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**A REVISION OF THE GENUS *SCYLLA* DE HAAN, 1833  
(CRUSTACEA: DECAPODA: BRACHYURA: PORTUNIDAE)**

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**ABSTRACT.** - There has been considerable confusion regarding the taxonomy of species in the genus *Scylla*, commonly known as mud or mangrove crabs. To resolve this confusion we collected material from the Red Sea (the original type locality of *Scylla serrata*), and from many other locations throughout the Indo-Pacific. Two independent genetic methods, allozyme electrophoresis and sequencing of two mitochondrial DNA genes, cytochrome oxidase I and 16s RNA, were employed in an attempt to discriminate species. The genetic data show that there are at least four distinct *Scylla* species. Using this knowledge their morphology was critically examined, and morphometric data analysed, to determine useful characters for field separation. Nomenclatural problems have been addressed with appropriate neotype and lectotype designations. The species recognised are: *S. serrata* (Forskål, 1775), *S. olivacea* (Herbst, 1796), *S. tranquebarica* (Fabricius, 1798), and *S. paramamosain* Estampador, 1949.

**KEYWORDS.** - mud crab, mangrove crab, taxonomy, genetics, morphology, morphometrics

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**INTRODUCTION**

Forskål (1775) described *Cancer serratus* from material collected from Jiddah on the Red Sea. His description, published posthumously, was of a crab without claws. His voyage ended tragically with his death, and the type specimen which should have been sent to Denmark, has never been located (for an historical account of the Danish expedition to "Arabia Felix" see Nielsen, 1993; Wolff, 1994). The lack of a type specimen has undoubtedly caused much of the confusion that was to follow. In subsequent years six additional species or

varieties were described, but the characters to discriminate between them have always been vague at best. The lack of type specimens for many of these has also caused difficult nomenclatural problems. Because the species of *Scylla* are remarkably similar, it has been difficult, without a large number of specimens from across the entire distributional range, to accurately define the juncture where intraspecific variation ends and real interspecific differences begin. To further illustrate the nomenclatural and practical difficulties in defining the *Scylla* species, the syntype specimens of *Portunus tranquebaricus* Fabricius, 1798, that we examined in the course of this work, represent all four species here recognised!

Estampador (1949a) published an important paper recognising three species and a new subspecies from the Philippines. Estampador's work was supported by Serène (1952) who also recognised four forms in Vietnam, but applied two species' names to different "morphotypes". However, the most recent revisionary work to be widely accepted was that of Stephenson & Campbell (1960), who felt that available evidence could only support the acceptance of a single species, *Scylla serrata*. Holthuis (1978) followed Stephenson and Campbell, pointing out the inconsistent and variable nature of the distinguishing characters. He also questioned the validity of the names used by Estampador and Serène.

Despite this, a number of recent regional workers have presented convincing arguments for the recognition of two or even three species within their study areas (Joel & Raj, 1980; Radhakrishnan & Samuel, 1982; Oshiro, 1991; Kathirvel & Srinivasagam, 1992; Fuseya & Watanabe, 1996; Overton et al., 1997). However, as pointed out by Fuseya & Watanabe (1995), it was still not clear whether *Scylla* consists of four species/subspecies, three species, or one species, and because of the importance of this aspect to other mud crab research, further hereditary or genetic work is necessary. An understanding of the taxonomy of *Scylla* populations throughout the Indo-Pacific is central to the development of a more successful aquaculture industry based on the mud crab, as well as improved wild-stock management of the different types. The uncertainty of genetic relationships is recognised as one of the primary constraints to the management of the wild fishery and development of aquaculture. This was recognised at the Regional Seminar on Mud Crab Culture and Trade in the Bay of Bengal Region in Surat Thani, Thailand in November 1991 (Infotish, 1992) and the need for such work was also addressed by Brown (1993).

Our research has endeavoured to resolve this confusion by collecting material from the Red Sea (the original type locality of *Scylla serrata*), and also from as many other locations as possible throughout the Indo-Pacific. We used two genetic methods, both allozyme electrophoresis (Keenan, 1996; in press) and mtDNA sequencing of cytochrome oxidase I (COI) and 16s RNA genes (Keenan & Lavery, in prep.), to unravel the problem.

Genetic data from our work (Keenan et al., 1995; Keenan, 1996; Keenan, in press; Keenan & Lavery, in prep.) show that there are at least four distinct species of mud crabs, with little evidence of hybridization despite being sympatric in many areas. This conclusion is supported by several recent independent studies. Fuseya & Watanabe (1996) and Watanabe & Fuseya (1997) determined using allozyme electrophoresis that three species of mud crab are present in the South China Sea. Sugama & Harianto (in press), also using allozyme electrophoresis, found three species in Indonesian waters. Examination of these independent studies show that they have in total covered the four species that we define in this paper.

To complete our study, we employed the knowledge gained from the genetic data to group the specimens into species groups, and morphometric data was analysed by discriminant

function analysis to produce an hierarchy of identifying characteristics for each species. Finally, available type specimens were examined and lectotypes and neotypes designated where necessary, to resolve the nomenclatural confusion. Synonymies are not intended to be complete. The confusion has been such that we felt that it was impossible to meaningfully attribute the majority of references to a particular species, although when a good illustration has been provided this has sometimes been done. It was considered most important to provide a sound nomenclatural and taxonomic base for the growing interest in the biology and aquaculture of this commercially important group.

With our new knowledge of the genetic relationships of mud crabs it now appears that Estampador (1949a,b) was correct in recognising four distinct groupings of mud crabs (after careful work on colour patterns, relative size, cheliped spination, chromosome 'form', and the process of gamete development). However, without reference to the type material he was not able to identify correctly *Scylla serrata*, and therefore his nomenclatural decisions were incorrect. Many authors subsequently followed Estampador's decisions, but others made their own interpretations of the taxonomy. Through examination of remaining type material and erection of neotypes where necessary, we have attempted to stabilise the nomenclature for all future workers.

#### *Abbreviations*

QM - Queensland Museum, Brisbane; MNHN - Museum National d'Histoire Naturelle, Paris; ZMUC - Zoological Museum, University of Copenhagen; ZRC - Zoological Reference Collection, National University of Singapore.

## MATERIAL AND METHODS

**Summary of genetic investigations.** - Genetic methods were used to first assess the species status of mud crabs from throughout the range of *Scylla*. Two independent techniques, allozyme electrophoresis and mitochondrial (mt) DNA sequencing were used to assess the genetic differences between crab specimens, and to determine the nature of relationships. Genetic methods can be used to resolve morphological taxonomy because breeding relationships and the absence of gene flow, indicating species level differences, can be quantified. Conclusions about breeding structure, based on the sharing or non-sharing of alleles, are more definitive than those based on morphology. Such conclusions can be used to derive morphological information, based on the known "biological" species, to enable visual identification of the different genetically defined morphs.

The allozyme electrophoresis and DNA studies are the basis for several papers (Keenan et al., 1995; Keenan et al., 1996; Keenan, 1996; Keenan, in press; Keenan & Lavery, in prep.), and will not be fully discussed here. The allozyme electrophoretic studies examined 36 protein coding loci and yielded species-specific expression of alleles at several diagnostic loci, summarised in Table 1. The absence of heterozygotes (i.e. hybrids) between the different species, for the protein coding loci where fixed differences were observed, provides evidence that there is no natural genetic exchange between them. As no heterozygotes were found between these "morphs" in sympatric samples, as defined on the basis of fixed genetic differences, then there is strong evidence that speciation has developed to a stage where hybridisation can no longer occur and that the "morphs" constitute "species". To further examine this conclusion, mitochondrial DNA sequences from selected samples were obtained (Keenan, in press; Keenan & Lavery, in prep). Unweighted pair-group [clustering] method

Table 1. Species-discriminating loci for the different species of mud crab, genus *Scylla*. TM (Shaw & Prasad, 1970), EBT & TRIC (Shaklee & Keenan, 1986) gel buffer systems.

