) (132.2 × 59.8mm) (ZRC 2007.0223), Chennai, India (photograph: Z. Jaafar); D, *Portunus armatus* (A. Milne-Edwards, 1861) (no specimen, photograph only) Brisbane, Queensland (photograph: P. J. F. Davie).

**Diagnosis.** – Carapace width 2.2–2.3 times wider than long; median teeth of frontal margin spinous, small but conspicuous; in larger adults, especially males, carapace regions relatively well indicated, branchial regions markedly swollen. Chelipeds with anterior margin of merus usually with 3 spines; normally without enlarged spine proximally near joint; in large males chelipeds narrow, elongated, merus up to 4.6 times longer than wide. Ambulatory legs elongated, slender, with ratio of 4<sup>th</sup> pereopod propodus length to width ranging from 3.7– 4.5 (median 4.1). Natatorial paddle elongate oval, obtusely angled distally, about 1.7 times longer than wide (Fig. 21A); relatively narrowest of species in complex. Sixth male abdominal somite relatively elongate, tapering (Fig. 22A). Base of G1 with round basal spur (Fig. 20A). In males, carapace patterning consists of spots and a broad reticulate network of bands, no obvious pattern of spotting on females but with a black mark on posterobranchial region. Largest known size is a male 155.7 × 73.4 mm (ZRC 2007.0235) from Singapore.

**Live colours (Figs. 6A, 7A, 10).** – Males, dark blue green carapace with purple blue chelipeds, tips rusty red; females, a uniformly brownish green carapace with red tipped chelipeds. Merus, carpus and manus of chelipeds speckled with pale white spots. Pale white broad bands and large blotches on carapace on background of blue green in males. Some females may also possess spots and bands on the posterior and branchial regions of carapace.

**Remarks.** – Linnaeus (1758: 626) described *Cancer pelagicus* as follows: “*C. brachyurus*, thorace laevi utrinque unispinoso, fronte octo-dentata, manibus multangulo-prismaticis. Osb. iter. 307. *C. manuum* articulis omnibus dentatis: extimoheptagono. Rumph. mus. t. 7. f. R. Brown jam. 421. t. 41. f. 2. Habitat in Pelagi universi orbis. Fuco natante.”

This description is brief and uninformative, and as noted by Holthuis (2004), it mentions three sources, viz., Osbeck (1757), Browne (1756) and Rumphius (1705). No type was designated and thus, any specimens Linnaeus may have had at the time of his description, as well as the material listed in the works he refers to, must all be regarded as syntypes. The extant Linnaean crustacean material is deposited in the Uppsala Museum in Sweden (Holm, 1957: 56). In this collection is a dried “type” specimen of *Cancer pelagicus* Linnaeus, 1758 (UUZM 243), however, it is also labelled as “from the collection of Gustav IV Adolf”, and was first reported by Linnaeus six years later in his 1764 work (Holm, 1957: 56; see also Wallin, 1997: 16). Consequently, this specimen cannot be a syntype of *Cancer pelagicus*.

Of the other authors referenced by Linnaeus (1758) in his description, Osbeck (1757: 307) described a swimming crab collected in 1752 from the Sargasso Sea in the mid-Atlantic; Browne (1756: 421, Pl. 47 Fig. 1) described and figured a crab collected from St. Mary’s in Jamaica; and Rumphius (1705: 11, Pl. 7 Fig. R) recorded his material

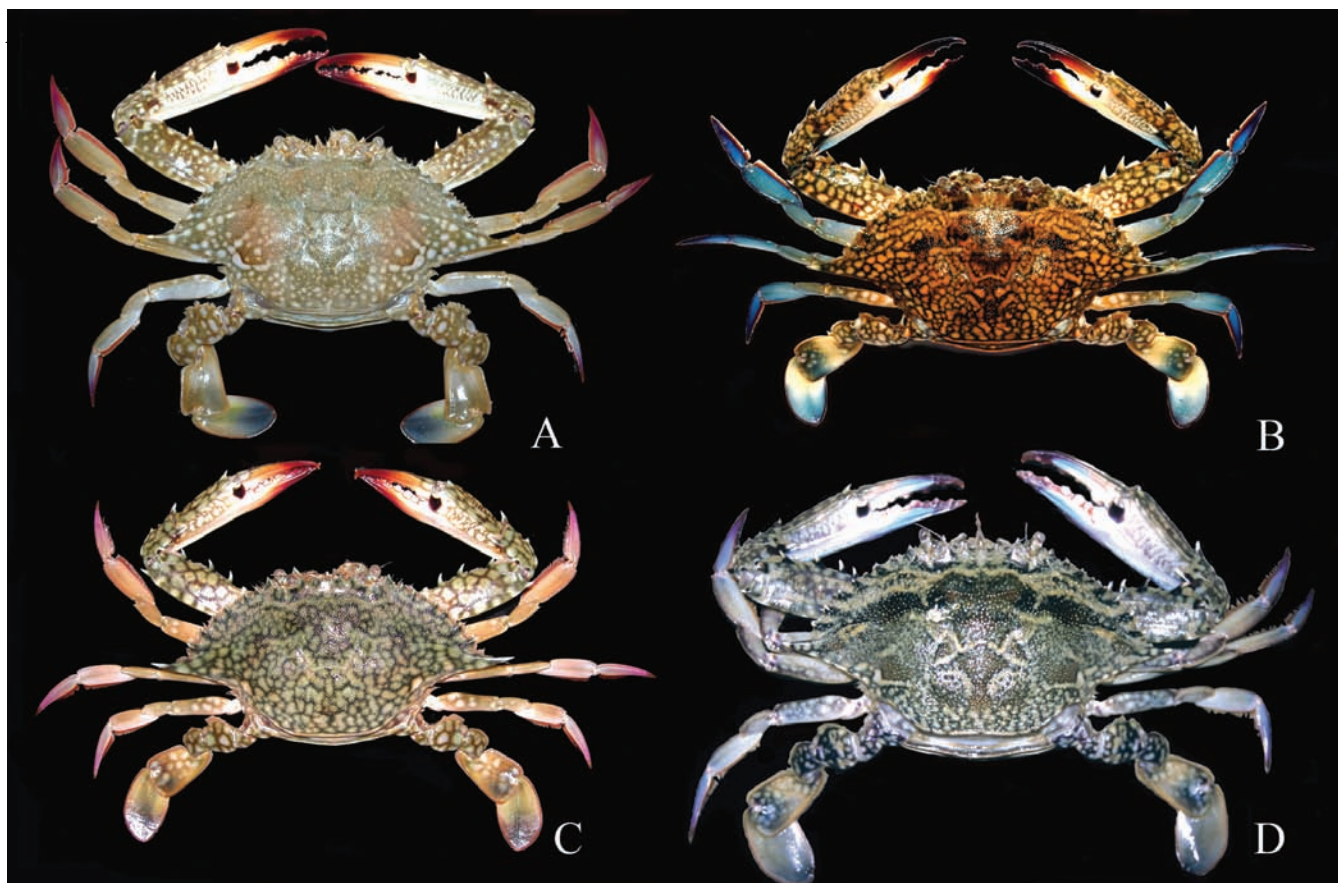


Fig. 7. Live colours of females. A, *Portunus pelagicus* (Linnaeus, 1758) (142.7 × 67.1mm) (ZRC 2007.0235), Pulau Tekong, Singapore; B, *Portunus segnis* (Forskål, 1775) (124.3 × 53.4mm) (ZRC 2007.0220), Madagascar, Tulear (photograph: H. H. Tan); C, *Portunus reticulatus* (Herbst, 1794) (132.2 × 59.8mm) (ZRC 2007.0223), Chennai, India (photograph: Z. Jaafar); D, *Portunus armatus* (A. Milne-Edwards 1861) (133.2 × 64.2 mm) (ZRC 2007.0232), Nelson Bay, New South Wales, Australia (photograph: S. Ahyong).

Table 7: List of morphological differences among the species in the *Portunus pelagicus* complex.

Character/Species	<i>Portunus pelagicus</i>	<i>Portunus segnis</i>	<i>Portunus reticulatus</i>	<i>Portunus armatus</i>
Median teeth frontal teeth	Small but conspicuous (Fig. 23A)	Minute and inconspicuous, almost obsolete; if present always small (Fig. 23B)	Small but conspicuous (Fig. 23C)	Strong, sharp (Fig. 23D)
Branchial region of carapace	Prominently swollen (Fig. 24A)	Convex but less prominently swollen compared to <i>P. pelagicus</i> (Fig. 24B)	Not swollen (Fig. 24C)	Not swollen (Fig. 24D)
Carapace granulation (adults)	Fine granules	Fine granules	Fine granules	Relatively markedly granular
Cheliped meri	Relatively long, slender	Relatively long, slender	Relatively shorter and stouter	The shortest and stoutest of all species
Spines on anterior margin of cheliped merus	3 (Fig. 23E)	3 (Fig. 23F)	3 (Fig. 23G)	4, rarely 3 (Fig. 24H)
Dactylus of P5	Ovate, relatively elongate (Fig. 21A)	Ovate, relatively elongate (Fig. 21B)	Relatively shorter and more rounded (Fig. 21C)	Relatively shorter and more rounded (Fig. 21D)
Sixth segment of male abdomen	Relatively shorter and broader (Fig. 22E)	Relatively shorter and broader (Fig. 22F)	Relatively narrower and more elongate (Fig. 22G)	Relatively narrower and more elongate (Fig. 22H)
G1 basal spur	Distinct, angled (Fig. 20A)	Distinct, angled (Fig. 20B)	Distinct, angled (Fig. 20C)	Distinct, rounded (Fig. 20D)
Carapace colour	Males possess a dark blue-green carapace with purple-blue chelipeds. Both males and females possess white spots on the carapace, often merging into broad almost banded reticulations, in particular on the posterior and branchial regions (Figs. 6A, 7A, 10)	Males with dark blue green carapace with discrete white spots on carapace, sometimes merging into thin reticulated bands. Females similar to males; spotting on the posterior third of carapace (Figs. 6B, 7B, 14)	Males have greenish-blue carapace, covered with large pale green spots, rarely merging into short bands. Female carapace tending to brownish-green; reticulated pattern as for males, tips of chelipeds rusty red (Figs. 6C, 7C, 16)	Colour variable; males typically with dark blue-green carapace, but South Australian specimens more blue than green. Spots on carapace sparser than other species, discrete, fusing into thin irregular short bands anteriorly; numerous small spots particularly postero-laterally. Females brownish with deep brownish-red cheliped tips; similar pattern of spots and reticulation to males (Figs. 6D, 7D, 19)

from Ambon, Indonesia. It is now clear that Osbeck's and Brownes' descriptions refer to *Portunus sayi* (Gibbes, 1850) and *Lupella forceps* (Fabricius, 1793), respectively (Holthuis, 2004). Only the specimen figured by Rumphius (1705) (reproduced in Fig. 8) clearly belongs to *P. pelagicus* sensu lato. To ensure there was no future confusion over the identity of all three names, Holthuis (2004: 1268) selected the "specimen figured by Rumphius, 1705, Pl. 7 Fig. R" as the lectotype of *Cancer pelagicus* Linnaeus, 1758. Although Holthuis knew that the specimen of Rumphius was no longer

extant, he considered there was no need for a neotype because the identity of *Portunus pelagicus* seemed clear at that time (pers. comm.). However, we have demonstrated that there are four species in the *P. pelagicus* species complex, and it is clear that the figure of Rumphius (1705) is insufficient to identify *P. pelagicus* sensu stricto. This is particularly important because *P. pelagicus* sensu stricto and *P. armatus* (A. Milne-Edwards, 1861) are sympatric in northern Australia and the potential for confusion is significant, especially since Ambon is relatively near this region of sympatry. As

the lectotype specimen is lost, we consider it necessary to designate a neotype for *P. pelagicus*.

The name *Portunus denticulatus* Marion de Procé, 1822, has not been used since it was first described from Manila, the Philippines. Checks at the MNHN as well as NMCR in Manila reveal no trace of the type specimens, and from what is known, all of Marion de Procé's material is now lost (D. Guinot, pers. comm.). On the basis of its description and the fact that we have so far identified only *P. pelagicus* sensu stricto from the north-west Pacific (including extensive material from Manila and Philippines), we are confident the two species are conspecific. Nonetheless, a neotype for *P. denticulatus* is needed to prevent future nomenclatural problems and we here designate a male specimen (119.7 × 54.0mm) (ZRC 2002.302), from Bohol, Philippines, as the neotype (Fig. 9). We consider this neotype to morphologically and genetically fall within the present concept of *P. pelagicus*.

*Cancer cedonulli* Herbst, 1794, is also regarded as a junior synonym of *P. pelagicus*. Herbst's (1794) original description was too brief to be informative. However, his accompanying illustration unambiguously depicts a male with a banding pattern of broad blotches and reticulations, and with a long and slender cheliped merus — characters that are diagnostic of *P. pelagicus* sensu stricto. Herbst (1794) indicated only that it was collected from "Ostindien" (East Indies), an area that was considered to extend from the east coast of India to the Indo-Malaysian region. The holotype is believed to be lost; it was not listed in Sakai's (1999) catalogue of the J. F. W. Herbst Collection in the Berlin Zoological Museum, and subsequent searches have also failed to find it (O. Coleman, pers. comm.). The east Indian Ocean and the Bay of Bengal area is likely a region of sympatry between *P. pelagicus* sensu stricto and *P. reticulatus* Herbst, 1799 (from genetic evidence), and this creates potential problems with the identity of *Cancer cedonulli*. Thus, a neotype is necessary to ensure there is no future taxonomic confusion. We here designate the neotype of *Cancer pelagicus* Linnaeus, 1758 (see above), as a simultaneous neotype of *Cancer cedonulli* Herbst, 1794, making both names objective synonyms.

A subadult male specimen of *P. pelagicus* (NHM 80.35) (determined by Miers, date unknown), purported to be collected from Hawaii during the voyage of H. M. S. Challenger, was examined. This specimen was not listed in Miers' (1886) "Challenger Report" on the Brachyura

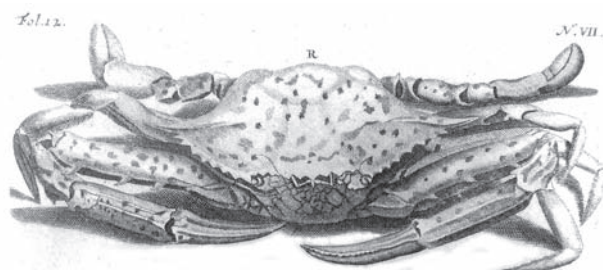


Fig. 8. *Portunus pelagicus* illustration from Rumphius (1705) from which Linnaeus based his description.

collected during the expedition. Barring this unpublished record, there have been no reports of *P. pelagicus* from the Hawaiian Islands and it is not listed in the latest checklist of Hawaiian Brachyura (<http://www2.bishopmuseum.org/HBS/invert/brachyura.htm>) or mentioned in Edmondson's (1954) study of the Portunidae of Hawaii. The main portunid utilized for food in Hawaii (although not commercially significant), is *P. sanguinolentus hawaiiensis* Stephenson, 1968. Although superficially similar to *P. pelagicus*, especially with regards to parts of the carapace colour pattern, the morphology of *P. sanguinolentus hawaiiensis* is clearly closer to *P. sanguinolentus* (see Stephenson, 1968b). Thus we believe the Challenger specimen, though clearly referable to *P. pelagicus*, was probably mislabeled. The presence of *P. pelagicus* in Hawaii is unlikely.

Most authors (Apel & Spiridonov, 1998; Boone, 1934; Stephenson, 1972b; Stephenson & Campbell, 1959; Tirmizi & Kazmi, 1996) accept that *P. pelagicus* occurs in Tahiti. However, the only verified record appears to be that of Heller (1865) based on specimens collected during the Novara Expedition (Poupin, 1996). All subsequent records have followed suit. Heller mentioned Tahiti as a locality for *P. pelagicus* along with others such as Singapore and India and his material is currently deposited at the Natural History Museum in Vienna. They are also damaged. There have been no subsequent published records from Tahiti, and the species has not been collected during extensive French collections made in this region over the last few decades (J. Poupin, pers. comm.). It is well documented that labels and localities from the Novara Expedition have been mixed-up (see McLaughlin & Dworschak, 2001; Rathbun, 1905, 1906), and there have been instances where Heller caused confusion by quoting wrong localities. For example, he described a species of freshwater crab from Chile in South America (*Telphusa chilensis* Heller, 1862) that later proved to belong to a genus endemic to Java and Borneo (Ng, 1989). Large edible crabs such as *P. pelagicus*, that typically inhabit shallow inshore coastal waters, are seldom overlooked. We thus consider it highly unlikely that *P. pelagicus* occurs in French Polynesia. However, it is also possible that the species may be confused with *P. sanguinolentus hawaiiensis* Stephenson, 1968, a species which superficially resembles

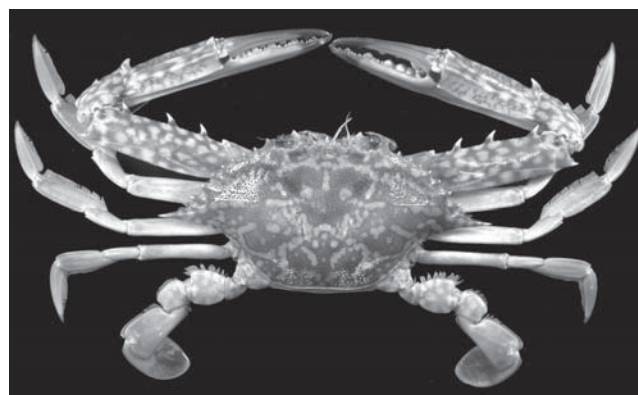


Fig. 9. *Portunus denticulatus* de Procé 1822, junior synonym of *P. pelagicus* (Linnaeus, 1758), neotype male (119.7 × 54.0 mm) (ZRC 2002.302), Tagbilaran Market, Bohol, Philippines.

*P. pelagicus* and is known from Hawaii and central Pacific (unpublished data).

Shen (1932) described *Portunus pelagicus* var. *sinensis* from China, but most of his specimens were small (average carapace width 24.0 mm) and he did not explicitly state why he considered them to be different from *P. pelagicus* sensu stricto. After comparing juvenile *P. pelagicus* with his description and the excellent figures of *P. pelagicus* var. *sinensis* (Shen, 1932: Pl.3 Fig. 6, Pl. 4, Fig. 2), we see no significant differences and thus regard the latter as a subjective synonym of *P. pelagicus* sensu stricto. Shen's (1932) record remains the only one of this species from northern China. Interestingly, *P. pelagicus* is not familiar to local fishermen or market traders at Qingdao, just south of Shandong, where *P. trituberculatus* is the dominant commercial species (unpublished data). The occurrence of several juveniles of *P. pelagicus* as recorded by Shen (1932) may have been due to accidental larval transport by northerly currents and the cold winters may have prevented further population establishment. It is also possible that the stated provenance of his material is wrong.

Herbst (1803: 159) compared *Cancer pelagicus* with *C. reticulatus* and *C. cedonulli*, but his accompanying drawing (Herbst, 1803: Pl. 8, Fig. 55) depicted *Charybdis natator* instead (Herbst, 1794). From his text, it is clear that he regards all three species as being highly similar and this error was most probably due to an editorial lapsus.

Bryars & Adams (1999) were the first to report the presence of two distinct forms of *P. pelagicus* found sympatrically in Darwin, northern Australia. One form is widely distributed all over Australia and the other was restricted to waters around Darwin. The former taxon was referred to as "*P. pelagicus*" and the latter, "*Portunus* species". The two populations occur sympatrically in Darwin, but with differing ratios of catch abundance from two localities. From their observations, individuals of "*Portunus* sp." were generally smaller in overall size than "*P. pelagicus*", with the ninth epibranchial spines longer (relative to the carapace) and more curved. Some differences in dorsal pigmentation between the two forms were also observed. Additionally, they reported the existence of hybrids based on allozyme data. We checked the specimens referred by Bryars & Adams (1999) as *Portunus* sp. and confirmed that they are *P. pelagicus* as defined in the present study. The species widely distributed around Australia that they referred to as "*P. pelagicus*" is *P. armatus*. Interestingly, the specimen that was described as a hybrid between the two species resembled both *P. armatus* and *P. pelagicus*: there are small sharp spines in the median part of the anterior margin and four teeth along the posterior margin of the merus of the cheliped. However, the specimen was heavily parasitized by *Sacculina*, altering the overall shape of the abdominal segments. Based on allozyme results and our examinations, we agree with their conclusions. Klunbuga et al. (2007) reported genetic heterogeneity in *P. pelagicus* populations collected off Thai waters. As sites chosen were within the Gulf of Thailand and along the coast of the Andaman sea, it is likely that both *P. pelagicus* and *P.*

*reticulatus* were analysed in the study. We were unable to confirm this as specimens analysed in their study were not deposited in any zoological collection.

**Habitat.** – Found in shallow sandy/muddy to sea grass lagoons and estuaries, brackish waters to a depth of 40 m (Ng, 1998).

**Distribution.** – This species has the widest distribution of all four species in the complex. It has been recorded from China, Japan (Okinawa and Kyushu), Korea, Philippines, Indonesia, and westwards to at least the straits of Malacca (Davie, 2002). There is evidence of hybridisation between *P. pelagicus* and *P. reticulatus* in the Bay of Bengal and the Andaman Sea based on COI data, but it is not known exactly where this hybridisation zone is (see general discussion). Based on our examination of material used by Bryars & Adams (1999), *P. pelagicus* is also present in the Northern Territory, Australia, and as mentioned, there is also some indication of occasional hybrids with *P. armatus*. Regrettably, attempts to collect fresh material of both species in the Northern Territory were not successful. As discussed, records of "*Portunus pelagicus*" from Hawaii and Tahiti are considered highly doubtful.

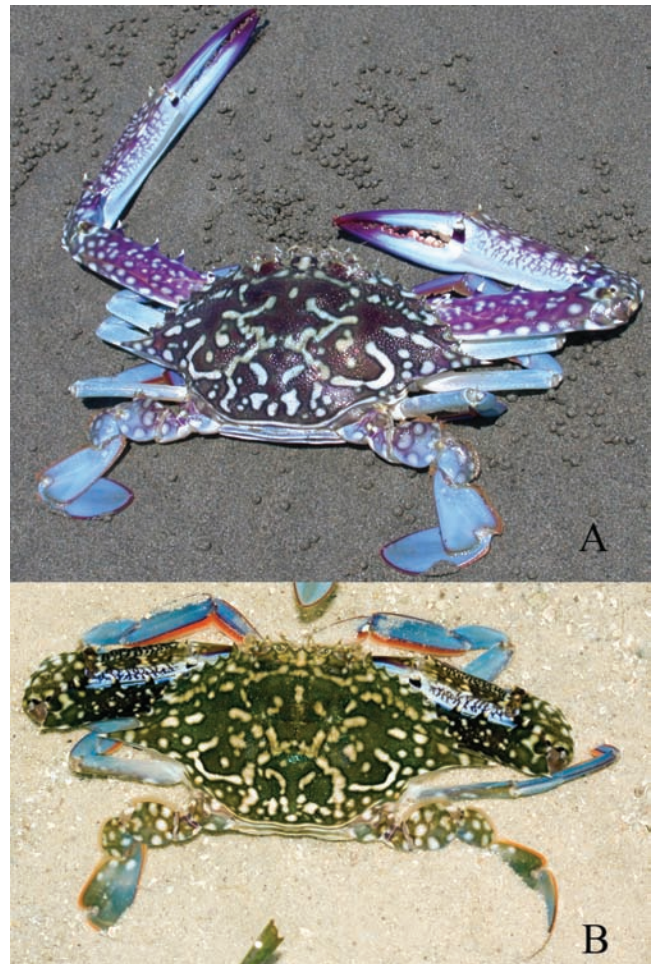


Fig. 10. Colour variation in *Portunus pelagicus* males. A, Taiwan (specimen not preserved) (photograph: C.Y. Tsai); B, Singapore (specimen not preserved) (photograph: M. Ng).



***Portunus segnis* (Forskål, 1775)**

(Figs. 6B, 7B, 11, 12, 13, 14, 20B, 21B, 22B, 23B, 23F, 24B)

- Cancer segnis* Forskål, 1775: 18, 91.  
*Cancer pelagicus* Forskål, 1775: 89.  
 Crabes-nageurs Savigny, 1826: Pl. 3, Fig. 1. 1–4.  
*Portunus mauritanus* Ward, 1942: 79, Pl. 5 Fig. 5.  
*Portunus trituberculatus* – Stephenson & Rees, 1967b: 51–53 (in part, material from the Red Sea) [not *P. trituberculatus* Miers, 1876].  
*Lupa pelagica* – Heller, 1861: 355 (part); Barnard, 1950: 152–154 Fig. 27b; Fourmanoir, 1954: 7, Fig. 7.  
*Neptunus (Neptunus) pelagicus* – Parisi, 1916: 171 (part); Stephensen, 1946: 124, 125, Fig. 26E; Hashmi, 1963a: 239; Hashmi, 1963b: 115, 117, 118.  
*Portunus (Portunus) pelagicus* – Audouin, 1826: 83; 1827: 261; Tirmizi & Kazmi, 1983: 369; Ng et al., 2008: 152.  
*Neptunus pelagicus* – Hoffmann, 1874: 7, 8; Paulson 1875: 61; De Man, 1888: 328; Nobili, 1906: 190; Klunzinger, 1913: 336 Pl. 7: Fig. 17; Kohli, 1921: 85; Monod, 1930: 138, 140, Fig. 6; 1938: 116; Gruvel, 1936: 50, 51, 71, 86, 94, 192, 195, 207, 215; Pretzmann, 1971: 471; Chandry, 1973: 402; Khan, 1975: 377 (list), 379–381, 390 (key), Fig. 2, Pl. 1.  
*Portunus pelagicus* – Crosnier, 1962: 43–45, Figs. 58, 61, 67; Guinot, 1962: 10; Heath, 1973: 2 (key), 13, Fig. 4b; Pretzmann, 1971: 47; Ramadan & Dowidar, 1972: 132; Khan & Ahmed, 1975: 77; Mustaqim & Rabbani, 1976: 163; Basson et al., 1977: 224, 227, 231, 235, 250, 256; Kensley, 1981: 42 (list); Titgen, 1982: 118–120, 250 (list); Jones, 1986: 161, Pl. 47; Tirmizi & Kazmi, 1996: 18–21; Bahmani, 1997: 2, 6, 8, 9, 12; Hornby, 1997: 75; Carpenter et al., 1997: 38; Apel & Spiridonov, 1998: 279 (key), 300–303, Pls. 10, 11; Neumann & Spiridonov, 1999: 21; Vannini & Innocenti, 2000: 266, Figs. 18, 23, 76; Galil et al., 2002: 114; Corsini-Foka et al., 2004: 83.  
*Portunus (Portunus) segnis* – Ng et al., 2008: 152.  
*Portunus pelagicus* or *P. segnis* – Guinot & Cleva, 2009: 70, Pl. 3, Fig. 1.

**Material examined.** – Neotype of *Cancer segnis* Forskål, 1775 (here designated); 1 male (SMF 3679) (144.4 × 70.1 mm), Red Sea, Egyptian coast, probably southern Gulf of Suez, coll. Dr E. Bannwarth, 1912. Others: BAHRAIN: 1 male (113.1 × 49.8 mm), 1 female (103.1 × 46.0 mm) (SMF 24424), from fisherman's nets (BRN-02). ISRAEL: 3 males (largest 147.2 × 66.8 mm), 1 female (143.3 × 62 mm) (ZRC 2007.225), off Ashjod, trawled by trawler MOTI, 12–14 fathoms, coll. B. Galil, 5 Dec.2003; 4 males (largest 141.3 × 66.9 mm), 9 females (154.8 × 72.5 mm) (ZRC 2007.226) off Haifa, coll. B. Galil, 2005; 1 male (134.5 × 62.6mm) (ZRC 2007.226), Mediterranean Coast. KENYA: 1 male (MZUF C898), Gazi, coll. M. Vannini, Dec.1997. KUWAIT: 1 male (56.8 × 25.2 mm) (NHM 1978.200), Khiran, Kuwait coast, coll. M. N. Mashmoom. MADAGASCAR: 8 males (largest 140.1 × 62.3 mm), 5 females (largest 153.2 × 69.4 mm), 6 juvs. (ZRC 2007.220), Belaza Tulear, coll. H. H. Tan, Jan.2004; 1 male (90.9 × 40.8 mm), 1 female (116.2 × 52.3 mm) (RMNH 47694), market at Morondava, west coast, coll. C. C. J. Jongkino, 11 Jan.1997; 1 juv. male (CL24.37 mm) (MNHN 844), Nosy Be, coll. A. Crosnier, 2 May 1961. MEDITERRANEAN SEA: 1 male (109.1 × 50.9 mm), 1 female (99.4 × 43.9 mm) (MNHN B12284), Gulf of Terente, coll. Perenzan, 1969. MOZAMBIQUE: 4 juv. males (largest 37.2 × 21.7 mm), 3 juv. females (largest 45.4 × 26.7 mm) (NHM 1951.9.13.416), Inyack Bay, Inhaca, Delagoa Bay (present day Maputo Bay), coll. O. S. Tattersall; 2 males, 1 female (126.6 × 60.00 mm) (ZRC 2007.230), Maputo Bay, coll. P. Clark, 2004. PAKISTAN: 5 males (largest 156.2 × 74.2 mm), 22 females (ZRC 2006.70), Karachi,