Locus, EC#, buffer	allele mobilities for each species			
	(two alleles indicate polymorphism, most common allele listed first)			
	<i>S. serrata</i>	<i>S. tranquebarica</i>	<i>S. paramamosain</i>	<i>S. olivacea</i>
alcohol dehydrogenase EC# 1.1.1.1, EBT	100	75	75	75, 100
alanine aminotransferase EC# 2.6.1.2, TM	100	95	100	95
arginine kinase EC# 2.7.3.3, TM	100	75	75	75, 100
mannose-6-phosphate isomerase EC# 5.3.1.8, EBT	100, 103	100	100	95, 90
phosphoglucomutase EC# 5.4.2.2, TRIC	100	107	100	85

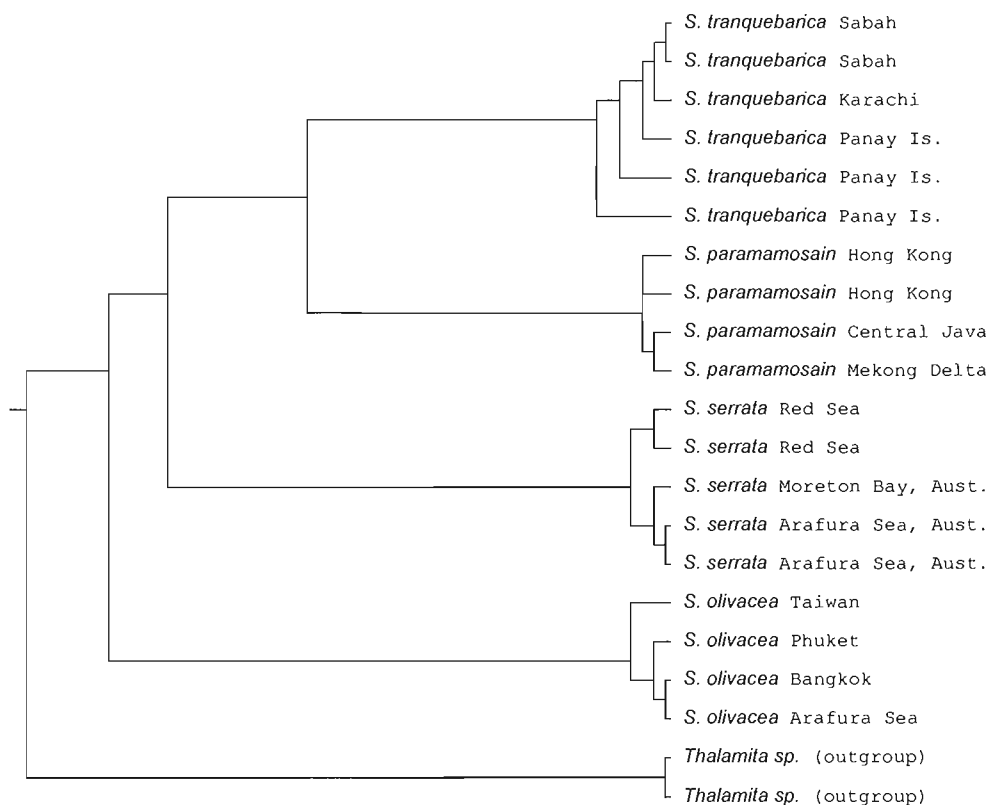


Fig. 1. UPGMA clustering of geographically isolated specimens from four species of mud crabs and an outgroup species based on the pairwise number of nucleotide differences for the 16S RNA subunit sequence of mtDNA (483 bases).

using arithmetic averages (UPGMA) (Sneath & Sokal 1973) analysis of pairwise codon differences in mitochondrial DNA sequences has been used to illustrate within and between species relationships for the 16S ribosomal RNA subunit (Fig. 1) and the cytochrome oxidase subunit I (COI) genes (Fig. 2). These figures clearly show that samples obtained from within a species, over a wide geographic range, show less than 2% sequence difference compared with between species sequence differences of greater than 8%. This provides additional conclusive evidence that there are at least four distinct species of mud crab.

**Morphometrics.** - Morphologically defining characters for each species were determined by discriminant function analysis (DFA) using the genetically defined groups, analogous to the work of Bratley (1995). Morphological data were collected from 253 crab samples taken from throughout the Indo-Pacific, for which genetic information was available. For DFA, 168 adult crabs with an internal carapace width (ICW) of 95 mm were used. This resulted in a sufficient representative sample of each species being obtained, without the confounding

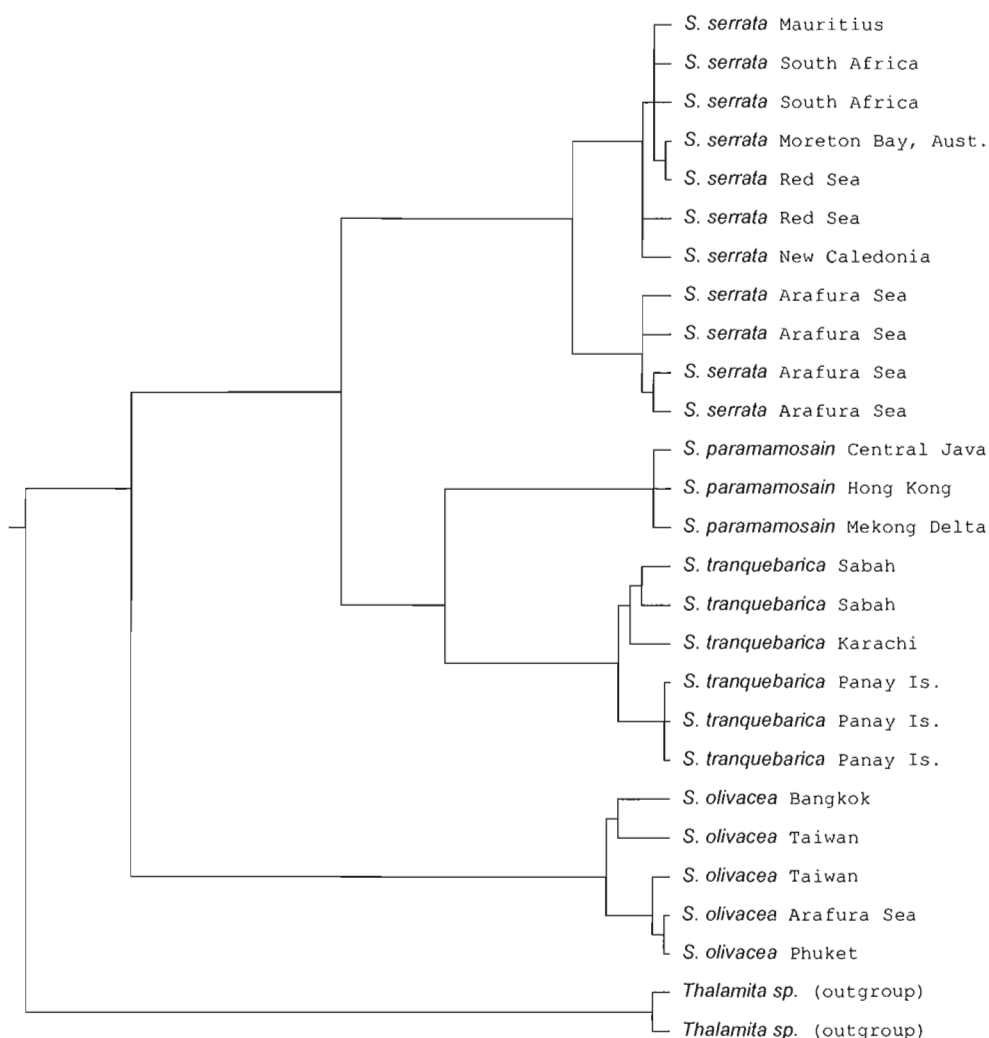


Fig. 2. UPGMA clustering of geographically isolated specimens from four species of mud crabs and an outgroup species based on the pairwise number of nucleotide differences for the COI mtDNA gene sequence (594 bases).