coll. Q. B. Kazmi, Sep.2005; 1 juv. male (37.0 × 21.6 mm) (SMF 21626), Korung Creek, Indus Delta, Sindh, coll. G. Pillen. PERSIAN GULF: 1 female (77.6 × 35.6 mm) (NHM 88.25), coll. Kurachee Museum. RED SEA: 4 males (SMF 10693) (94.9 × 43.1 to 115.5 × 55.1 mm), Jeddah Fish Market, Saudi Arabia, Red Sea, W. John, 20 Aug.1982; 1 male (114.5 × 53.4 mm) (MNHN B6032), coll. 1929; 1 juv. female (70.2 × 39.3 mm) (NHM), El Tor Presed, coll. Major Macdonald, 4 Sep.1966; 2 females (larger 72.2 × 40.4 mm) (NHM), Gulf of Ilat, Aryab, coll. F. Day. SAUDI ARABIA: 5 male, 1 female (48.2 × 21.6 mm) (NHM), Jeddah, coll. A. C. Trott; 1 female (106.9 × 62.1 mm) (SMF 24427), Jubail Marine Wildlife Sanctuary Al-Jubayl, W. Qurma Island, PTL-01 (27°07.090'N 49°27.300'E) sand/mud bottom, coll. M. Apel, 4 Dec.1991; 2 females (larger 132.7 × 60.6 mm) (SMF 24430), Eastern, N. Jubail (27°25.410'N 049°16.010'E), sandy bottom, coll. M. Apel, 26 Nov.1991; 2 males (larger 56.4 × 25.7 mm), 2 females (larger 80.5 × 35.0 mm) (SMF 24417), Eastern, Ras Az-Zawr (27°26.000'N 49°17.000'E) sublittoral sand flats, coll. M. Apel, 17 May 1995; 1 juv. male (31.7 × 15.0 mm), 1 juv. female (32.4 × 15.3 mm) (SMF 24418), Eastern Ras Az-Zawr (27°26.000'N 49°17.000'E), beachrocks and sand, coll. M. Apel, 17 May 1995; 1 male (130.7 × 59.5 mm) (SMF 24428), Eastern Jubail Marine Wildlife Sanctuary, N. Al-Jubayl, W. Jinna Island, PTL-04 (27°21.490'N 49°14.200'E) on rock and sand, coll. M. Apel, 28 Nov.1991; 1 male (95.9 × 43.0 mm) (SMF 24429), Eastern Jubail Marine Wildlife Sanctuary, N. Al-Jubail, SW bank of Dauhat al Musallamiya, PTL-07 (27°23.330'N 49°10.150'E) on rock and mud, coll. M. Apel, 10 Dec.1991. SOMALIA: 1 male (117.2 × 51.9 mm), 1 female (MZUF C811), Gresira, coll. M Vannini, Nov.-Dec.1976; 1 male (76.9 × 34.4 mm) (MZUF C2672), 2 males (larger 127.8 × 58.3 mm), 4 females (135.8 × 61.2 mm) (MZUF C2673), Sar Vaule, coll. M. Vannini, 1976; 1 juv. male (38.9 × 18 mm), 1 male (113.8 × 51.7 mm) (NHM 1950.8.851), Zeilah, coll. A. Fraser-Bronner; 1 male (114.5 × 53.5 mm) (MZUF C890), Mida Creek, Kenya, coll. M. Vannini, 1991; 2 females (94.1 × 43.7; 122.4 × 53.9 (ovig.) mm), 2 males (68.1 × 33.1; 84.3 × 38.2 mm) (MZUF C890), Mtwapa, Mombasa, Kenya, coll. M. Vannini, Nov.–Dec.1993. SOUTH AFRICA: 1 male (NHM 1917.6.19.37), Durban Bay, Natal, from Durban Bay Natal Government Museum, coll. F. Toppin, Mar.1905; 1 male (168.8 × 75.8mm) (ZRC), coll. Institute of Aquatic Biodiversity, South Africa, Nov.2006. SUDAN: 1 male (newly moulted) (SMF 24487), Küsta ca. 8 km Port Sudan, SAN-53, in *Avicennia marina* mangrove, coll. M. Apel, 23 Mar.1991. GULF OF SUEZ: 2 females (larger 130.5 × 60.1 mm) (MNHN B6031), from SS *Al Sayad*, Station II, 1928. SYRIA: 1 male (144.7 × 68.0 mm), 2 females (larger 158.4 × 75.4 mm) (SMF 8768), fish market, Latakia, coll. R. Kinzelbach, 31 Aug.1978. UNITED ARAB EMIRATES: 2 males (larger 119.9 × 54.4 mm), 3 females (largest 125.7 × 57.9 mm) (ZRC 2007.224), Abu Dhabi, market facing Oman coast, coll. L. W. H. Tan, 26 Mar.2004, 2 juv. males (larger 48.3 × 21.8 mm) (NHM 1999.68-69), Trucial Coast, Abu Dhabi, coll. D. J. J. Kinsman, Imperial College; 1 juv. male (28.4 × 13.3 mm) (NHM 1966.10.4.23), Khor al Bazam PS/34, Trucial Coast, Abu Dhabi, coll. Imperial College; 1 damaged female (58.0 × 26.5 mm) (NHM 1966.10.4.22), Khor al Bazam, PG/B/449, Trucial Coast Abu Dhab, coll. Imperial College; 1 male (SMF 24422), mangroves of Umm al Qaiwai, UAE95-29 (25°35.000'N 55°34.000'E), 0-1m around small islands, Khor al Beidah, coll. M. Apel, 9 Jul.1995. OMAN: 2 females (larger 38.4 × 86.1 mm), 2 males (larger 37.7 × 83.2 mm) (UF7745), south end of Bar al Hikman peninsula, silty pebbly sand spit, coll. U. Bonito et al., 24 Jan.2005. MAURITIUS: 1 male (carapace width 170.0 mm, side of carapace damaged) (MPL MAU-231) (damaged) (holotype of *Portunus mauritanus* Ward, 1942).

**Type material.** – The holotype of Forskål (1775) from Djedah (present day: Jeddah) in the Red Sea is lost, and a neotype for *Cancer segnis* is thus necessary to stabilise the nomenclature of this species.

We have selected a specimen collected from the original locality, a male (SMF 3679) (144.4 × 70.1 mm), as the neotype.

**Diagnosis.** – Carapace width 2.2–2.3 times wider than long, median frontal teeth minute or obsolete, usually inconspicuous, appearing confluent or with wide gap between lateral median teeth, except sometimes in larger individuals (carapace width > 140 mm). Compared with adult male *P. pelagicus*, carapace regions relatively poorly defined, branchial regions not as swollen compared with *P. pelagicus*. Chelipeds narrow, elongated, merus length of adult males maximum 4.5 times longer than wide; most specimens with shorter, stouter chelipeds than *P. pelagicus*; anterior margin of merus of cheliped usually with 3 spines. Ambulatory legs relatively more elongated, slender, merus of 4<sup>th</sup> pereopod 3.3–4.4 (median 3.6) longer than wide (Fig. 21B). Natatorial paddle elongate oval, obtusely angled distally, similar to *P. pelagicus*. Sixth male abdominal somite relatively shorter, less tapering (Fig. 22B). Base of G1 with slight basal spur (Fig. 20B). Largest specimen known is a female from Syria, 158.4 × 75.4 mm) (SMF 8768).

**Life colours (Figs. 6B, 7B, 14).** – Males with dark olive green blue carapace with many pale white spots on surface particularly posteriorly and anterolaterally; spots do not tend to merge to form reticulating bands, however, such banding if present is typically thinner than in *P. pelagicus*. Females similar in pattern to male except that tips of chelipeds are red tinged with a brownish red instead of blue tinged with deep rust red.

**Remarks.** – Forskål (1775) described *Cancer segnis* from material collected from Jeddah, on the Red Sea coast of Saudi Arabia. His description is as follows: “*Cancer segnis*; brachyurus; thoracae laevi, utroque latere novem-dentato; fronte quatuor-dentata. Descr. Transverse-ovalis: latitudine spithamae, sed longitudine inferior. Color superne obscure-viridis, nebulosus; subtus albidus. Antennae setaceae, nigrae, breves. In fronte spinae 4, inter oculos erectae, obtusiusculae: sub quovis oculo una validior. Oculorum pedicelli teretes, virides, oculi hemisphaerici; nitentes, obscuro-rubri, maculis albis: profunde inserti. Chelae viridi-caeruleae, apice albae: in forcicis latere interiore una series callorum in singulo digito; in chela superne post basin pollicis spinae duae, contiguae, antrorsum spectantes: ad basin juxta carpum superne spina valida, conica, caerulea apice ferruginea, Praeterea nullae in chelis spinae; fed duae in carpis extrorsum, una introrsum, longior, fortior, Femora depressa, ob-cuneata, Secundum tertium par pedum subteres, versus apicem compressum, pollice nullo, leave, digito subulato. Quartum par longe crassius, articulis duobus postremis compressissimis, membranaceis, dilatatis, ovatis, margine ciliates. Cauda lata, albida, fusco-rivulata. In Mari rubro. Tarde procedit in aqua.”

Forskål’s description is relatively detailed for its time, and generally fits *P. pelagicus* sensu lato. While there are some discrepancies, there does not seem to be any other likely candidate amongst the Red Sea fauna. Interestingly, most live portunids are active and aggressive, not “slow” as implied

by Forskål with the Latin name “*segnis*”. The presence of a white tip at the apex of the cheliped (*Chelae viridi-caeruleae, apice albae*), and the presence of a blue green spine with a red tip near the carpus (*ad basin juxta carpum superne spina valida, conica, caerulea apice ferruginea*) is peculiar — the *P. pelagicus*-complex conversely have red tips to the chelipeds and white tipped carpal spines. However, Forskål’s description of a dark green blue carapace with white cloud like markings (*color superne obscure-viridis, nebulosus*) does not fit any other portunid known from the Arabian Gulf other than *P. pelagicus* sensu lato (Apel & Spiridonov, 1998). This description matches the illustration of “Crabes-nageurs” presented in Savigny (1826: Pl. 3, Fig. 1. 1–4) (reproduced as Fig. 12, from Guinot & Cleve, 2009: 70, Pl. 1, Fig. 3) and may explain some of his observations. The name “*Cancer segnis*” has not been used or discussed since its description. Unfortunately, Forskål’s voyage ended with his premature death and the type specimen which ought to have been sent to Denmark was never located (for an historical account of the Danish expedition to “Arabia Felix” see Nielsen, 1993; Wolff, 1999). Interestingly, Forskål (1775) referred to *C. pelagicus* on page 89 before describing the new species, *C.*

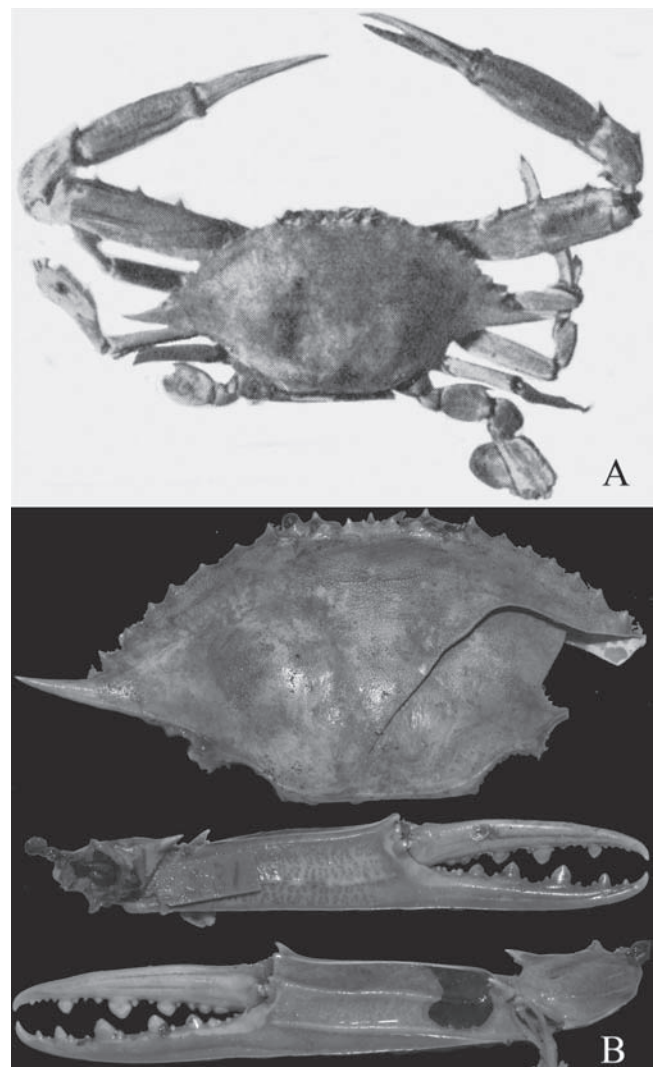


Fig. 11. *Portunus mauritanicus* Ward, 1942. A, holotype male (carapace width 170.0 mm) (MPL MAU-231) (after Ward, 1942); B, present condition of specimen showing damaged carapace.

*segnis* on page 91. As there is marked sexual dimorphism in the species, perhaps like Herbst, Forskål (1775) had mistaken males and females as different species (see discussion for *P. reticulatus*), and inadvertently established *C. segnis* for one sex. Another consideration is that his account is published posthumously and was most likely based on his field notes. Thus, it may also be possible that errors in description could have been the result of wrong interpretations of his notes or errors in typesetting. In any case, *P. segnis* is restricted to the West Indian Ocean (Red Sea and African coast) and differs from *P. pelagicus* of eastern Asia both morphologically and genetically.

*Portunus mauritanus* Ward, 1942, was described from Mauritius, southwest Indian Ocean. From Ward's (1942) description, it is apparent that what he conceived to be the true "*P. pelagicus*" was the Australian species, *P. armatus*. Consequently, he was correct in recognising the Mauritius material as a separate species. *Portunus armatus* has more clearly defined carapace granulation, sharper teeth and spines on the frontal and anterior margins, a differently shaped natatorial paddle, as well as four spines on the anterior margin of the merus of the cheliped versus three in *P. mauritanus*. The holotype of *P. mauritanus* is housed in the Mauritius Institute, but the specimen is badly damaged and all trace of colour patterning has been lost (Fig. 11). Examination of photographs of the holotype from different angles shows it to be distinct from *P. armatus*, but its poor condition and broken carapace make it difficult to clearly separate it from *P. pelagicus* and *P. reticulatus*. Unlike typical *P. segnis*, the holotype has two distinct median teeth, but the specimen is large and larger specimens of *P. segnis* are also known to have prominent median teeth. Attempts were made to collect topotypes of *P. mauritanus* for further morphological and genetic study. However, the species is apparently uncommon in Mauritius (C. Michel, pers. comm.) and no specimens were collected. Anecdotal evidence also suggests that at



Fig. 12. *Portunus segnis* (Forskål, 1775) (photograph based on a re-edition of the plates of Savigny by Institut d'Orient (1988), © Institut d'Orient/Naguib-Michel Sidhom, in Guinot & Cleva, 2009), Red Sea.

least some *P. pelagicus* sensu lato sold in Mauritius may be imported from Mozambique or Madagascar although this could not be verified with actual collected material in the present study. Nevertheless, from the recent photographs we have of the holotype (Fig. 11) and Ward's figures of the chelipeds and gross morphology, along with the fact that only *P. segnis* is otherwise known from the western Indian Ocean, it is likely that *P. mauritanus* is a subjective junior synonym of *P. segnis*.

Stephenson & Rees (1967b) recorded one male and three female specimens of *P. trituberculatus* from the Red Sea, but Stephenson (1976) later clarified that this was a mistake and that the species attributed to *P. trituberculatus* was in fact *P. pelagicus* (= *P. segnis* in present study). The figure by Stephenson & Rees (1967b: Fig. 17a, b) compares "*P. trituberculatus*" from the Red Sea with *P. pelagicus* from the Philippines. It is possible that they used the absence of median frontal teeth in the Red Sea material to distinguish between the two species. When viewed dorsally, the lack of median frontal teeth coupled with the projection of the epistomial spine along the underside of the frontal margin gives the illusion of three teeth along the frontal margin and this was presumably the reason for their misidentification as *P. trituberculatus*.



Fig. 13. *Portunus segnis* (Forskål, 1775), neotype male (144.4 × 70.1 mm) (SMF 3679), Red Sea, Egyptian coast (photograph: M. Türkay, SMF).



Fig. 14. *Portunus segnis* (Forskål, 1775) (specimen not preserved), Doha fish market, Qatar, (photograph: H. Q. Ng).

**Habitat.** – Under rocks and in rock pools, on sandy or muddy substrate, intertidal to 55 m (Galil *et al.*, 2002). Common in fish landings in Pakistan (Tirmizi & Kazmi, 1996).

**Distribution.** – Western Indian Ocean, from Pakistan westwards to the Arabian Gulf, and extending to the east coast of South Africa, Mozambique, Madagascar and Mauritius. It has also entered eastern Mediterranean Sea, as a Lessepsian migrant through the Suez Canal (Ekman, 1967; Ozcan *et al.*, 2005; Yokes *et al.*, 2007) and become established as far north as the northern Tyrrhenian Sea (Crocetta, 2006).

***Portunus (Portunus) reticulatus* (Herbst, 1799)**

(Figs. 6C, 7C, 15, 16, 20C, 21C, 22C, 23C, 23G, 24C)

*Cancer reticulatus* Herbst, 1799: 65, Pl. 50.

*Portunus pelagicus* – Sakai, 1999: 29, Pl. 15C.

*Portunus trituberculatus* – Stephenson & Rees, 1967a: 17 (material from the Bay of Bengal and India) [not *Neptunus trituberculatus* Miers, 1876, fide Stephenson 1976: 18].

*Neptunus (Neptunus) pelagicus* – Alcock, 1899: 34; Chopra, 1935: 476, 477, Fig. 3; Chhapgar, 1957: 418, Pl. 6a-c, colour Pl. A6.

*Neptunus pelagicus* – De Man, 1888: 328; Henderson, 1893: 367.

*Portunus pelagicus* – Fabricius, 1798: 367; Stephenson, 1972a: 15 key; Stephenson, 1972b: 137 (part); Stephenson, 1976: 18; Sethuramalingam & Ajmal Khan, 1991: 9 (key), 27, Pl. 18d; Fernando & Fernando, 2002: 62; Vongpanich, 2006: 77.

*Portunus (Portunus) reticulatus* – Ng *et al.*, 2008: 152.

**Type locality.** – “Das Vaterland ist Ostindien” [somewhere within the region stretching from the east coast of India to the Indo-Malayan Archipelago].

**Material examined.** – Lectotype of *Cancer reticulatus* Herbst, 1799, female (167.0 × 70.0 mm) (ZMB Herbst 0312) (photographs examined). Others. – INDIA: 14 males (largest 132.2 × 59.8 mm), 3 females (largest 135.0 × 59.5 mm) (ZRC 2007.223), Marina Beach Market, Chennai, coll. Z. Jaafar, 23 Nov.2004; 1 male (111.9 × 63.7 mm) (ZRC 2007.231), Midnapure, Cantai, Danthadhpatribar, West Bengal, coll. Z. Jaafar; 1 male (ZRC 2001.894), Porto Novo market, Tamil Nadu, coll. A.S. Fernando, 10 Mar.2001; 2 males (largest 85.6 × 37.6 mm), 1 female (75.7 × 34.3 mm) (ZRC 2007.209), Porto Novo market, Tamil Nadu, coll. N. K. Ng, Mar.2001; 5 males (largest 38.1 × 17.4 mm) (NHM 1892.715.330), Pamban, Rameswaran, coll. J. R. Henderson. SRI LANKA: 5 males (largest 141.4 × 62.3 mm) (ZRC 2007.222), Colombo Market, coll. M. Bahir, 16 Jun 2003; 1 male (132.8 × 58.5 mm) (NHM 1974.50), coll. Osman Hill; 1 female (49.9 × 20.4 mm) (NHM 60: 15), Ceylon (?), coll. Schlagintweck, Pres. Sec. India. BOARD. THAILAND: 8 males (largest 163.4 × 77.23mm), 2 females (larger 134.9 × 61.4mm) (ZRC 2009.1005), Phuket Pichai fish port, coll. J. C. Y. Lai, 13 Oct.2008; 1 male (116.9 × 53.7mm) (ZRC 2002.295) Phuket Pichai fish port, coll. J. C. Y. Lai, 2–3 Sep.2001; 1 male (126.6 × 56.0 mm), 1 female (107.0 × 50.1 mm), Phuket Pichai fish port, coll. J. C. Y. Lai, 22–25 Aug.2002; 2 males (larger 65.6 × 29.9 mm) (ZRC 2000.1058), Phuket, Ao Tang Khen, NE Cape Panwa, coll. H. H. Tan, 19 Jun.2000.

**Diagnosis.** – Carapace width 2.2–2.3 times wider than long, median frontal teeth spinous, small but conspicuous, similar to *P. pelagicus*. Adults with regions relatively poorly indicated,

branchial regions not markedly swollen. Cheliped merus relatively short, 3.5–3.9 times longer than wide (median 3.6); anterior margin usually with 3 spines; normally without enlarged spine proximally near joint; cheliped manus/dactylus ratio = average  $2.30 \pm 0.048$  (differs significantly from *P. pelagicus* ( $P = 0.03$ , ANOVA)). Ambulatory legs relatively less slender than *P. pelagicus*; merus of 4<sup>th</sup> pereopod 3.5 to 3.9 (median 3.7) times longer than wide (Fig. 21C). Natatorial paddle oval but less elongate, more rounded distally than *P. pelagicus* or *P. segnis* (Fig. 21C). Sixth male abdominal somite relatively elongate, tapering (Fig. 22C). Base of G1 with small but conspicuous rounded basal spur (Fig. 20C). In males, patterns on carapace may be variable, from dense spots merging into broad reticulating network of bands or few spots and thin reticulations, females similar to males (Figs. 6C, 7C, 16). The maximum size of *P. reticulatus* (present study) is the lectotype female, 167.0 × 70.0 mm (ZMB Herbst 0312).

**Live colour (Figs. 6C, 7C, 16).** – Males with greenish blue carapace. Patterns of carapace variable, large pale green spots that rarely merge into broad net like bands, to sparsely spotted, with thick reticulations. Females with green brown carapace, surface of carapace marked with numerous dense spots and blotches, without black marking on posterobranchial region. Tips of chelipeds marked bright red.

**Remarks.** – Herbst described two species of swimming crabs that were subsequently synonymised with *Portunus pelagicus* by Alcock (1899): *Cancer cedonulli* Herbst, 1794, and *Cancer reticulatus* Herbst, 1799. Like *C. cedonulli*, *C. reticulatus* was described from “Das Vaterland ift Ostindien” (East Indies), an area considered to extend from the east coast of India to the Indo-Malaysian region. Herbst (1799) described *C. reticulatus* from a female, and it closely matches females we have collected from India (see Figs. 7C, 15). On the other hand, *C. cedonulli* appears to be based on a male (Herbst 1794: Pl. XXXIX), and agrees well with male *P. pelagicus* specimens we have examined from eastern Indonesia. Our earlier neotype designation for *C. cedonulli* has effectively fixed



Fig. 15. *Portunus reticulatus* (Herbst, 1799), lectotype female (167.0 × 70.0 mm) (ZMB HERBST 0312) (photograph: C. O. Coleman, ZMB).

its identity as an objective junior synonym of *P. pelagicus*. Nevertheless, as both Herbst's species were described based on different sexes, and were originally separated largely on colour differences, some comment on sexual dimorphism in colour within this species-complex is needed.

Herbst's male *C. cedonulli* (Herbst 1794: tab. XXXIX) was described as follows: "grün mit vielen grossen und kleinen gelben flecken, die ein e dunkelgrüne Einfassung habe ... unten violett, oben grün, mit gelben Flecken ... Handwurzeln gruen, purpur und gelb gefleckt". Five years later, Herbst (1799) noted that his new *C. reticulatus* was very similar to *C. cedonulli* except that markings on the carapace of *C. reticulatus* were netlike and purple red ("die netzformigen Züge sind purpurroth"), while *C. cedonulli* possesses a green carapace with many large and small yellow spots, and dark green edge with the underside of merus violet, upper side green with yellow spots, claws green, purple with yellow spots.

Alphonse Milne-Edwards (1861: 321) simply stated that *C. cedonulli* was blue with yellow spots, while *C. reticulatus* was red with yellow spots. It must be considered that as species in this group are sexually dimorphic in colouration, carapace ratios, and cheliped merus and manus dimensions, it is possible that first Herbst and then A. Milne-Edwards subsequently, may have incorrectly concluded that males and females represented two different species. However, differences in colour patterning between the two species are real despite sexual differences, and Herbst's original illustration of *P. cedonulli*, does show the broad white bands, and spotting size diagnostic of *P. pelagicus*, as well as matching it in cheliped merus dimensions.

A type specimen of *Cancer reticulatus* (ZMB Herbst 0312) (Fig. 15) is extant and part of the Herbst Collection in the Berlin Zoological Museum (Sakai, 1999). An additional label with this specimen also identifies it as "*Portunus armatus*", a related species described by A. Milne-Edwards 60 years later in 1861 (see discussion for *P. armatus*). However, O. Coleman (Curator of Crustacea at ZMB) does not recognise the penmanship or initials of the label writer; nor was its presence reported by Sakai in his Herbst catalogue (1999).



Fig. 16. *Portunus reticulatus* (Herbst, 1799), male (163.4 × 77.2mm) (ZRC 2009.1005), Phuket, western Thailand.

While this label casts some slight doubt over the type status of this specimen, nevertheless its striking similarity to the figure in Herbst (1799: Pl. L), and its presence within the Herbst Collection in the ZMB (which has never been moved or mixed; O. Coleman, pers. comm.), indicates that this specimen can reasonably be regarded as part of the type material of *C. reticulatus*. As no holotype was originally selected by Herbst (1799), we therefore designate this specimen as the lectotype in accordance with Article 74b of the ICZN.

**Habitat.** – Found in shallow sandy lagoons; commonly caught with gill nets or trawls (Ameer Hamsa, 1978).

**Distribution.** – *Portunus reticulatus* (Herbst, 1799) appears to be restricted to the Bay of Bengal, and is so far only known from the southeastern coast of the Indian subcontinent, waters off Sri Lanka, and from the Andaman coast of southern Thailand (present study). There appears to be evidence of introgression or incomplete lineage sorting within this species with *P. pelagicus* based on genetic data, and this will be further elaborated on in the following general taxonomic discussion.

***Portunus armatus* (A. Milne-Edwards, 1861)**

(Figs. 6D, 7D, 17, 18, 19, 20D, 21D, 22D, 23D, 23H, 24D)

*Neptunus armatus* A. Milne-Edwards, 1861: 322, Pl. 33, Fig. 2.

*Neptunus pelagicus* – A. Milne-Edwards, 1873: 156.

*Portunus pelagicus* – Hale, 1927: 149-150, Fig. 150; Stephenson & Campbell, 1959: 96-98, Figs. 2A, 3A, Pl. 1 Fig. 1; McNeill, 1968: 54; Stephenson & Rees, 1967b: 34, 35 (part); 1968: 21; Stephenson, 1968b: 84, Fig. 1A-D, Pl. 11; Stephenson, 1972a: 15 (key); Stephenson, 1972b: 137 (part); Stephenson, 1976: 18; Healy & Yaldwyn, 1970: 86, Fig. 46; Türkay, 1971: 123 (part); Heath, 1973: 2 (key), 13, Fig. 4b; Poupin, 1996: 32; Davie, 1998: 100 (col. Fig.); 2002: 467; Davie, 2005: 157; Rice, 1999: 222 (figure); Jones & Morgan, 2002: 157, 158 (top), 159 (top); Laboute & Richer de Forge, 2004: 401(top).

*Portunus (Portunus) armatus* – Ng et al., 2008: 152.

**Type locality.** – Shark Bay, Western Australia.

**Material examined.** – Lectotype of *Neptunus armatus* A. Milne-Edwards, 1861, male (36.0 × 15.0 mm) (NHM 1858.172.115) (photograph examined), Shark Bay, Western Australia. Paralectotype – 1 male (34.0 × 16.0 mm) (NHM 1858.172 .114) (photograph examined), Shark Bay, Western Australia. Others – AUSTRALIA: 1 female (133.3 × 61.4 mm) (WAM C38994), Rottneest Island, Western Australia, otter trawl at 29 m, 32°02.43'S 115°31.67'E to 32°02.60'S 115°31'E, coll. A. Sampey, 27 Apr.2007; 1 female (carapace length 72.5 mm, sides broken) (WAM C38996), Southwest Cape, Western Australia, trawled at 37 m, 33°33.24'S 115°00.00'E to 33°37.98'S 114°59.99'E, coll. A. Sampey, 30 May 2007; 1 male (85.4 × 41.0 mm) (WAM C38995), Southwest Cape, Western Australia, trawled at 37 m, 33°37.59'S 115°00.13'E to 33°37.72'S 115°00.14'E, coll. A. Sampey, 30 May 2007; 1 male (93.5 × 43.8 mm) (WAM C38997), Southwest Cape, Western Australia, trawled at 37 m, 33°38.24'S 115°00.00'E to 33°37.98'S 114°59.99'E, coll. A. Sampey, 30 May 2007; 2 juv. males (larger 34.0 × 14.5 mm) (WAM C39101), Denham, Shark Bay, Western Australia, coll. B. R. Wilson, 29 Dec.1959; 2 juv. males (larger 26.8 × 10.9 mm)