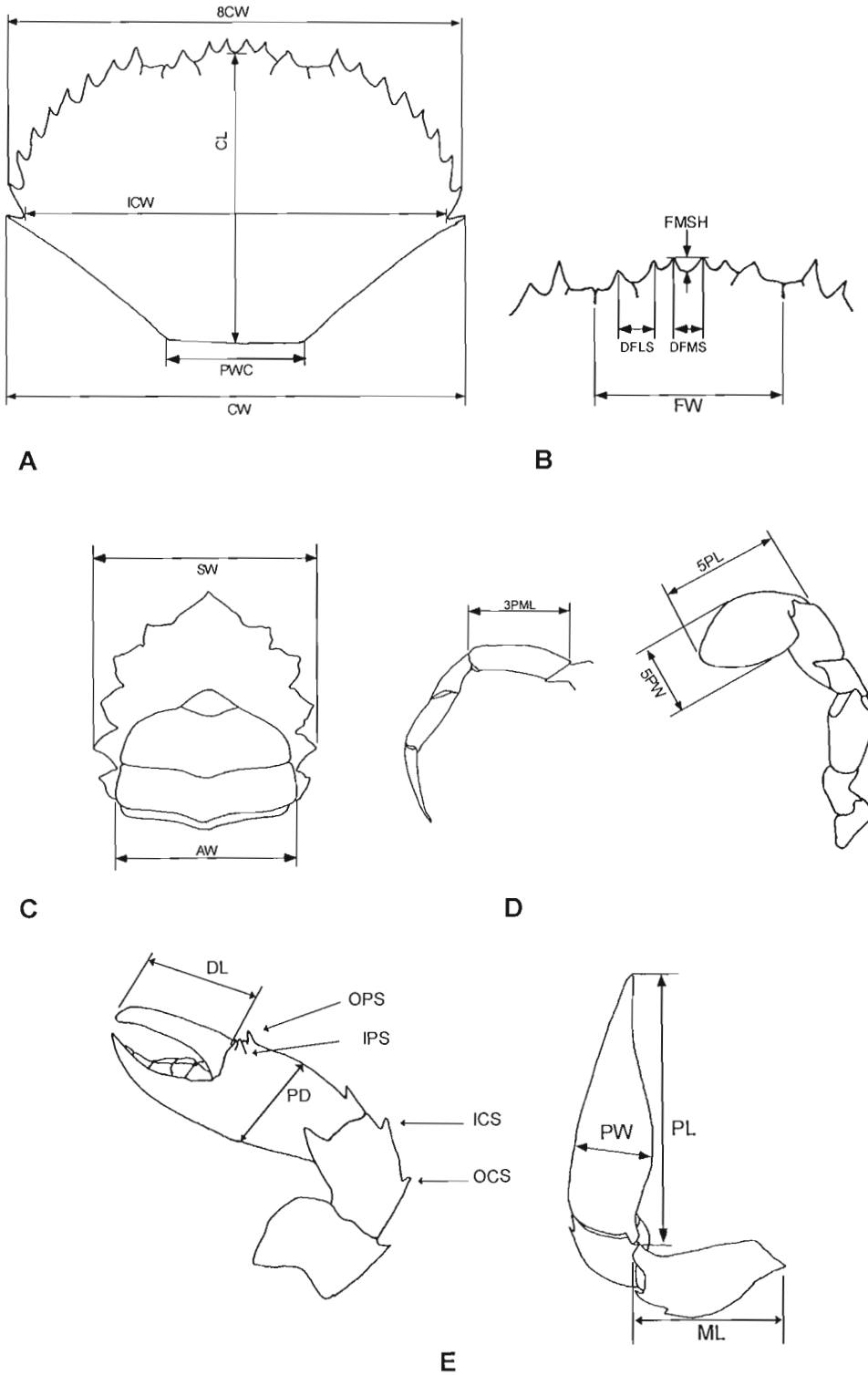


Fig. 3. Measurements taken from; (A) carapace, (B) frontal lobe, (C) sternum, (D) periopods and (E) chelipeds.

influence of juvenile ontogenetic changes. Oshiro (1991) mentions that species differences in frontal spines ("rostrum") are only recognisable in crabs greater than 8 cms carapace width.

Apart from recording the sex of the specimens, 24 measurements were taken with digital calipers to the nearest 0.1 mm. Diagrams of the positions of the measurement points are presented in Fig. 3 (A-E). Many of the crabs had broken or missing appendages and spines — these were recorded as missing data. The characters were size standardised through the creation of 27 ratios, some of which are often used in describing morphological variation of *Scylla*. Details of the calculation of these ratios are provided in Table 2.

Stepwise discriminant function analyses (StatSoft Inc., 1996) were conducted to determine the characters that best discriminate the four genetically recognised species. Each specimen was assigned to its species group based on its allozyme characters (Keenan, 1996; in press). Missing values were substituted by group means. An F-value of 3.0, which approximately represents the 0.05 significance level for the number of samples examined, was used as the minimum F value for variables to enter the model.

Table 2. Size standardised mud crab morphometric data used for discriminant function analysis.

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**A. Carapace data**

1. 9th Lateral spine height (LSH) / Internal carapace width (ICW)  
where  $LSH = (CW - ICW) / 2$
2. Carapace width (CW) / Carapace width at spine 8 (8CW)
3. Carapace length (CL) / Internal carapace width (ICW)
4. Posterior width of carapace (PWC) / Internal carapace width (ICW)
5. Carapace frontal width (FW) / Internal carapace width (ICW)
6. Posterior width of carapace (PWC) / Frontal width (FW)
7. Frontal median spine height (FMSH) / Frontal width (FW)
8. Frontal median spine height (FMSH) / Distance between frontal median spines (DFMS)
9. Distance between frontal median spines (DFMS) / Frontal width (FW)
10. Distance between frontal lateral spines (DFLS) / Frontal width (FW)
11. Distance between frontal median spines (DFMS) / Distance between frontal lateral spines (DFLS)
12. Sternum width (SW) / Internal carapace width (ICW)
13. Abdomen width (AW) / Sternum width (SW)

**B. Cheliped data**

14. Propodus length (PL) / Internal carapace width (ICW)
15. Dactyl length (DL) / Propodus length (PL)
16. Propodus width (PW) / Propodus length (PL)
17. Propodus depth (PD) / Propodus length (PL)
18. Propodus width \* Propodus depth ( $PW*PD*0.7854$ ) / Propodus length (PL)
19. Inner propodus spine (IPS) / Propodus length (PL)                      0 = no spine
20. Outer propodus spine (OPS) / Propodus length (PL)
21. Inner propodus spine (IPS) / Outer propodus spine (OPS)
22. Inner carpus spine (ICS) / Propodus length (PL)
23. Outer carpus spine (OCS) / Propodus length (PL)
24. Inner carpus spine (ICS) / Outer carpus spine (OCS)
25. Merus length (ML) / Propodus length (PL)

**C. Periopod data**

26. 5th periopod dactyl width (5PW) / 5th periopod dactyl length (5PL)
  27. 3rd periopod merus length (3PML) / Internal carapace width (ICW)
-



Figure 4 (A)

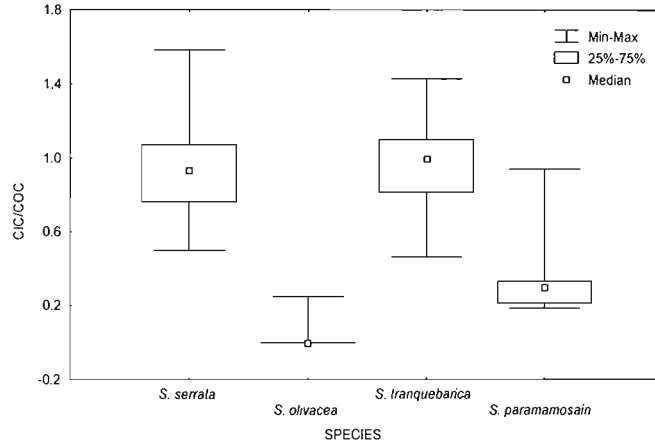


Figure 4 (B)

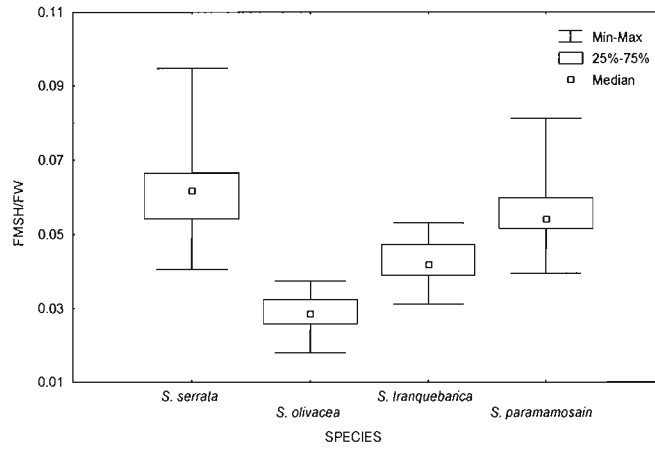


Figure 4 (C)