(WAM C39179), Denham, Shark Bay, Western Australia, sand flats at low tide just north of Denham jetty, coll. B. R. Wilson, 29 Dec.1959; 1 juv. male (38.6 × 16.4 mm) (WAM C39180), Monkey Mia, Shark Bay, Western Australia, coll. B. R. Wilson, 2 Jan.1960; 1 female (56.9 × 24.0 mm), 1 juv. male, (damaged) (WAM C20194), Goulet Bluff, south of Denham, Shark Bay, W.A., coll. BTH, 7 Mar.1986; 1 juv. male (30.7 × 13.89 mm) (WAM C20682), Kuri Bay, Kimberleys, Western Australia, UIRB G1 33, intertidal, coll. G. Morgan, 23 Aug.1991; 1 juv. female (48.2 × 27.4 mm) (NHM), Cape Boileau, NW Australia, coll. B. Grey, 13 Mar.1930; 1 male (27.7 × 11.1 mm) (QM-W20210), western side of Mermaid Is, Kimberley coast, Western Australia, 16°19'S 123°21'E, muddy reef flat, coll. J. W. Short, 18 Nov.1994; 1 male (40.0 × 17.7 mm), 1 female (83.4 × 40.9 mm, one lateral tooth chipped) (QM-W21064), Reveley Island, Cambridge Gulf, Kimberley Coast, Western Australia, 14°22'S 127°50'E, sand flat, in pools, coll. J. W. Short, 21 Nov.1995; 1 male (49.8 × 19.9 mm) (QM-W21203), Mackenzie Anchorage, Napier Broome Bay, south of Anjo Peninsula, W. A., 14°20'06"S, 126°30'03"E, rocky cove, pools, muddy sand, backed by *Rhizophora* mangroves, coll. J. W. Short, 24 Nov.1995; 1 male (46.6 × 19.9) (QM-W21247), West Governor Island, NW side, Napier Broome Bay, Kimberley Coast, Western Australia, 13°55'07"S 126°38'00"E, netted, coll. J. W. Short, 26 Nov.1995; 1 male moult (75.5 × 31.1 mm) (QM-W21267), Sandy Island, Cape Talbot, Kimberley Coast, Western Australia, 13°45'03"S 126°48'05"E, coll. J. W. Short, 27 Nov.1995; Sandy Island, Cape Talbot, Kimberley Coast, Western Australia, 13°45'03"S 126°48'05"E, coll. J. W. Short, 28 Nov.1995; 1 male (124.6 × 54.2 mm) (SAM C15787), 1 male (136.5 × 65.4 mm) (SAM C15788), 1 male (105.6 × 48.1 mm) (SAM C15789), 1 male (119.1 × 52.0 mm) (SAM C15786), Darwin area, Northern Territory; 1 male (81.1 × 36.6 mm) (QM-W2205), trawled, SE of Wellesby Island, Gulf of Carpentaria, NW Queensland, 16°26'S 139°22'E; 1 male (54.4 × 25.5 mm) (QM-W2865), trawl, Gulf of Carpentaria, off Karumba, NW Queensland, 17°29'S 140°50'E, coll. B. Campbell, 1966; 1 female (138.8 × 66.7 mm, one lateral tooth chipped), 1 male (134.4 × 65.6 mm, one lateral tooth chipped) (QM-W20688), 0.5 m, netted over mud and rubble, Karumba Point, NW Queensland, 17°28'05"S 140°49'04"E, coll. J. W. Short, 23 Jun.1995; 1 male (27.7 × 13.3 mm) (QM-W27092), SW coast Sweers Island, Gulf of Carpentaria, Queensland, 17°06'S 139°37'E, coll. P. Davie, 22 Nov.2002; 1 female (74.4 × 35.5 mm, one lateral tooth chipped) (QM-W8903), Norman River, Gulf of Carpentaria, Australia, coll. CSIRO; 1 female (57.7 × 28.8 mm, one lateral tooth broken off) (QM-W8904), Bynoe River, NW Queensland, 17°32'S 140°43'E, coll. CSIRO; 1 male (90.3 × 38.0 mm) (QM-W12470), Torres Strait, northern Queensland, 10°02'S 142°31'E, coll. Queensland Fisheries Service, 13 m, 21 Apr.1974; 1 male (55.4 × 25.6 mm) (QM-W12434), Darnley Island, northern Queensland, 9°35'S 143°46'E, coll. Tosh; 1 male (55.4 × 25.6 mm) (QM-W12434), 4 females (66.6 × 28.8 mm, 61.1 × 26.6 mm, 54.4 × 23.3 mm, 57.7 × 25.5 mm), 2 males (58.9 × 25.5 mm, 49.9 × 22.2 mm) (QM-W12430), Cape York; 1 male (62.2 × 26.6 mm) (QM-W6428), Quintell Beach, Iron Ra., northern Queensland, 12°50'00"S 143°20'00"E, mangroves, coll. M. J. Bishop, Jul.1976; 1 male (51.1 × 23.4 mm) (QM-W9920), 70 km East Coen, northern Queensland, Australia, 13°55'04"S 143°48'06"E, 21.9 m, coll. Queensland Fisheries Service, Sep.1979; 1 male (108.8 × 50.0 mm) (QM-W9915), 40 km west Cape Melville, northern Queensland, 14°10'04"S 144°9'04"E, coll. Queensland Fisheries Service, 22 m, Sep.1979; 1 female (122.2 × 51.1 mm) (QM-W18142), Starcke R, northern Queensland, 14°47'08"S 144°59'09"E, netted, mid-estuary, sandy mud bottom, salinity 35 ppt, 0.3 m, coll. P. Davie & J. W. Short, 10 Nov.1992; 1 male (95.6 × 39.8 mm) (QM-W18215), beach S of Starcke R mouth, northern Queensland, 14°47'09"S 145°01'03"E, netted, 1m, gravel/mud, seagrass salinity 35 ppt, coll. P. Davie & J. W. Short, 13 Nov.1992; 1 male (52.2 × 23.3 mm) (QM-W6085), 13 miles due east of Oyster

Reef, 17 miles NE Green Island, Queensland, 16°39'S 146°11'E, 73.2 m, coll. L. R. G. Cannon, 21 Feb.1979; 2 females (73.3 × 32.2 mm, 45.5 × 21.1 mm, one anterolateral tooth chipped), 1 male (37.8 × 19.8 mm, one anterolateral tooth missing) (QM-W2675), Machan's Beach, NE Queensland, 16°51'S 145°45'E, 26 Dec.1960; 3 males (67.5 × 28.8 mm, 57.7 × 25.5 mm, 63.3 × 27.7 mm) (QM-W12776), SE end of Hinchinbrook Is., NE Queensland, 18°27'5"S 146°22'7"E, trawled, coll. C. Jones, Queensland Fisheries Service, 17 Mar.1985; 2 males (68.8 × 29.7 mm, 41.3 × 20.01 mm) (QM-W15209), Gladstone, Queensland, 23°51'S 151°16'E, coll. P. Saenger, Queensland Electricity Commission Survey, 1974–1983; 1 male (15.5 × 6.7 mm) (QM-W2705), Burnett R. Heads, SE Queensland, 24°26'S 152°25'E, coll. N. Milward, 20 Apr.1966; 1 male (20.0 × 9.9 mm) (QM-W2674), Burnett River Heads, SE Queensland, 24°46'S 152°25'E, coll. N. Milward, 26 Aug.1965; 1 female (44.4 × 20.0 mm) (QM-W5344), south of Urangan Boat Harbour, Hervey Bay, SE Queensland, 25°18'S 152°55'E, estuarine, coll. P. Davie & R. Timmins, 23 Jul.1975; 1 female (47.6 × 21.1 mm), 3 males (41.1 × 18.8 mm, 40.0 × 18.8 mm, 39.9 × 18.8 mm) (QM-W5398), mud flats S. of Urangan Boat Harbour, Hervey Bay, SE Queensland, 25°18'S 152°55'E, coll. P. Davie, 23 Jul.1975; 1 female (71.1 × 20.0 mm) (QM-W9461), Susan River, SE Queensland, 25°26'S 152°56'E, coll. A. Ellis, 31 Oct.1970; 2 males (22.2 × 10.0 mm, 21.1 × 10.0 mm), 2 females (36.5 × 15.6 mm, 30.0 × 12.3 mm) (QM-W9470), Susan River, SE Queensland, 25°26'S 152°56'E, coll. A. Ellis, 25 Dec.1970; 1 female (108.8 × 43.4 mm), 1 male (63.6 × 41.1 mm, lateral teeth missing, measurement taken from the 8th anterolateral tooth) (QM-W3393), 5–6 miles E. Pt. Cartwright Light, SE Queensland, 26°41'S 153°15'E, 35 m., coll. F. Wallace, 6 Mar.1970; 1 juv. male (52.2 × 24.4) (QM-W1060), east flat, Green Island, SE Queensland, 27°26'00"S 153°14'00"E; 2 females (129.9 × 55.5 mm, 117.6 × 53.3 mm), 3 males (117.6 × 53.3 mm, 111.1 × 50.0 mm, 122.1 × 58.8 mm) (QM-W2492), off St. Helena Island, SE Queensland, 27°24'S 153°14'E, coll. L. Wale, University of Queensland, 28 Jul.1966, trawled; 2 females (82.3 × 37.7 mm, 63.4 × 31.0 mm), 4 males (32.2 × 15.5 mm, 29.9 × 14.5 mm, 35.5 × 17.7 mm, 35.5 × 17.7 mm) (QM-W26681), Scarborough Spit, Moreton Bay, SE Queensland, 27°11'05"S 153°7'00"E, 0.5 m, netted over sand and shell substrate, coll. J. Johnson, 21 Jan.2003; 2 males (52.3 × 22.2 mm, 42.2 × 19.9 mm) (QM-W797), Moreton Bay, SE Queensland, 27°25'S 153°20'E; 1 male (17.7 × 8.8 mm) (QM-W2474), beach at Sandgate, Moreton Bay, SE Queensland, 27°20'S 153°04'E, 9 Oct.1962; 1 male (42.2 × 18.8 mm) (QM-W5232), Serpentine Creek, SE Queensland, 27°23'S 153°5'E, coll. B. Campbell et al., 12 Oct 1972; 5 males (25.6 × 11.1 mm, 12.3 × 6.6 mm, 16.6 × 8.8 mm, 21.2 × 10.0 mm, 28.8 × 12.4 mm) (QM-W12005), Serpentine Creek, Cribb Island, Nudgee Beach, SE Queensland, 27°21'S 153°7'E, coll. I. Stejskal, 1984; 1 male (19.9 × 10.0 mm) (QM-W8726), mouth of Brisbane R., SE Queensland, 27°24'S 153°10'E, 1 m, coll. Zoology Department, University of Queensland, 19 Sep.1975; 1 male (18.8 × 9.9 mm) (QM-W1203), mud flat, Myora, SE Queensland, 27°29'S 153°25'E, coll. University Science Students Association; 1 male (55.4 × 24.4 mm), 1 female (60.0 × 26.7 mm) (QM-W12432), Sandgate, SE Queensland, 27°20'S 153°4'E, coll. R. Hamlyn-Harris; 1 juv. female (22.2 × 10.0 mm) (QM-W836), Goat I., SE Queensland, 27°31'S 153°23'E, 1 Jan.1938; 1 female (107.7 × 48.8) (QM-W19588), Moreton Bay, SE Queensland, 27°17'S 153°15'E, trawled, coll. S. Cook, 3 Jun.1993; 2 males (15.6 × 8.7; 15.5 × 7.7), 1 female (17.7 × 8.8) (QM-W7231), Deception Bay, Moreton Bay, SE Queensland, 27°10'S 153°5'E, coll. CSIRO, 6 Nov.1972; 3 males (15.5 × 7.7; 21.1 × 9.9; 15.5 × 7.7), 1 female (18.8 × 8.8 mm) (QM-W7217), Deception Bay, Moreton Bay, SE Queensland, 27°10'05"S 153°30'00"E, coll. CSIRO, 6 Nov.1972; 1 male (152.1 × 74.4 mm) (QM-W2515), Moreton Bay, near Mud Island, SE Queensland, 27°20'S 153°15'E, trawled, 20 Oct.1966; 1 male (22.2 × 10.0 mm) (QM-W2356), South Dunwich, SE Queensland, 27°30'S 153°24'E, coll. F. C.

Vohra; 1 male (144.4 × 68.7 mm) (QM-W1931), Lake Macquarie, New South Wales, 32°59'S 151°38'E, 26 Sep.1953; 1 male (143.2 × 65.5 mm) (QM-W1933), Lake Macquarie, New South Wales, 32°59'S 151°38'E, 26 Sep.1953; 1 female (136.5 × 62.2 mm) (QM-W1932), Lake Macquarie, New South Wales, 32°59'S 151°38'E, 26 Sep.1953; 3 males (largest 150.9 × 73.4 mm), 2 females (largest 135.6 × 67.5 mm) (ZRC 2007.0232), Nelson Bay, Port Stephen, New South Wales; 6 juv. males (largest 14.6 × 31.4 mm) (ZRC 2007.0236), Sandringham, Botany Bay, on *Zostera* flats, Sydney, New South Wales, netted at 0.5 m, coll. S. Ah Yong, 4 Jul.2003; 3 males (largest 134.7 × 65.1 mm), 3 females (largest 132.4 × 65.2 mm) (ZRC 2007.0212), Spencer Gulf, South Australia, coll. S. Ah Yong; 3 male, 1 female (183.7 × 86.4 mm) (ZRC 2007.0227), Brighton Beach, Gulf St. Vincent, South Australia, coll. S. Ah Yong & M. Middleton, Dec.2003; 1 female (159.1 × 76.2 mm) (ZRC 2007.0228), Whyalla, Spencer Gulf, South Australia, trapped 1-2m, coll. M & L. Middleton, Dec.2003; 1 male (133.0 × 66.0 mm) (ZRC 2007.0229), Spencer Gulf vicinity, South Australia, coll. S. Ah Yong. NEW CALEDONIA: 2 males (largest 133.0 × 75.6 mm), 1 female (97.1 × 54.6 mm) (MNHN), Navlie Vauban Croisiere St. Vincent St 4, 14 m (22°05'06"S 166°04'05"E), 24 Apr.1985; 1 male (124.0 × 70.7 mm), 1 female (110.5 × 62.7 mm) (MNHN), ORSTOM Vauban, Chalutage 12, 4–6 m 21°56'06"S 166°02'02"E, 30 Apr.1985; Banc Gail, Prof 30m, 1 female (106.4 × 60.8 mm) (MNHN), coll. Tivard, 30 Jul.1986; 1 female (101.0 × 58.0 mm) (MNHN), Baie de St Vincent, Chalutage 1, coll. M. Kulbichi, 20 Aug.1985; 1 female (132.5 × 88.0 mm) (MNHN), Lagoon Nord-Ouest St. CP 1060, 12–14m (20°14'03"S 164°15'04"E), coll. B. Richer de Forges, 5 May 1988; 2 juv. males (largest 83.6 × 47.2 mm) (MNHN), Bourake, St CP2 from the "Alis", coll. M. Kulbichi, 30 Jan.1989; 2 males (28.8 × 12.3 mm, 25.6 × 11.2 mm) (QM-W19909), Dumbéa, coll. P. Davie, 7 Dec.1993, mangroves.

**Diagnosis.** – Carapace width 2.0–2.3 times wider than long, however, on average, carapace width of *P. armatus* less elongated compared to other species, more quadrate in appearance. Median frontal teeth very sharp, spinous, conspicuous. Carapace regions relatively poorly indicated, branchial regions not markedly swollen, surface with coarser granulations compared with other species. Chelipeds in large males stout, more robust than other species, 3.5 times longer than wide (median ratio of 3.2). Anterior margin of cheliped merus usually with 4 (occasionally 5) spines (including extra enlarged spine proximally near joint). Ambulatory legs relatively stouter compared with *P. pelagicus*, ratio of 4<sup>th</sup> pereopod propodus length to width ranging from 2.9–3.7 (median 3.6). Natatorial paddle relatively broader, rounder compared with other three species (Fig. 21D). Sixth male abdominal somite relatively elongate, tapering (Fig. 22D). Base of G1 without round basal spur, or if present blunt, rounded (Fig. 20D). Colour pattern with spots tending to remain relatively discrete, though sometimes fusing into thin irregular short bands thinner than those on *P. pelagicus*. Female patterns similar to males but differs in colour compared with females of other three species (Fig. 7D). Maximum size of 200 mm carapace width (Kailola et al., 1993).

**Life colours (Figs. 6D, 7D, 19).** – Carapace colouration varies from dark blue and purple to green in males, brown in females. Banding patterns present on carapace present, but thinner and sparse in comparison to the other three species; posterior part of carapace ocellated, markings on carapace

resemble thin reticulations, never as thick or as dense as markings on the others. Females with a background colour in varying shades of brown, but similar banding patterns to male. Within *P. armatus*, there appears to be regional variation in the colour of males around Australia, especially from South Australia in Spencer Gulf and Gulf St. Vincent, where males typically are brighter blue and exhibit less reticulation than those from other localities (Fig. 19D) (S. Ah Yong, pers. comm.). They are otherwise indistinguishable morphologically and genetically.

**Remarks.** – Alphonse Milne-Edwards described *Neptunus armatus* in 1861 based on at least one juvenile male collected from Shark Bay, Western Australia, commenting that the shape of its frontal and anterolateral teeth seemed broader at the base than *P. pelagicus* to which it was otherwise similar. *Portunus armatus* was accepted as a valid species by both Miers (1884) and Henderson (1893), although Alcock (1899: 34) tentatively regarded it as a junior synonym of *P. pelagicus*. Following Alcock's action, the species was essentially forgotten and not mentioned in recent Australian literature. In particular, it was overlooked by Stephenson & Cambell (1959) in their review of the Australian *Portunus* species, Stephenson (1972a), in his checklist of the Indo-West Pacific Portunidae, Jones (1994), in her checklist of marine decapod crustaceans from Shark Bay (the type locality), and by Davie (2002), in his synopsis of the Australian fauna.

The confusion over the identity of *P. armatus* and subsequent lack of records in Australia may be attributed to the fact that the original description was based on a juvenile of only carapace length 15 mm (large adults are typically more than 150 mm), and the length of the last anterolateral

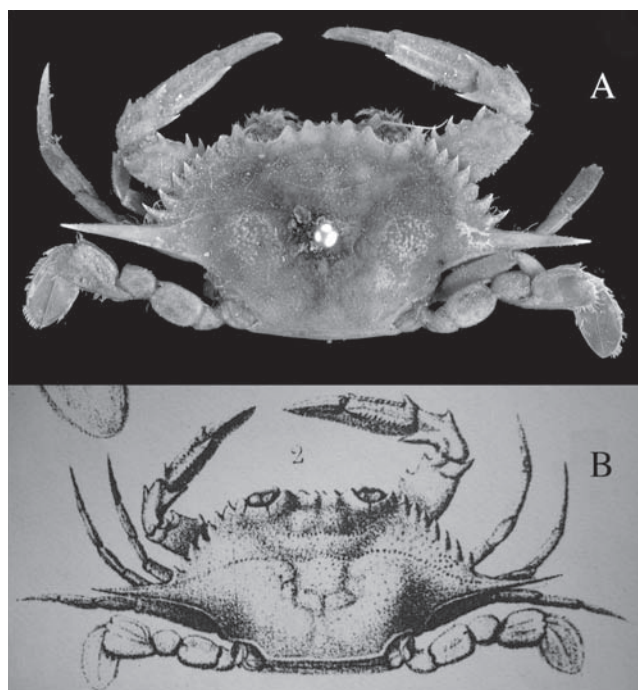


Fig. 17. *Portunus armatus* (A. Milne-Edwards, 1861). A, Lectotype male (36.0 × 15.0 mm) (NHM 1858.172.115) (photograph: P. Crabb, NHM photo unit); B, original figure in A. Milne-Edwards (1861).

spine is much longer than in adult specimens. Secondly, the accompanying illustration (reproduced in Fig. 17B) differs from the lectotype and paralectotype specimens in at least two key features: 1) the posterolateral corner of the carapace is square in the illustration, but rounded in reality; and 2) the carapace proportions of the drawing are distorted so that it appears wider than the type specimen on which it was based. Henderson (1893) first commented that A. Milne-Edwards gave incorrect carapace dimensions, and that the length of the last anterolateral spine was inaccurately drawn. Photographs of a syntype (NHM 1858.172.115) (Fig. 17A) kindly provided by P. Clark (NHM), leave us in no doubt that this is the specimen figured by A. Milne-Edwards (1861), and we here designate it as the lectotype. The general features, positions of the legs and chelipeds all match, although as already mentioned, the last anterolateral spine is exaggerated in the drawing, and the measurements originally given are different.

Stephenson (1968b) had access to a series of specimens collected from across the Indo-West Pacific and Australia, and concluded that perceived differences between samples from different localities may be attributed to regional clines or varieties. Indeed, there does appear to be some regional colour variation between *P. armatus* specimens collected from localities around Australia. In particular, the colour of specimens collected from Spencer Gulf/Vincent Gulf in South Australia deviate the most from “typical” *P. armatus* collected in other localities (Fig. 9D). However, the fundamental shape and positioning of the underlying patterning is retained, and females are consistently the same as elsewhere. It was also noted by Bryar & Adams (1999) that allozyme data provide no evidence that the marked colour and pattern variations in *P. armatus* from different regions around Australia are due to the presence of cryptic species or subspecies. Rather, they speculated that variation in pigmentation is probably due to phenotypic plasticity as reported by Meagher (1971) and Bryars (unpublished data) from laboratory held individuals.

Initially, the extreme length of the last anterolateral spine in the lectotype cast some doubt as to whether it was conspecific with the “*P. pelagicus*”-like species occurring in Australia, but a comparison with juvenile specimens collected from both the type locality in Shark Bay, Western Australia, and from New South Wales indicates that spine length is significantly variable, and that longer spined juveniles similar to the lectotype do occur, and seem to be more common in Western Australia (Fig. 18).

Other specimens identified by Henderson (1893) as *P. armatus* from outside Australian waters have also been re-examined. Five small specimens (the largest being 30.5 mm wide) from Pamban, Rameswaran, India, are actually juvenile *P. reticulatus*; and similarly, specimens identified as *P. armatus* from Chefoo, China, belong to *P. trituberculatus*.

While we are sufficiently certain that the specimen here designated as lectotype (NHM 1858.172.115) is the same as that described and illustrated by A. Milne-Edwards (1861), a

second specimen of *P. armatus* with the same register number (NHM 1858.172) but a different specimen number (114) was uncovered by P. Clark. As these two specimens were listed together as a single lot in the accession book, it is likely that A. Milne-Edwards examined both specimens. However, he did not indicate how many specimens he had seen. As no holotype was selected, we here recognise both specimens as syntypes and designate a lectotype and paralectotype as earlier indicated.

*Portunus armatus* appears to be the largest of the four species in the *P. pelagicus*-complex, with the biggest specimen recorded attaining 200 mm in carapace width (Kailola et al., 1993). It is of significant economic importance in Australian fisheries and subject to stringent catch quotas and size restrictions. As such, its population dynamics and biology in Australian waters are relatively well studied (see Shields, 1992; Sumpton et al., 1994; Weng, 1987, 1992; Xiao & Kumar, 2004).

**Habitat.** – Lives in a variety of inshore and continental shelf waters from low intertidal to 50 m depth; prefers flatter sandy to muddy bottoms with algal and seagrass communities (Edgar, 1990; Williams, 1982). Juveniles are common near low water mark on intertidal flats; adults can also sometimes be found in shallow water near low tide mark, but mostly crabs move into deeper water as they age in response to changes in water temperature and inshore salinity (Potter et al., 1983). At least in Moreton Bay, ovigerous crabs move into deeper more oceanic water for spawning (Potter et al., 1987).

**Distribution.** – In Australia from Cape Naturaliste, Western Australia, around northern Australia south to about the southern border of New South Wales; also found in the warmer waters of the South Australian Gulfs, as far south as Barker Inlet in Gulf St Vincent (Kailola et al., 1993). Lord Howe Island; Arafura Sea off southern Papua; occasional records from the North Island of New Zealand, but apparently not able to form a sustainable population (Dell, 1964). In New Caledonia, they are present but rare within the shallow lagoon fringing the island. *P. armatus* has no commercial value in New Caledonia, and is more often regarded as a pest as they tend to congregate around floating fish holding pens within the lagoon and damage nets as well as fish stocks kept within. With the decline in fish holding aquaculture in New Caledonia, *P. armatus* density within the lagoon has also diminished (B. Richer de Forges, pers. comm.).

## INCERTAE SEDIS

The following records are attributed to *P. pelagicus* sensu lato. However, due to a lack of description or specimens, it is impossible to determine which of the four species the description is based on. Hence they are listed here as incertae sedis.

***Lupa pelagica*** – H. Milne Edwards, 1834: 450. No particular specimen(s) listed, but the Red Sea and Indian Ocean listed as localities. As specimens could not be examined, it could either be *P. segnis* or *P. reticulatus*.



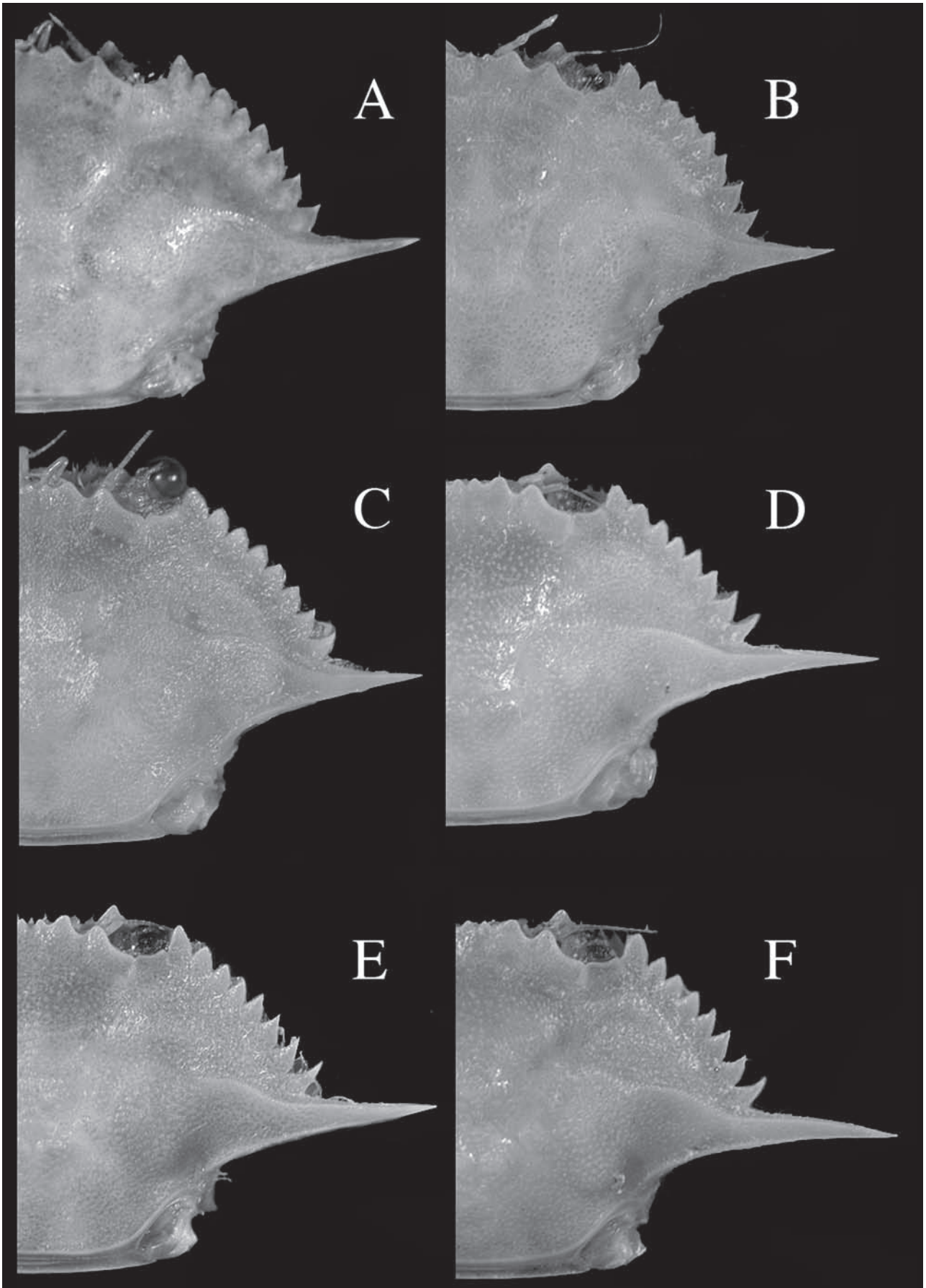


Fig. 18. Lateral spine length variation in juvenile *Portunus armatus* (A. Milne-Edwards, 1861). A, B, Botany Bay, New South Wales; C-F, Shark Bay, Western Australia. A, male (27.14 × 12.4 mm) (ZRC 2007.236); B, male (28.5 × 13.9mm) (ZRC 2007.236); C, male (30.7 × 13.9 mm) (WAM C20682); D, male (29.5 × 12.3 mm) (WAM C39181); E, male (34.0 × 14.5 mm) (WAM C39181) F, male (26.8 × 10.9 mm) (WAM C39179).

*Neptunus pelagicus* – A. Milne-Edwards, 1861: 320. No particular specimen(s) listed; localities ranged from the Red Sea to “New Holland” (presently Australia). Potentially includes some or all of the four species.

*Portunus pelagicus* – Sankarankutty, 1961: 102 (list), 103, 104. The specimen was collected from Andaman and Nicobar Islands, but no photographs or illustrations are shown. It may be *P. reticulatus* based on the locality.

*Portunus pelagicus* – Turkey, 1971: 123 (part). Turkey examined material from both New Caledonia and Indian Ocean. While *P. armatus* is the name designated to the New Caledonia population, there is uncertainty with regards to the Indian Ocean material (either *P. segnis* or *P. reticulatus*). Hence, his record is here regarded as incerta sedis.

*Portunus pelagicus* – Pretzmann, 1971: 477. His record of “Vorderasien” seems to indicate the region of the Eastern Mediterranean to the Middle East. In this area, only *P. segnis* is known thus far. The specimens were photographed by P. Dworschak of Naturhistorisches Museum in Vienna at our request and consist of three juveniles and one sub-adult

female. The frontal margin of the female is damaged but based on what can be seen, the specimens are likely to be *P. segnis*.

*Portunus pelagicus* – Stephenson & Rees, 1967b: 34-35. Their material from the Smithsonian Institution came from various parts of the Pacific and Indian Ocean. All are probably *P. pelagicus* with the exception of material collected from the Gulf of Carpentaria which is more likely to be *P. armatus*.

*Portunus pelagicus* – Stephenson, 1976: 18. Material reported from the collections of the Smithsonian Institution acquired from expeditions carried out in the Seychelles, central Indian Ocean and the Marquesas. No list of specimens examined were listed, his only remark was “the previous record of *P. trituberculatus* by Stephenson and Rees (1976a, b) belongs to the present species”. A check by R. Lemaitre (USNM) indicated that there is no record of *P. pelagicus* from the Marquesas lodged at the Smithsonian. As there are no known or reliable records of *P. pelagicus* from French Polynesia, the specimen(s) examined by Stephenson is likely to have been collected from the Seychelles or the central Indian Ocean. As such, it was probably *P. segnis* or *P. reticulatus*.



Fig. 19. Regional colour variation in *Portunus armatus* (A. Milne-Edwards, 1861). A, figure by F. Bauer from voyage of H.M.S Investigator to Australia (after Rice, 1999), exact locality unknown; B, adult male (photograph only), Hacking River, Sydney C, male (132.4 × 65.2 mm) (ZRC 2007.0212) (Nelson Bay, Port Stephen, New South Wales), incomplete specimen; D, male (133.0 × 66.0 mm) (ZRC 2007.0229) (Spencer Gulf vicinity, South Australia). (Photographs B, C and D taken by S. Ahyong).

**KEY TO THE SPECIES OF  
PORTUNUS PELAGICUS SPECIES-COMPLEX**

1. Median teeth frontal teeth minute, inconspicuous, almost obsolete (Fig. 23B); western Indian Ocean ..... *P. segnis*
  - Median teeth frontal teeth conspicuous, either small or prominent; eastern Indian Ocean and Western Pacific ..... 2
2. Four spines on anterior margin of cheliped merus (Fig. 23H); Australia ..... *P. armatus*
  - Three spines on anterior margin of cheliped merus ..... 3

3. Sixth segment of male abdomen relatively shorter, broader (Fig. 22A); white spots on the carapace, often merging into broad almost banded reticulations, in particular on the posterior and branchial regions (Figs. 6A, 10); Southeast Asia to northwestern Australia, western Pacific to Japan ..... *P. pelagicus*
  - Sixth segment of male abdomen relatively narrower, more elongate (Fig. 22C); carapace covered with spots, rarely merging into short bands (Figs. 6C, 16); eastern Indian Ocean but not Australia ..... *P. reticulatus*

**DISCUSSION**

Three methods of data analysis were employed: morphological examination, morphometrics and DNA sequencing to determine species variability within this complex at the COI locus. The morphometric discriminate function analysis gave the weakest resolution, only unequivocally splitting *P. armatus* from the rest of the *P. pelagicus*-species complex, e.g., a one-way ANOVA for cheliped merus length width proportions differed significantly between *P. pelagicus* and *P. armatus* ( $P = 0.025$ ). However, morphological and genetic analyses generally gave much clearer discrimination indicating the presence of four species.