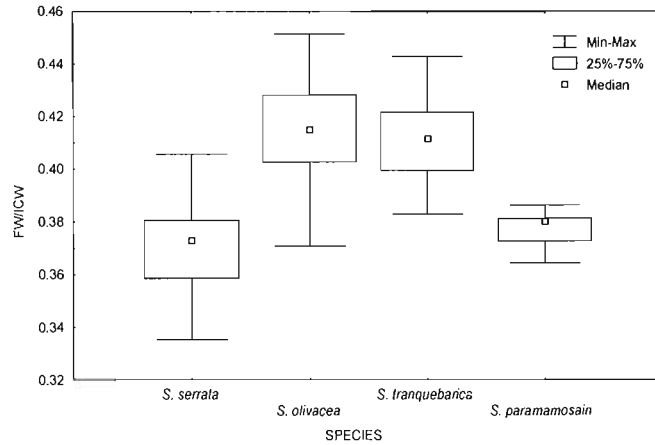


Fig. 4. Graph of median, quartiles and range for the three ratios with the highest species discrimination: (A) ICS/OCS; (B) FMSH/FW; (C) FW/ICW.

RESULTS

Examination of the morphological data for the four *Scylla* species revealed that several characters displayed distinct differences with no overlap in the range of observations between some species-pairs e.g. ICS/OCS and FMSH/FW for *S. serrata* and *S. olivacea* (Table 3, Fig. 4A, B). However there was no single character that provided clearly discriminating information between all four species.

Forward stepwise discriminant function analysis produced three significant discriminant functions, incorporating 16 characters, which together provided 100% discrimination between the four species. The separation of specimens achieved, according to their score on each of the 3 discriminant function roots, is illustrated in Fig. 5 (A, B). Three ratios contributed most to discrimination among species: ICS/OCS, FMSH/FW and FW/ICW (F-remove =

Figure 5 (A)

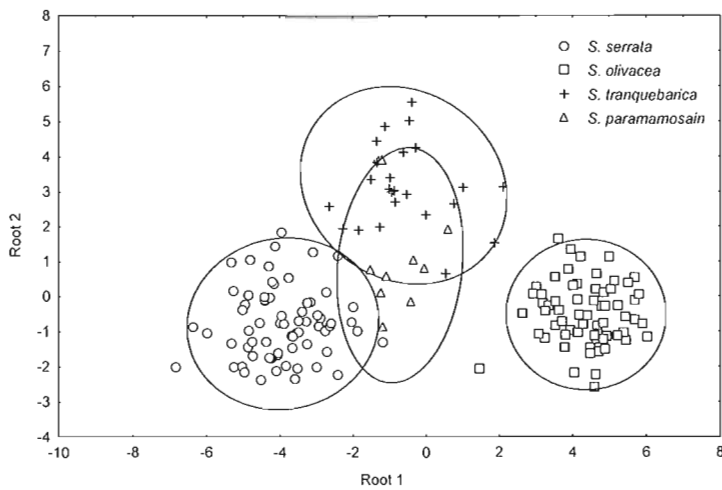


Figure 5 (B)

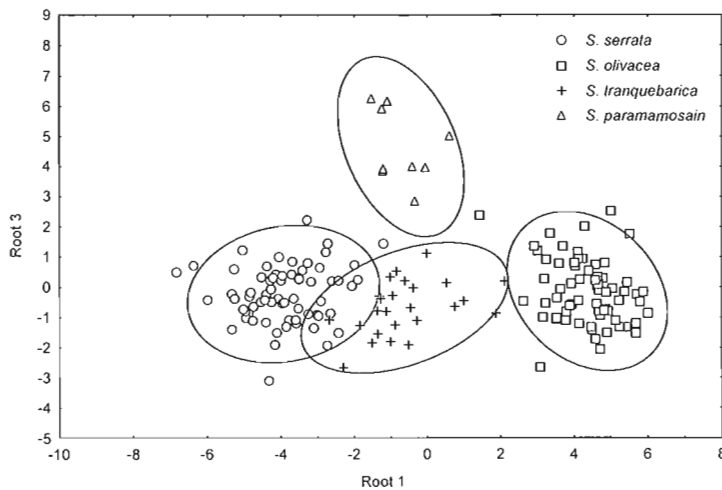


Fig. 5. Graphs of individual discriminant function scores with superimposed 95% confidence ellipses around each species centroid: (A) DFA Root 1 vs Root 2; (B) DFA Root 1 vs Root 3.

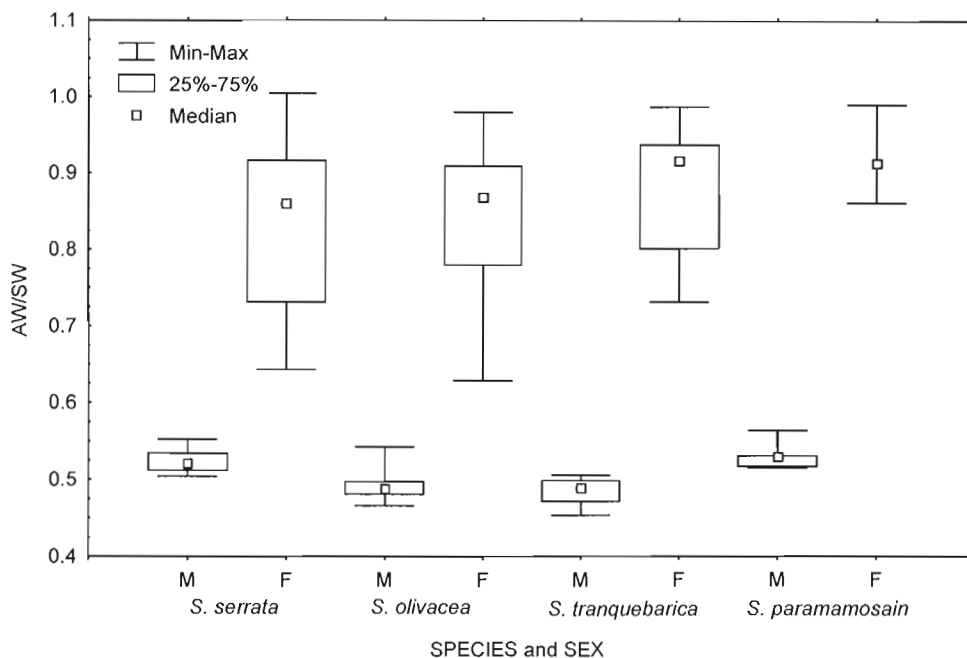


Fig. 6. Graph of median, 75% & 25% quartiles and range for the ratio AW/SW, grouped by species and sex.

54.4, 38.3 and 47.0 respectively, all  $P < 0.0001$ ). If only these three characters were included in the model there was 94.05% discrimination between the four species. Inclusion of the remaining 13 ratios increased the discrimination power by decreasing amounts. Many variables showed a degree of overlap between species and also a degree of sexual dimorphism.

A similar analysis was conducted using sex as the grouping factor (across all species). Variables that were significant in this model were the ones that displayed the greatest amount of sexual dimorphism. Surprisingly, several ratios showing sex based differences were also included in the species' model, AW/SW, PW\*PD/PL and IPS/PL. The AW/SW ratio contributed the most to discrimination between sexes ( $F=441.6$ ,  $P < 0.0001$ ) (Fig. 6).

The most useful characters to distinguish between species were determined by comparing results from forward and backward DFA. Seven characters appeared in both analyses; Inner carpus spine (ICS) / Outer carpus spine (OCS), Frontal median spine height (FMSH) / Frontal width (FW), Carapace frontal width (FW) / Internal carapace width (ICW), Merus length (ML) / Propodus length (PL), Abdomen width (AW) / Sternum width (SW), Propodus length (PL) / Internal carapace width (ICW), and Inner propodus spine (IPS) / Propodus length (PL). Data for these characters are presented in Table 3.

Likewise, the characters that best described sexual differences and tended to confuse species differences are: Abdomen width (AW) / Sternum width (SW), Posterior width of carapace (PWC) / Internal carapace width (ICW), Propodus width \* Propodus depth (PW\*PD\*0.7854) / Propodus length (PL), Inner propodus spine (IPS) / Propodus length (PL), Sternum width (SW) / Internal carapace width (ICW).

Table 3. Means, ( $\pm$ SD) and ranges of 2 morphometric characters and 27 ratios for four species of mud crab over 95 mm ICW collected from throughout the Indo-Pacific oceans. Data are based on N specimens of each species for each character.

#	Ratio	<i>S. serrata</i>			<i>S. tranquebarica</i>			<i>S. paramamosain</i>			<i>S. olivacea</i>		
		N	Mean $\pm$ SD	Range	N	Mean $\pm$ SD	Range	N	Mean $\pm$ SD	Range	N	Mean $\pm$ SD	Range
	CW (mm)	60	147.3 $\pm$ 25.0	102.4-204.4	24	120.8 $\pm$ 12.3	102.5-143.8	9	122.5 $\pm$ 10.5	111.1-145.7	63	112.2 $\pm$ 10.4	98.8-138.1
	ICW (mm)	68	138.4 $\pm$ 23.2	95.5-191.7	25	113.7 $\pm$ 11.4	97.1-137.8	9	114.7 $\pm$ 9.0	104.8-134.1	66	107.5 $\pm$ 10.1	95.0-133.9
1	LSH/ICW	60	0.031 $\pm$ 0.006	0.018-0.046	24	0.031 $\pm$ 0.006	0.022-0.044	9	0.034 $\pm$ 0.009	0.022-0.049	63	0.022 $\pm$ 0.005	0.015-0.037
2	CW/8CW	57	1.013 $\pm$ 0.009	0.997-1.038	21	1.014 $\pm$ 0.011	0.995-1.042	8	1.028 $\pm$ 0.018	1.010-1.056	62	0.999 $\pm$ 0.011	0.982-1.025
3	CL/ICW	68	0.695 $\pm$ 0.011	0.661-0.721	24	0.695 $\pm$ 0.010	0.680-0.716	8	0.686 $\pm$ 0.010	0.674-0.703	65	0.697 $\pm$ 0.009	0.676-0.715
4	PWC/ICW	65	0.331 $\pm$ 0.018	0.287-0.371	24	0.323 $\pm$ 0.017	0.295-0.355	8	0.339 $\pm$ 0.019	0.312-0.371	63	0.315 $\pm$ 0.016	0.285-0.362
5	FW/ICW	68	0.371 $\pm$ 0.016	0.335-0.406	25	0.412 $\pm$ 0.016	0.383-0.443	9	0.377 $\pm$ 0.007	0.364-0.386	66	0.415 $\pm$ 0.017	0.371-0.451
6	PWC/FW	65	0.892 $\pm$ 0.075	0.724-1.058	24	0.787 $\pm$ 0.064	0.691-0.884	8	0.899 $\pm$ 0.065	0.807-1.003	63	0.762 $\pm$ 0.059	0.671-0.928
7	FMSH/FW	67	0.061 $\pm$ 0.010	0.041-0.095	23	0.043 $\pm$ 0.006	0.031-0.053	9	0.058 $\pm$ 0.012	0.040-0.081	64	0.029 $\pm$ 0.005	0.018-0.037
8	FMSH/DFMS	63	0.418 $\pm$ 0.059	0.254-0.544	23	0.310 $\pm$ 0.042	0.216-0.371	8	0.369 $\pm$ 0.068	0.283-0.483	64	0.221 $\pm$ 0.036	0.143-0.316
9	DFMS/FW	63	0.145 $\pm$ 0.009	0.127-0.165	24	0.139 $\pm$ 0.009	0.123-0.169	8	0.149 $\pm$ 0.011	0.132-0.164	64	0.130 $\pm$ 0.012	0.112-0.165
10	DFLS/FW	67	0.134 $\pm$ 0.006	0.116-0.150	25	0.133 $\pm$ 0.007	0.120-0.147	9	0.136 $\pm$ 0.008	0.119-0.148	65	0.136 $\pm$ 0.008	0.111-0.152
11	DFMS/DFLS	62	1.084 $\pm$ 0.077	0.908-1.244	24	1.047 $\pm$ 0.077	0.924-1.200	8	1.097 $\pm$ 0.093	0.946-1.176	63	0.952 $\pm$ 0.087	0.826-1.172
12	SW/ICW	55	0.525 $\pm$ 0.013	0.500-0.570	25	0.522 $\pm$ 0.012	0.501-0.545	9	0.526 $\pm$ 0.011	0.503-0.546	66	0.531 $\pm$ 0.011	0.499-0.549
13	AW/SW	55	0.705 $\pm$ 0.176	0.504-1.005	25	0.611 $\pm$ 0.194	0.454-0.987	9	0.704 $\pm$ 0.208	0.515-0.991	66	0.576 $\pm$ 0.158	0.466-0.980
14	PL/ICW	60	0.716 $\pm$ 0.084	0.607-0.943	23	0.801 $\pm$ 0.099	0.640-0.954	9	0.747 $\pm$ 0.084	0.644-0.838	62	0.784 $\pm$ 0.078	0.645-0.917
15	DL/PL	57	0.448 $\pm$ 0.013	0.423-0.484	23	0.455 $\pm$ 0.013	0.432-0.480	9	0.473 $\pm$ 0.028	0.435-0.530	61	0.451 $\pm$ 0.020	0.382-0.498
16	PW/PL	60	0.427 $\pm$ 0.022	0.366-0.481	23	0.434 $\pm$ 0.031	0.381-0.488	9	0.442 $\pm$ 0.025	0.403-0.468	62	0.433 $\pm$ 0.039	0.359-0.511
17	PD/PL	60	0.269 $\pm$ 0.012	0.239-0.293	23	0.258 $\pm$ 0.015	0.222-0.284	9	0.280 $\pm$ 0.013	0.251-0.296	62	0.281 $\pm$ 0.021	0.225-0.322
18	PW*PD/PL	60	8.817 $\pm$ 2.207	4.315-13.69	23	8.221 $\pm$ 2.288	4.853-14.061	9	8.415 $\pm$ 1.768	5.922-11.363	62	8.338 $\pm$ 2.606	4.440-14.785
19	IPS/PL	54	0.031 $\pm$ 0.009	0.013-0.047	21	0.030 $\pm$ 0.008	0.017-0.045	9	0.042 $\pm$ 0.013	0.029-0.059	61	0.020 $\pm$ 0.009	0.005-0.045
20	OPS/PL	56	0.019 $\pm$ 0.006	0.009-0.033	22	0.015 $\pm$ 0.006	0.006-0.032	8	0.021 $\pm$ 0.009	0.009-0.031	59	0.006 $\pm$ 0.005	0.000-0.018
21	IPS/OPS	53	1.691 $\pm$ 0.291	0.577-2.278	22	2.107 $\pm$ 0.574	0.926-3.300	8	2.202 $\pm$ 0.501	1.857-3.375	51	3.917 $\pm$ 1.280	1.800-7.500
22	ICS/PL	56	0.020 $\pm$ 0.007	0.007-0.035	23	0.015 $\pm$ 0.006	0.004-0.029	9	0.005 $\pm$ 0.004	0.003-0.014	61	0.000 $\pm$ 0.000	0.000-0.003
23	OCS/PL	57	0.021 $\pm$ 0.006	0.009-0.033	23	0.015 $\pm$ 0.006	0.007-0.033	9	0.014 $\pm$ 0.004	0.010-0.020	61	0.009 $\pm$ 0.005	0.000-0.027
24	ICS/OCS	55	0.940 $\pm$ 0.233	0.500-1.583	24	0.980 $\pm$ 0.251	0.467-1.429	9	0.352 $\pm$ 0.235	0.188-0.941	63	0.006 $\pm$ 0.035	0.000-0.250
25	ML/PL	58	0.456 $\pm$ 0.064	0.338-0.608	22	0.463 $\pm$ 0.054	0.400-0.604	9	0.575 $\pm$ 0.016	0.550-0.604	60	0.459 $\pm$ 0.061	0.389-0.622
26	SPW/SPL	51	0.620 $\pm$ 0.027	0.541-0.682	18	0.627 $\pm$ 0.021	0.585-0.660	6	0.593 $\pm$ 0.038	0.549-0.637	53	0.608 $\pm$ 0.021	0.545-0.648
27	3PML/ICW	47	0.375 $\pm$ 0.037	0.303-0.449	11	0.421 $\pm$ 0.025	0.381-0.450	7	0.395 $\pm$ 0.034	0.357-0.430	54	0.427 $\pm$ 0.036	0.343-0.487

## TAXONOMY

### Genus *Scylla* de Haan, 1833

*Scylla* de Haan, 1833: 11; Milne Edwards, 1861: 347; Alcock, 1899: 27; Stephenson & Campbell, 1960: 111; Crosnier, 1962: 71.