**Morphological Differences.** – Species of the *Portunus pelagicus*-complex are morphologically most similar to *P. trituberculatus* Miers, 1876, and *P. sanguinolentus* Herbst, 1783. *Portunus trituberculatus* is the most important commercial *Portunus* species in China, Japan and Korea, but does not appear to extend as far south as the Indo-Malaysian region. Bryars & Adams (1999) speculated that the cryptic lineage of “*Portunus pelagicus*” revealed by their allozyme study of northern Australian populations may have been records of *P. trituberculatus*, though subsequent examination has shown this is not the case. *Portunus trituberculatus* can be differentiated from all four members of the *P. pelagicus* complex by having three spines on the frontal margin of carapace vs. four (medial pair variably conspicuous); a typically shorter and stouter merus of the cheliped with four spines on the anterior margin vs. slender and elongate with three spines on the anterior margin in most of the *P. pelagicus* species-group (but similar to *P. armatus* in this respect). The posterior third of the carapace in *P. trituberculatus* is smooth whereas it is granular in the *P. pelagicus* complex.

Species of the *P. pelagicus* complex can also be simply and quickly differentiated from *P. sanguinolentus* by different life colour patterns. Male specimens of the complex possess a greenish blue carapace with a variable network of white reticulations and spots, while *P. sanguinolentus* is brown-olive in colour with three blood-red spots posteriorly. The *P. pelagicus* species complex also has a more granulate carapace and the presence of a postero-distal spine on the cheliped merus that is absent in *P. sanguinolentus*. No obvious sexual dimorphism is observed in *P. sanguinolentus* and *P. trituberculatus*, unlike in *P. pelagicus*. Nonetheless, a subspecies of *P. sanguinolentus*, *P. s. hawaiiensis* Stephenson, 1968 (type locality Hawaii) resembles a cross between *P. sanguinolentus* and *P. pelagicus*, having both reticulated patterns on the carapace and three red spots on the posterior

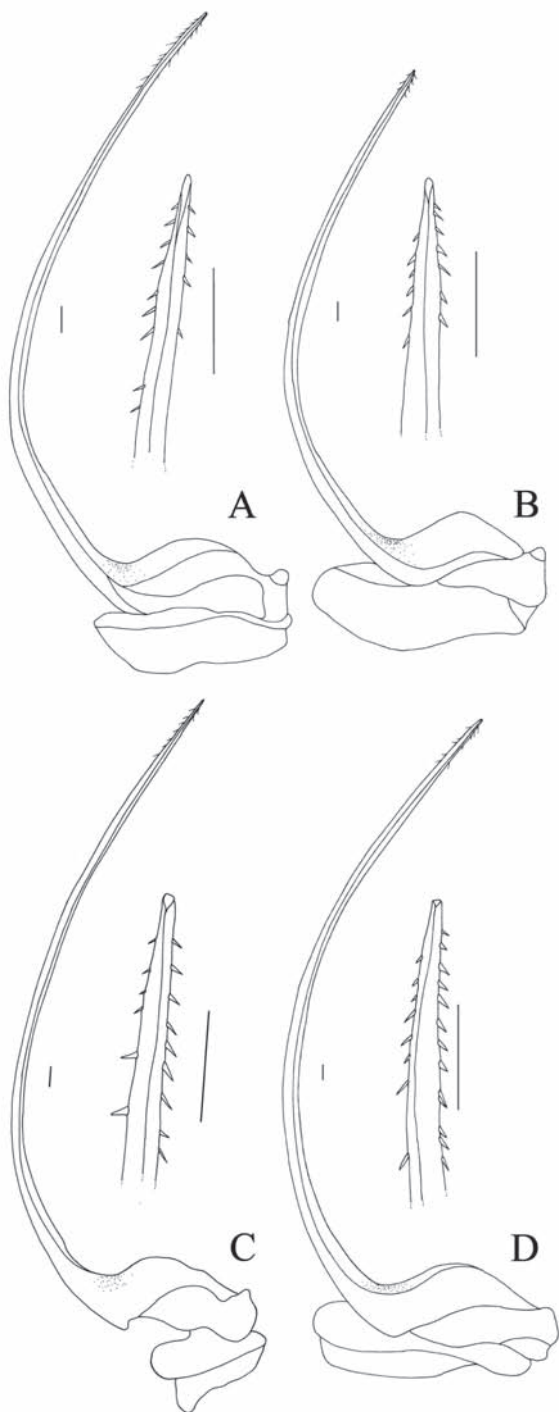


Fig. 20. G1 and distal part of G1 structures. A, *Portunus pelagicus* (110.7 × 48.8 mm) (RMNH D384); B, *P. segnis* (147.2 × 66.8 mm) (ZRC 2007.225); C, *P. reticulatus* (138.5 × 60.7 mm) (ZRC 2007.222); D, *P. armatus* (150.8 × 73.6 mm) (ZRC 2007.232). Scale = 1 mm.

part of the carapace (Stephenson, 1968: Fig. 2A). The identity of this isolated subspecies/species is currently being elucidated (Lai et al., in preparation). Aside from morphology, these three species are also clearly distinct genetically (Table 6).

The differences between the four species recognised here are summarised in Table 7 and only key identifying characters will be further discussed. All four species can be separated

based on various combinations of morphological characters, primarily on the prominence of the frontal teeth, the length and armature of the cheliped merus, live colour patterns, male sixth abdominal segment shape, paddle shape of P5, and other characters as enumerated fully in Table 7.

Two discrete species-pairs can be recognised both on morphological and molecular grounds (Fig. 3): *P. pelagicus*/*P. segnis* and *P. armatus*/*P. reticulatus*.



Fig. 21. Fourth and fifth pereopod merus, carpus, dactylus. A, *Portunus pelagicus* (152.9 × 68.0 mm) (ZRC 2007.233); B, *P. segnis* (134.5 × 62.6 mm) (ZRC 2007.226); C, *P. reticulatus* (138.5 × 60.7 mm) (ZRC 2007.222); D, *P. armatus* (133.0 × 66.0 mm) (ZRC 2007.229).

*Portunus pelagicus* and *P. segnis* both have relatively long, slender cheliped meri (most obvious in adult male specimens) compared to *P. reticulatus* and *P. armatus* (Fig. 23E–H). *Portunus pelagicus* and *P. segnis* also possess similarly shaped, relatively more elongated paddles on their swimming legs compared with other two species, which tend to be shorter and rounder (Fig. 21). Similarly, the sixth segment of the male abdomen is relatively shorter and broader in *P. pelagicus* and *P. segnis* versus appearing relatively narrower and more elongate in *P. reticulatus* and *P. armatus* (cf. Fig. 22A, B with Fig. 22C, D).

Apel & Spiridonov (1998) have already noted that “*P. pelagicus*” specimens (= present *P. segnis*) from the Western Indian ocean tend to have low and obtuse or even indistinct frontal median teeth, and this is an important and simple

character for recognising this species. However, relatively prominent median teeth may occasionally be observed in larger individuals (1 female; 158.4 × 75.4 mm, SMF 8768); in this specimen the branchial regions are also swollen but less so when compared to *P. pelagicus* sensu stricto (Fig. 24B). To further underline the distinctiveness of *P. segnis*, Ward (1942) described *P. mauritanus* as a new species (here considered *P. segnis*), after comparing his material with what he thought was real “*P. pelagicus*” from Australia (= *P. armatus*).

*Portunus armatus* is the most distinctive of the four species in the *P. pelagicus* complex due to its distinctive colouration and banding patterns of both sexes (Figs. 6D, 7D). Its carapace appears to be more granular than the other three, and spines appear to be larger and broader at the base as noted by A.

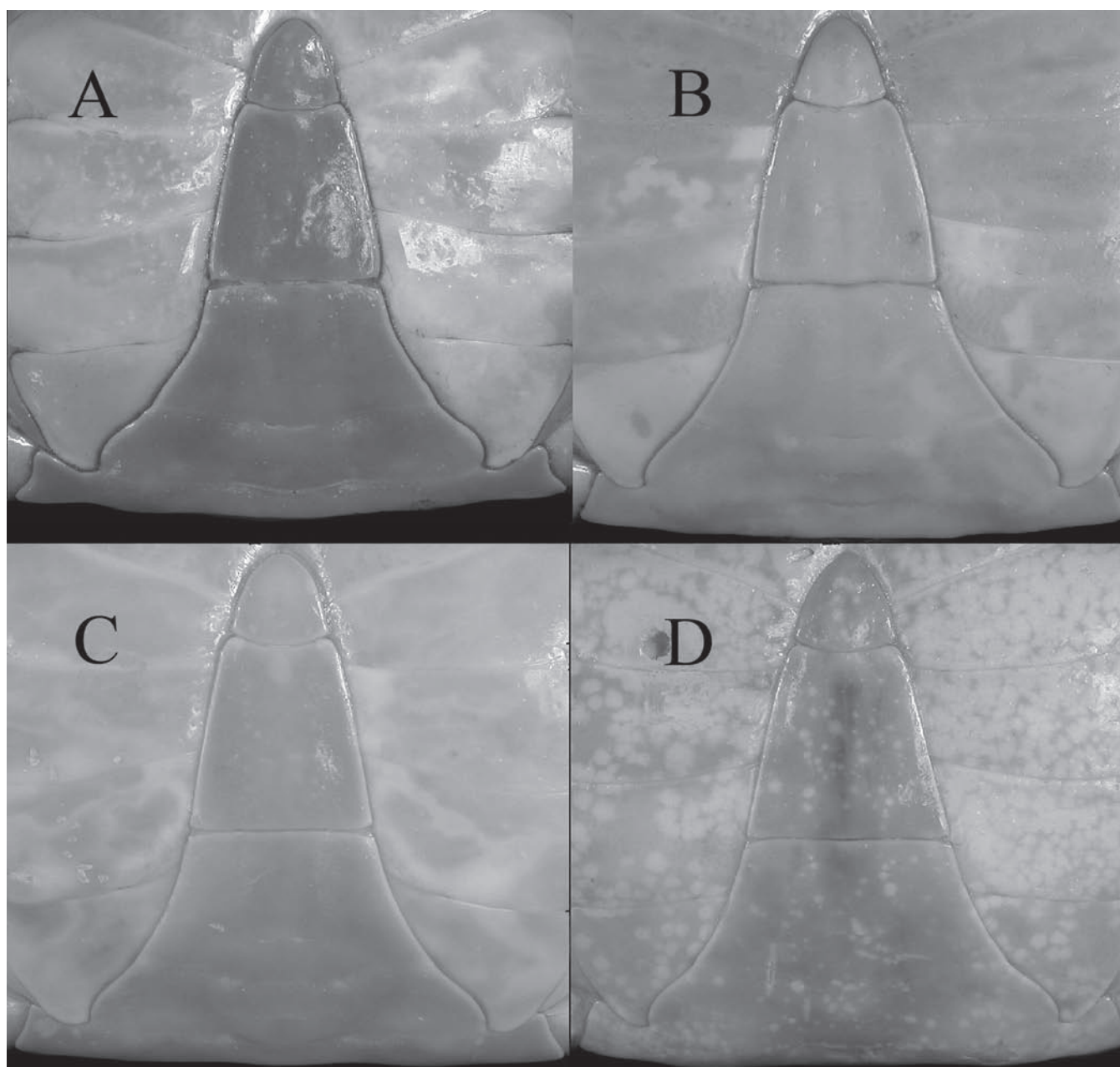


Fig. 22. Male abdominal somites. A, *Portunus pelagicus* (152.9 × 68.0 mm) (ZRC 2007.233); B, *P. segnis* (134.5 × 62.6 mm) (ZRC 2007.226); C, *P. reticulatus* (138.5 × 60.7 mm) (ZRC 2007.222); D, *P. armatus* (133.0 × 66.0 mm) (ZRC 2007.229).

Milne-Edwards (1861). The four spines on the anterior margin of the cheliped merus (rarely three) and the four acute spines on the frontal margin (Fig. 23D) are distinctive. The meri of the chelipeds of *P. armatus* and *P. reticulatus* appear stouter relative to carapace width (Fig. 23H), but this did not show as significant in the morphometric analysis. *P. armatus* differs from *P. pelagicus* ( $P = 0.025$ ) and *P. reticulatus* ( $P = 0.003$ ) in cheliped merus length and width proportions, and from *P. pelagicus* in cheliped manus and dactylus proportions ( $P = 0.001$ ) (Fig. 23H). Finally, the carapace width of *P. armatus* appears to be less laterally elongated compared to the other three species, giving it more a quadrate appearance.

**Morphometric Analyses.** – One-way ANOVA demonstrated reciprocal differences between pairs of species (see diagnosis of each species in the systematic account), but a confidence interval of 95% on the scatter plot of canonical scores did not allow the four species to be significantly discriminated. Although statistically not significant, the morphometric ratios of *P. armatus* appear to be slightly different from the other three species, accounting for the segregation of groups into two broad clusters, one of *P. armatus* and the other comprising the remaining three species. This suggests a large degree of overlap between measurements of any specific ratio — something reported in morphometric studies

of other closely related species complexes (see Burton & Davie, 2007; Keenan et al., 1998; Pfenninger et al., 2006; Reuschel & Schubart, 2006).

**Genetic Separation.** – The genetic data supports the morphological division of these four species into two affiliated groups. Based on total sequence divergence at the COI locus, *P. armatus* and *P. reticulatus* form a sister group to *P. pelagicus* and *P. segnis*, with average genetic distance of ~2% between *P. armatus* and *P. reticulatus*, 3.14% between *P. pelagicus* and *P. segnis*, and ~7% divergence between *P. armatus*/*P. reticulatus* and *P. pelagicus*/*P. segnis* (Table 6, Fig. 4). The topology of the ME tree (Fig. 3) shows the close relationships between these species pairs. The genetic divergence of only 2% between *P. armatus* and *P. reticulatus* is relatively low by the standards of the early barcoding recommendations (Hebert et al., 2003) but the use of percentiles for species and genus delimitations based on a single gene has been criticised (Meier et al., 2006; Rubinoff, 2006; Will & Rubinoff, 2004). Burton & Davie (2007) discussed this issue in some detail, and indeed interspecific divergences within the slipper lobster genus *Thenus* of their study, similarly ranged from 2.0–11.8%. For North American birds, the average value of is 1.9% difference for sister species (Johnson & Cicero, 2004).