**Type species.** - *Cancer serratus* Forskål, 1775, designated by Rathbun, 1922. Gender feminine.

**Diagnosis.** - Carapace oval, wider than long (CL/ICW range 0.66-0.72); moderately convex, surface smooth, gastro-cardiac grooves poorly to moderately well defined; front clearly separated from supra-orbital angles, divided into four teeth ranging from low rounded lobes to prominent sharp spines, frontal width variable between species (FW/ICW range 0.33-0.45); anterolateral margins convex, bearing nine similar-sized teeth, longer than smooth posterolateral margins; supra-orbital margin with closed median and outer fissures; infra-orbital margins prominently toothed; antennules folded nearly transversely; basal antennal article produced into the orbit, flagellum lying in the orbital hiatus. Chelipeds massive, smooth, longer than legs; merus with three large spines on anterior border, two smaller spines on posterior border; carpus with acute tooth at inner angle, 1-2 spines on outer margin varying from strong to obsolete; propodus with strong spine at carpal articulation, a pair of dorsal spines above base of dactyl varying from strong to obsolete, inner face with a large tubercle immediately behind base of gape. Legs stout, moderately compressed, first three pairs similar, fourth pair natatorial. Male abdomen narrow, segments 3-5 fused; female abdomen broadly oval. Colour variable, with or without polygonal patterning.

### *Scylla serrata* (Forskål, 1775)

(Figs. 7A, 8A, 9A, 10)

*Cancer serratus* Forskål, 1775: 90.

*Portunus serratus* - Rüppell, 1830: 10, pl. 2.

*Achelous crassimanus* MacLeay, 1838: 61; Stebbing, 1910: 308.

*Portunus (Scylla) serratus* - De Haan, 1833: 44.

*Scylla tranquebarica* var. *oceanica* Dana, 1852: 270.

*Scylla oceanica* - Estampador, 1949a: 101-102, pl. 1, fig. 2.

*Scylla serrata* - Barnard, 1950: 160-161, fig. 31b,c; Crosnier, 1962: 72-73, figs 128,129; Guinot, 1967: pl 1, fig. 1; Melo, 1983: 159-167, figs1-3.

*Scylla serrata* var. *paramamosain* - Serène, 1952: 1-5, fig. 1D, pl. I(4), pl. II(4&D).

*Scylla tranquebarica* - Joel & Raj, 1980: 39-50, figs 1, 3, 5, 7, 9a, b.

**Material examined.** - Neotype - *Cancer serratus* Forskål, 1775: (QM W20917), Male (153.0 mm CW), central coast of Yemen, Red Sea, Sep.1993, J. Thoroughgood.

Neotype - *Achelous crassimanus* MacLeay, 1838: (QM W21553), Male (141.7 mm CW), Richard's Bay, South Africa, Jan.1996, R. McGeer.

Neotype - *Scylla tranquebarica* var. *oceanica* Dana, 1852: (QM W21555), Female (130.9 mm CW), Western Samoa, Jun.1996, M. King.

Other material - female (149.4 mm) (QM W21554), Richard's Bay, South Africa, coll. R. McGeer, Jan.1996; male (143.6 mm) (SAM unreg), Richard's Bay, South Africa, coll. R. McGeer, Jan.1996; female (149.4 mm) (QM W20882), Mauritius, coll. M. Munbodh, Aug.1994; male (132.0 mm) (QM W20875), Mauritius, coll. M. Munbodh, Aug.1994; male (125.5 mm) (QM W20886), Red Sea, coll. J. Thoroughgood, Sept.1993; female (125.9 mm) (QM W20874), Red Sea, coll. J. Thoroughgood, Sept.1993; male (96.3 mm) (QM W20885), Okinawa, Japan, coll. N. Shikatani, Feb.1994; female (116.7 mm) (QM W20878), Okinawa, Japan, coll. N. Shikatani, Feb.1994; male (ZRC 1998.377),

Tunkang, Kaohsiung, southern Taiwan, coll. P. Ng, May 1997; male (128.4 mm) (QM W20879), Panay Is., Philippines, coll. A. Marasigan, Feb. 1994; female (185.9 mm) (QM W20881), Solomon Islands, coll. J. Bell, June 1994; male (152.9 mm) (QM W20873), Solomon Islands, coll. J. Bell, June 1994; female (126.0 mm) (QM W21556), Western Samoa, coll. M. King, June 1996; male (139.5 mm) (QM W21557), Western Samoa, coll. M. King, June 1996; male (167.0 mm) (QM W21558), Western Samoa, coll. M. King, June 1996; male (129.5 mm) (QM W20877), Fiji, coll. K. Swamy, Sept. 1993; female (104.4 mm) (QM W20883), Fiji, coll. K. Swamy, Sept. 1993; male (152.1 mm) (QM W20884), New Caledonia, coll. T. Lewis, Aug. 1994; female (157.2 mm) (QM W20876), New Caledonia, coll. T. Lewis, Aug. 1994; female (182.7 mm) (QM W20880), Moreton Bay, Qld, Australia, coll. L. Serafini, May 1994.

Photograph examined - ZMUC CRU1885, Indian Ocean, coll. D. Daldorff (sometimes cited with the initials "I.K"). Paralectotype of *Portunus tranquebaricus* Fabricius, 1798.

**Diagnosis.** - Frontal lobe spines high (mean height c. 0.06 times frontal width measured between medial orbital sutures), bluntly pointed with tendency to concave margins and rounded interspaces. Anterolateral carapace spines narrow, with outer margin straight or slightly concave. Carpus of chelipeds with two obvious spines on distal half of outer margin, palm of cheliped with a pair of distinct spines on dorsal margin behind insertion of the dactyl. Chelipeds and legs all with polygonal patterning for both sexes and on abdomen of female only. Male first gonopod as in Fig. 9A. Colour variable from purple through green to brown/black depending on habitat. Means and standard deviations of the most important morphological ratios for species discrimination are presented in Table 4.

**Remarks.** - *Scylla serrata* can be separated from its congeners using the characters presented in Tables 4 and 5, and Figs 7 and 8.

Forskål (1775) described *Cancer serratus* from material collected from Jiddah on the Red Sea. The type specimen was destined for Denmark along with a large number of other animals collected during the Danish "Arabia Felix" expedition. Although a significant part of this collection did reach Copenhagen Zoological Museum (Nielsen 1993, Wolff 1994), the specimen of *Cancer serratus* has never been located and is considered lost. The lack of a type specimen has caused much confusion, and therefore we here designate a neotype male (QM W20917) collected from near the type locality.

*Achelous crassimanus* MacLeay, 1838, has for a very long time been considered a junior synonym of *Scylla serrata*. As Barnard (1950: 161) states "MacLeay's species is obviously the common *serrata*, as there is no other crab in South African waters of the size given by him". The type has not been found in the collections of the MacLeay Museum, University of Sydney (Griffin & Stanbury, 1970), now transferred to the Australian Museum, and can be considered lost. To remove any doubt as to the identity of this species we have erected a neotype for *Achelous crassimanus* using a specimen (QM W21553) from South Africa we consider conspecific with *S. serrata*.

Table 4. Means and standard deviations of the three most useful morphological ratios for discriminating between the four species of mud crab.

Species	ICS/OCS	FMSH/FW	FW/ICW
<i>S. serrata</i>	0.940 ± 0.233	0.061 ± 0.010	0.371 ± 0.016
<i>S. tranquebarica</i>	0.980 ± 0.251	0.043 ± 0.006	0.412 ± 0.016
<i>S. paramamosain</i>	0.352 ± 0.235	0.058 ± 0.012	0.377 ± 0.007
<i>S. olivacea</i>	0.006 ± 0.035	0.029 ± 0.005	0.415 ± 0.017

*Scylla tranquebarica* var. *oceanica* Dana, 1852, was elevated to full species rank by Estampador (1949a), and following his work *Scylla oceanica* has been used widely as an available name for a species distinct from *S. serrata*. Dana (1852) tentatively proposed his name for a specimen obtained from the Navigator Islands (Western Samoa). We treat it here as a junior synonym of *S. serrata* because no other species to our knowledge has such a wide easterly distribution into the Pacific Ocean, and the remarks and figures given by Dana (1852) are insufficient to distinguish his specimens from true *Scylla serrata*. We here designate a female (QM W21555) collected from the type locality as the neotype, and identify it as being conspecific with *S. serrata*.

**Habitat.** - Associated with mangrove forests inundated with full salinity oceanic water for the greater part of the year. Can tolerate reduced salinity.

**Distribution.** - Samples have been positively identified for this study from a wide range of locations in the Indo-West Pacific. Indian Ocean: Red Sea; Richard's Bay, South Africa; Mauritius; Broome, Western Australia; the Arafura Sea; Darwin, Northern Territory; Gulf of Carpentaria; and Kupang, Timor, Indonesia. From the Pacific Ocean: Fiji; Solomon Islands; New Caledonia; Western Samoa; Panay Is., Philippines; Okinawa, Japan; southern Taiwan; and the east coast of Australia.

This is the most widespread *Scylla* species. It occurs naturally throughout the Indo-Pacific, from South Africa to Tahiti, north to Okinawa, and south to Port Hacking in Australia, and the Bay of Islands, New Zealand (McLay, 1988). There is also a report of the species from the South Atlantic Ocean off Brazil (Melo, 1983), although there is no evidence that it has viable populations there.

### *Scylla tranquebarica* (Fabricius, 1798)

(Figs. 7B, 8B, 9B, 11)

*Portunus tranquebaricus* Fabricius, 1798: 366.

*Lupa lobifrons* H. Milne Edwards, 1834: 453.

*Scylla tranquebarica* - Estampador, 1949a: 103, pl. 3, fig. 1; Serène, 1952: 1-5, fig. 1B, plate I(2), plate II(2&B).

**Material examined.** - Lectotype - *Portunus tranquebaricus* Fabricius, 1798: female (ZMUC CRU1881), Indian Ocean, presumably Tranquebar, S.E. India, coll. D. Daldorff. (Fig. 12).

Lectotype - *Lupa lobifrons* H. Milne Edwards, 1834: male (MNHN B1085 S). Paralectotype - *Lupa lobifrons* H. Milne Edwards, 1834: male (MNHN B1087 S).

Other material. - male (137.5 mm) (QM W20902), Karachi, Pakistan, coll. T. Burton, Aug. 1993; female (135.0 mm) (QM W20911), Karachi, Pakistan, coll. T. Burton, Aug. 1993; male (143.3 mm) (QM W20909), Karachi, Pakistan, coll. T. Burton, Aug. 1993; male (113.3 mm) (QM W20903), Sabah, Malaysia, coll. J. Peng, Apr. 1994; female (114.8 mm) (QM W20901), Sabah, Malaysia, coll. J. Peng, Apr. 1994; female (97.1 mm) (QM W20906), Bako, Malaysia, coll. J. Peng, Mar. 1994; female (127.9 mm) (QM W20912), Bako, Malaysia, coll. J. Peng, Mar. 1994; male (ZRC 1998.376), Tunkang, Kaohsiung, southern Taiwan, coll. P. Ng, May 1997; female (115.0 mm) (QM W20905), Panay Is., Philippines, coll. A. Marasigan, Feb. 1994; male (117.4 mm) (QM W20913), Panay Is., Philippines, coll. A. Marasigan, Feb. 1994; male (106.3 mm) (QM W20908), Panay Is., Philippines, coll. A. Marasigan, Feb. 1994; male (121.6 mm) (QM W20910), Panay Is., Philippines, coll. A. Marasigan, Feb. 1994; female (118.6 mm) (QM W20907), Panay Is., Philippines, coll. A. Marasigan, Mar. 1994; male (120.5 mm) (QM W20914), Panay Is., Philippines, coll. A. Marasigan, Mar. 1994; male (126.4 mm) (QM W20904), Panay Is., Philippines, coll. A. Marasigan, Mar. 1994.

**Diagnosis.** - Frontal lobe spines of moderate height (mean height c. 0.04 times frontal width measured between medial orbital sutures), blunted with rounded interspaces. Anterolateral carapace spines broad, with outer margin convex. Carpus of chelipeds with two obvious spines on distal half of outer margin, palm of cheliped with a pair of distinct spines on dorsal margin behind insertion of the dactyl. Polygonal patterning weak on chelipeds and first two pairs of legs; last two pairs of legs with stronger patterning for both sexes; patterning variable on abdomen of female, absent on male. Male first gonopod as in Fig. 9B. Colour variable, similar to *Scylla serrata*. Means and standard deviations of the most important morphological ratios for species discrimination are presented in Table 4.

**Remarks.** - *Scylla tranquebarica* can be separated from its congeners using the characters presented in Tables 4 and 5, and Figs 7 and 8. Following our lectotype designation this species corresponds with the *Scylla tranquebarica* of Estampador (1949a) and Serène (1952).

The lectotype (Fig. 12) has been selected from a series of six specimens held in the collection of the Zoological Museum, University of Copenhagen. Four specimens were listed as syntypes of *Portunus tranquebaricus* in the catalogue of Zimsen (1964: 651) under the catalogue number "150". Zimsen noted there were three specimens held at Kiel and one specimen in Copenhagen, however the Kiel specimens have since been transferred to Copenhagen. Dr N. Bruce sent us photographs of all six syntypes, and it is apparent that the collection represents four species. The above female specimen was originally housed in the Kiel collection and it is the unique representative of this species. It was selected in the interests of maintaining nomenclatural stability. The other specimens in the series belong to *S. serrata* (one specimen, ZMUC CRU1885), *S. olivacea* (one specimen, ZMUC CRU1880) and *S. paramamosain* (three specimens, ZMUC CRU1882, 1883, 1884).

The description of *Lupa lobifrons* H. Milne Edwards, 1834, collected from "les Indes orientales" was based on juvenile specimens (lectotype male = 44 x 29 mm). Two dry syntype specimens have been located in the MNHN, Paris; the male (MNHN B1085 S) is in the best condition and is designated the lectotype, the other male (MNHN B1087 S) is thus a paralectotype. Because of their small size it is impossible to be completely certain of their identity. Juveniles of all four species are typically spinous and the characters used to separate the adults are less useful. However, the combination of strong carpal and propodal spines on the chelipeds, and the blunted frontal spines, indicate *Scylla tranquebarica*, and we here identify it as such.

**Habitat.** - Associated with mangrove forests and coastlines inundated with reduced salinity seawater for part of the year. Reported to be found berried within estuaries.

**Distribution.** - A widespread species of *Scylla*, *S. tranquebarica* is commonly found from the South China Sea but also occurs in specific locations around the Indo-Pacific. It is often associated with *S. olivacea*.

Samples have been positively identified for this study from the Indian Ocean: Karachi, Pakistan; Penang, Malaysia. From the Pacific Ocean: Panay Is., Philippines. From the South China Sea: Sarawak, Malaysia; Sabah, Malaysia; Singapore.



***Scylla paramamosain* Estampador, 1949**

(Figs 7C, 8C, 9C, 13)

*Scylla serrata* var. *paramamosain* Estampador, 1949a: 104, pl. 3, fig. 2.

*Scylla oceanica* – Serène 1952: 1-5, fig. 1A, pl. I(1), pl. II(1&A).

*Scylla serrata* – Holthuis 1978: 15-16; Chen, 1989: 352-353, fig. 321.

**Material examined.** - Neotype - *Scylla serrata* var. *paramamosain* Estampador, 1949: male (118.3 mm)(QM W22174), Timbulloko, Central Java, Indonesia, coll. C. Keenan, 3.02.1997.