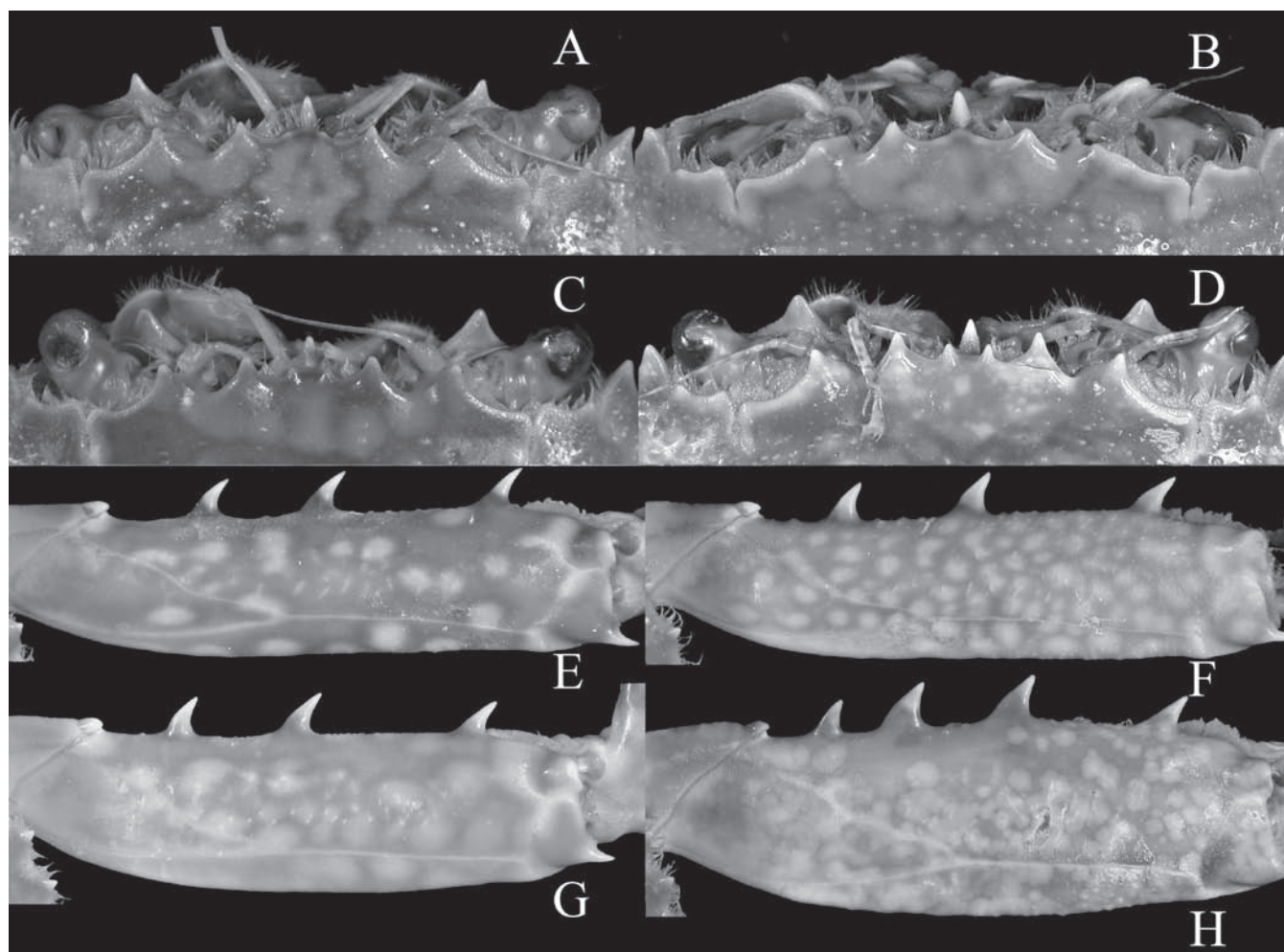


Fig. 23. Frontal margin and merus of left cheliped A, E, *Portunus pelagicus* (152.9 × 68.0 mm) (ZRC 2007.233); B, F, *P. segnis* (134.5 × 62.6 mm) (ZRC 2007.226); C, G, *P. reticulatus* (138.5 × 60.7.0 mm) (ZRC 2007.222); D, H, *P. armatus* (133.0 × 66.0 mm) (ZRC 2007.229).

Although *P. segnis* and *P. pelagicus* are closely related to each other, their distribution is disjunct; the western-most range of *P. pelagicus* is in the Andaman Sea, the eastern edge of the Indian Ocean, while *P. segnis* is restricted to waters west of the Indian subcontinent. They are separated from each other by *P. reticulatus*, so far known to be restricted to the eastern Indian Ocean in the Bay of Bengal.

Interestingly, *P. pelagicus* mt DNA haplotypes are present in 21 of 77 specimens of *P. reticulatus* for which COI data was available, despite the fact that all specimens are clearly *P. reticulatus* in external morphology. Closely related species may share haplotypes and this has been reported in the crustacean genus *Xantho*; *X. hydrophilus* and *X. depressus* are two closely related species found in the Atlantic/Mediterranean that share the same COI haplotype between individuals of the two species (Reuschel & Schubart, 2006). Verheyen et al. (2003) reported a similar situation for cichlid superflocks in Lake Victoria. This could be due to hybridisation between the two species in the Bay of Bengal leading to introgression where the mitochondrial genome of *P. portunus* is introduced to *P. reticulatus*. This is apparently not uncommon and is widely reported in a range of taxa from birds (Vallender et al., 2007) to mysid crustaceans (Audzijonyte & Väinölä, 2006). While the putative sympatric zone between the two species is thought to be the Bay of Bengal based on the distribution the two species, we were unable to collect enough material from this specific region to confirm our hypothesis.

Our genetic data also point to the possible existence of a fifth species in this complex in northern Japan. Two individuals out of 26 collected from Kyushu differed from the rest of the population by 25 mutational steps and showed a higher genetic affinity with *P. reticulatus* and *P. armatus* (Fig. 3). Unfortunately, voucher specimens for these two individuals were not properly preserved and therefore were unavailable for follow-up morphological examination. As this locality represents the northernmost range of *P. pelagicus* in Japan

(and Pacific), they could represent an incipient fringe species sympatric with *P. pelagicus* sensu stricto. A more extensive collection with fresh material and a reanalysis of morphology and genetic data sets will be needed to confirm this hypothesis.

Based on our examination of material of Bryars & Adams (1999), we conclude that Northern Territory is a zone of sympatry for *P. armatus* and *P. pelagicus*, although attempts to collect fresh material for the present study were unsuccessful.

Marine connectivity between the Bay of Bengal and the Indo-Malayan Archipelago occurs along the eastern edge of the Bay of Bengal, and thus this would form a zone where hybridisation and introgression may occur between *Portunus pelagicus* and *P. reticulatus* (indicated by the presence of *P. pelagicus* “specific” haplotypes amongst *P. reticulatus* individuals). This possibility is supported by the presence of circulating surface currents within the Bay of Bengal during both the Northeast and Southwest monsoons (Eigenheer & Quadfasel, 2000). However, the large disjunction of COI sequence data obtained from *P. reticulatus* compared with *P. segnis* and *P. pelagicus* (that it shares an almost ‘continuous’ distribution with), hints at an unusual zoogeographical cline within the Bay of Bengal that bears further investigation. In investigating the identity of the box crab *Calappa lophos* (Herbst, 1782), Lai et al. (2006) observed that while *C. lophos* has a broad Indo-West Pacific distribution ranging from Japan to South Africa, most of the material that was previously identified as *C. lophos* in Chennai, India, Pakistan and the Persian Gulf was, however, a closely related sibling species, *C. guerini* Brito-Capello, 1871. The present study suggests that the zone of introgression may exist in Phuket where *P. reticulatus* populations all share the same dominant haplotype as Pacific populations of *P. pelagicus*

It is clear that aside from a putative hybridisation zone for *P. pelagicus* and *P. reticulatus* in the Bay of Bengal/Andaman

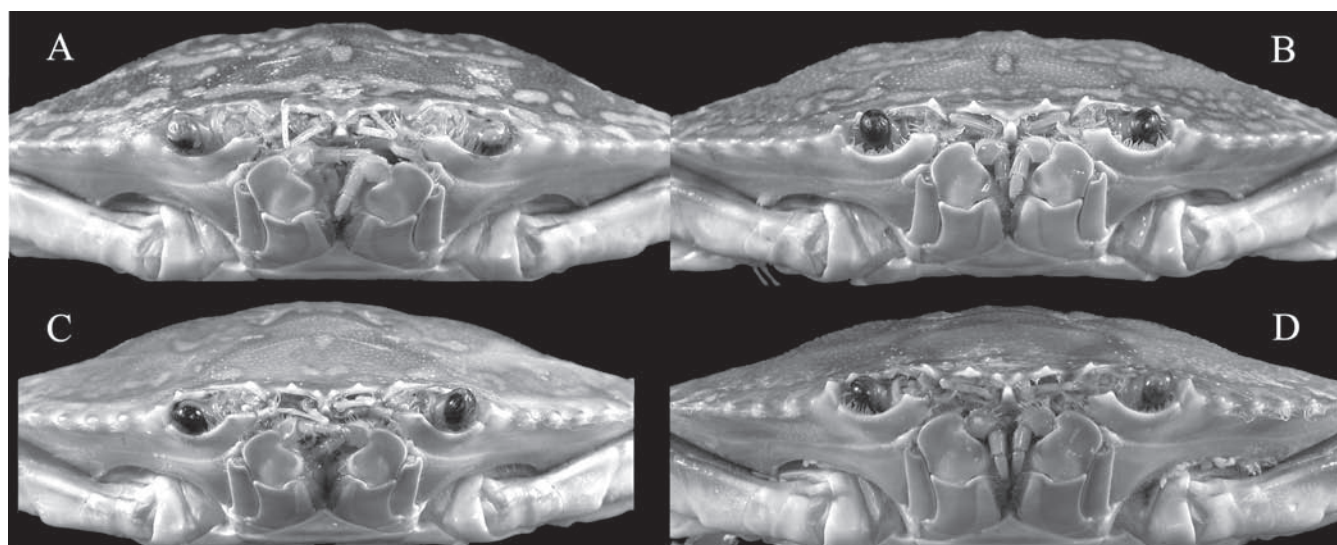


Fig. 24. Frontal view showing differences in branchial swelling. A, *Portunus pelagicus* (152.9 × 68.0 mm) (ZRC 2007.233); B, *P. segnis* (134.5 × 62.6 mm) (ZRC 2007.226); C, *P. reticulatus* (141.7 × 63.0 mm) (ZRC 2007.222); D, *P. armatus* (150.8 × 73.6 mm) (ZRC 2007.232).

Sea and perhaps also between *P. pelagicus* and *P. armatus* in Northern Australia, most populations of the four species are reproductively isolated from one another and should be managed accordingly.

Genetic data for *P. segnis* uncovered two common co-dominant haplotypes of COI separated from each other by two base pair mutations and no shared haplotypes between populations sampled from Madagascar/Mozambique and Israel/UAE (Fig. 5B). The *P. segnis* population from Israel is non-native and probably resulted from Lessepsian migration of *P. segnis* from the Arabian Sea (Galil et al., 2002). This segregation of COI haplotypes is also reflected in pairwise Fst differences between the populations (data not shown).

This dichotomous COI haplotype network may indicate phylogeographic structuring owing to isolation by divergent ocean currents. During the Southwest monsoon season, the South Equatorial Current (SEC) flowing westwards splits into two divergent currents, the northward flowing Somali Current (SC) that enters the Arabian Sea as the East Arabian Current (EAC) and the southward flowing Agulhas Current (AC) (Schott et al., 2002; Swallow et al., 1988). During the Northeast monsoon, SC flows southwards from the Arab Sea but is a deflected eastward after encountering the East African Coast Current (EACC) south of the equator, subsequently supplying the SEC (Düëing & Schott, 1978; Schott & McCreary, 2001) while the direction of AC remains unchanged. These divergent currents may prove to be a barrier to dispersal between marine taxa north and south of the equator along the African coast, and is observed for the first time in the present study. In the light of current patterns and isolation of *P. segnis* along the African subcontinent, these areas should be managed as independent fisheries resources.

Although situated geographically in the Indian Ocean, the COI haplotype patterns of various taxa collected from Western Australia typically show strong affinities with those in either the Pacific or Indian Ocean and at other times a mix of both (Benzie et al., 2002; Williams et al., 2002). Eastern and Western Australia, which are influenced by the Pacific and Indian Ocean respectively, are normally regarded as separate biogeographic regions. Imron et al. (2007) reported a 3.68% divergence rate in COI sequences between the abalone *Haliotis asinina* collected from East and Western Australia, a break they consider to be due to cryptic speciation. On the other hand, Williams et al. (2002) and Benzie et al. (2002), using *Alpheus lottini* (Crustacea: Alpheidae), *Penaeus monodon* (Crustacea: Penaeidae) and *Linckia laevigata* (Echinodermata: Ophidiasteridae) as model organisms, showed that while there is a clear genetic break, nuclear and mitochondrial data demonstrate that West Australian haplotypes either join a central Indo-Malayan Pacific clade, or are affiliated with both Indian and Pacific Oceans clades.

In the present study, *P. armatus* shows no such geographic distinction for Eastern and Western Australia populations

based on COI data. Haplotypes from all individuals of *P. armatus* collected from around Australia and New Caledonia revealed that the populations are heterogeneous (based on significant population pairwise Fsts), but no associations can be deduced. NCA was not performed on the present data set as our sample size of *P. armatus* in the present study was insufficient (i.e., no sampling saturation was reached in the form of an overwhelmingly dominant haplotype) to draw any statistically significant conclusions in the haplotype makeup of populations of *P. armatus*.

While genetic results for *P. armatus* from the present study should be treated with caution, they nonetheless highlight a genetically distinct Australian and South Pacific species that has a heterogeneous distribution of haplotypes. This result is concordant with the genetic patterns reported by Sezmis (2004), and the outcomes of the allozyme work undertaken by Bryars & Adams (1999). In particular, Sezmis (2004) reported that phylogenetic lineages of *P. armatus* showed variable geographical distribution, a trend that is seen from the haplotype network obtained from this study. Haplotypes from individuals obtained from Western Australia and New Caledonia are observed to be “private” (i.e. restricted to a particular population). This is most likely the result of geographic isolation, and barriers to dispersal between the Indian and Pacific Oceans.

Based on the molecular clock of COI mutation rates suggested by Schubart et al. (1998), species within the *P. pelagicus* sensu lato complex diverged at different times (between 0.78 and 5.4 million years ago). This corresponds with fossil records of *P. sanguinolentus*-like crabs found from the Miocene (23–5.3 MYA) (Glaessner, 1969; Müller, 1984).

**Larval differences.** – Although larvae were not cultured in the present study, a literature search revealed some morphological differences between the first zoea of *P. pelagicus* sensu stricto, *P. reticulatus* and *P. armatus*. These differences are summarised in Table 8. Among others, there are discrepancies in the number of setae on the coxal and basal endites of the maxillule and antennule structure. Following Stephenson’s (1972a) comment, the possibility that such differences reflect the presence of a cryptic species was suggested by Shinkarenko (1979). However, it is also well documented in the literature (see Clark, 1984; Lim & Ng, 1988; Ng & Clark, 1994) that setal morphology of congeneric larvae are highly similar and differences between larvae of closely allied species are typically slight, and often based on precise setal numbers (after discounting variation). Interestingly, while *P. pelagicus* and *P. armatus* are reported to pass through four zoeal stages and a megalopa stage (Cowan, 1984; Motoh et al., 1978; Shinkarenko, 1979), Jose et al. (1996) reported five zoeal stages in *P. reticulatus* (as *P. pelagicus*) in Mandapam, southern India. As pointed out by Clark et al. (1998), the quality of larval descriptions varies greatly between workers and eras, and therefore it is probably only possible to make a definitive assessment after direct comparison of a range of material representing each putative species.



Table 8: Comparison of setae on the antennule and coxal and basal endites of the maxillule, as given by Prasad & Tampi (1953), Shinkarenko (1979), and Yatsuzuka & Sakai (1980) of the first zoea of *Portunus reticulatus*, *P. armatus* and *P. pelagicus* respectively.

	<i>Portunus reticulatus</i>	<i>Portunus armatus</i>	<i>Portunus pelagicus</i>
Antennule asethetasc	3	2	3
Maxillule endites			
Coxal	4	7	6
Basal	5	5	5

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