Other material. - 1 male, 1 female (ZRC 1998.379), Tunkang, Kaohsiung, southern Taiwan, coll. P. Ng, May 1997; male (116.0 mm)(QM W22171), Hong Kong, coll. K.H. Chu, Dec.1996; male (115.4 mm)(QM W22172), Hong Kong, coll. K.H. Chu, Dec.1996; female (129.6 mm)(QM W22173), Hong Kong, coll. K.H. Chu, Dec.1996; 2 females, (ZRC 1996.119-120), Beihai City Markets, southern China, coll. N.K. Ng, 8 Dec.1996; male (120.7 mm)(QM W22160), Tam Giang III Enterprise, Lower Mekong Delta, Vietnam, coll. C. Keenan, 29 Jan.1997; male (85.1 mm)(QM W22161), Tam Giang III Enterprise, Lower Mekong Delta, Vietnam, coll. C. Keenan, 29 Jan.1997; female (117.0 mm)(QM W22162), Tam Giang III Enterprise, Lower Mekong Delta, Vietnam, coll. C. Keenan, 29 Jan.1997; male (145.7 mm)(QM W22166), Ca Mau Markets, Lower Mekong Delta, Vietnam, coll. C. Keenan, 29 Jan.1997; male (90.5 mm)(QM W20887), Vietnam, coll. Le thanh Hung & Nguyen Tac An, 1 Feb.1994; male (95.0 mm)(QM W20916), Vietnam, coll. Le thanh Hung & Nguyen Tac An, 1 Feb.1994; 4 males, 1 female (ZRC 1997.133), Trat Wet Market, Thailand, coll. H.H. Tan, 15 Jan.1997; 2 males, 1 female (ZRC 1996.2626) Pasar Lima Beton (market) Banjarmasin, Sth Kalimantan, coll. H.H. Ng & O. Chia, Jun.1996; male (112.1 mm)(QM W22167), Timbulloko, Central Java, Indonesia, coll. C. Keenan, 3 Feb.1997; female (125.2 mm)(QM W22168), Timbulloko, Central Java, Indonesia, coll. C. Keenan, 3 Feb.1997; female (123.0 mm)(QM W22169), Timbulloko, Central Java, Indonesia, coll. C. Keenan, 3 Feb.1997; male (111.1 mm)(QM W22170), Semarang, Central Java, Indonesia, coll. C. Keenan, May 1996.

Photographs examined. - Three specimens, ZMUC CRU1882, 1883, 1884, Indian Ocean, coll. D. Daldorff. Paralectotypes of *Portunus tranquebaricus* Fabricius, 1798.

**Diagnosis.** - Frontal lobe spines high (mean height c. 0.06 times frontal width measured between medial orbital sutures), typically triangular with straight margins and angular interspaces. Anterolateral carapace spines broad, with outer margin convex. Carpus of chelipeds with one small blunt prominence (spinous in juveniles) ventro-medially on outer margin. On juveniles, reduced second spine may be present dorso-distally. Palm of cheliped with a pair of distinct spines on dorsal margin behind insertion of the dactyl, followed by ridges running posteriorly. Chelipeds and legs with weak polygonal patterning for both sexes. Male first gonopod as in Fig. 9C. Colour varies from purple through green to brown/black depending on habitat. Means and standard deviations of the most important morphological ratios for species discrimination are presented in Table 4.

**Remarks.** - *Scylla paramamosain* can be separated from its congeners using the characters presented in Tables 4 and 5, and Figs 7 and 8.

It appears that no type material is extant for this species and it is unclear whether or not Estampador kept a holotype or syntypes, because no mention is made of his collection being lodged with an institution. His original description is sufficient for us to confidently identify it as part of our revisionary study, but considering the difficulty of species discrimination in this genus (as exemplified by all four species being represented in the syntype series of *Scylla tranquebarica*), we still consider that a neotype designation is required. It is very unlikely that material from Estampador's collection will be found. Dr Peter Ng (in litt.) tried to trace Estampador's material in the Philippines ... "According to his colleagues, his collections (presumably his *Scylla* specimens as well) were bequeathed to the University of

the Philippines, but they are not there. I have searched their invertebrate collections (and their crab lots) but only a few are Estampador's...". Unfortunately we do not have access to topotypic material from the Philippines. We have chosen instead the best available specimen, from near Semarang, Central Java, Indonesia. This species has a broad distribution, and the genetic data clearly show that all the examined specimens are conspecific.

The specimen from Sumba, Indonesia, recorded as *Scylla serrata* by Holthuis (1978) is almost certainly this species. His description states that the specimen was intermediate between Serène's (1952) *S. serrata* (= *S. olivacea*) and *S. tranquebarica*. However, his description of the frontal teeth fits well with our definition of *S. paramamosain*.

**Habitat.** - Associated with shallow denuded coral (reef rubble) in Singapore; shallow subtidal flats and estuarine ponds in Central Java; and in mangrove forests in the Lower Mekong Delta, Vietnam.

**Distribution.** - An abundant species of *Scylla* where it occurs, *S. paramamosain* is known from the continental coast of the South China Sea, south into the Java Sea.

Samples have been positively identified for this study from the South China Sea: Xiamen, China; Hong Kong; Beihai, south China; Kaohsiung, south Taiwan; Labrador Beach, Singapore; and Trat, Cambodia. Also from the Java Sea: Banjarmasin, south Kalimantan; and Central Java, Indonesia.

### *Scylla olivacea* (Herbst, 1796)

(Figs 7D, 8D, 9D, 14)

*Cancer olivaceus* Herbst, 1796: 157, pl.38, fig.3.

*Scylla serrata* - Estampador, 1949a: 99-101, pl. 1, fig. 1; Serène, 1952: 1-5, fig. 1C, pl. I(3), pl. II(3&C); Joel & Raj, 1980: 39-50, figs 2, 4, 6, 8, 10a, b.

**Material examined.** - Neotype - *Cancer olivaceus* Herbst, 1796: male (112.7 mm CW) (QM W20895), Kupang, Indonesia, coll. C. Lee, Jun.1994.

Other material. - female (96.4 mm) (QM W20900), Phuket, Thailand, coll. T. Burton, Aug.1993; male (125.1 mm) (QM W20897), Singapore, coll. P. Davie, Jul.1994; male (111.6 mm) (QM W20890), Kupang, Indonesia, coll. C. Lee, Jun.1994; male (112.7 mm) (QM W20895), Kupang, Indonesia, coll. C. Lee, Jun.1994; male (139.9 mm) (QM W20889), Western Australia, coll. G. Thailuer, Feb.1993; male (132.5 mm) (QM W20891), Western Australia, coll. G. Thailuer, Feb.1993; male (113.9 mm) (QM W20888), Buntal, Sarawak, coll. J. Peng, Mar.1994; male (90.1 mm) (QM W20887), Vietnam, coll. L. Hung, Feb.1994; male (95.0 mm) (QM W20916), Vietnam, coll. L. Hung, Feb.1994; 2 males, (ZRC 1996.117-118), Beihai City Markets, southern China, coll. N.K. Ng, 8 Dec.96; 1 male, 1 female (ZRC 1998.378), Tunkang, Kaohsiung, southern Taiwan, coll. P. Ng, May 1997; female (94.0 mm) (QM W20899), Taiwan, coll. T-Y. Chan, Feb.1994; male (121.2 mm) (QM W20915), Panay Is., Philippines, coll. A. Marasigan, Feb.1994; male (112.7 mm) (QM W20896), Panay Is., Philippines, coll. A. Marasigan, Feb.1994; female (93.3 mm) (QM W20898), Panay Is., Philippines, coll. A. Marasigan, Mar.1994; male (105.3 mm) (QM W20893), Panay Is., Philippines, coll. A. Marasigan, Mar.1994; male (122.7 mm) (QM W20894), Mindanao Is., Philippines, coll. A. Marasigan, Feb.1994.

Photograph examined. - One specimen, ZMUC CRU1880, Indian Ocean, coll. D. Daldorff. Paralectotype of *Portunus tranquebaricus* Fabricius, 1798.

**Diagnosis.** - Frontal lobe spines low (mean height c. 0.03 times frontal width measured between medial orbital sutures), rounded with shallow interspaces. Anterolateral carapace

spines broad, with outer convex. Carpus of chelipeds usually with one small blunt prominence (may be spinous in juveniles) ventro-medially on outer margin; reduced second spine may be present dorso-distally in juveniles and young adults. Palm of cheliped usually with a pair of blunt prominences on dorsal margin behind insertion of the dactyl, inner larger than outer; may be spinous in juveniles and young adults. Chelipeds, legs and abdomen all without obvious polygonal patterning for both sexes. Male first gonopod as in Fig. 9D. Colour varies from red through brown to brown/black depending on habitat. Means and standard deviations of the most important morphological ratios for species discrimination are presented in Table 4.

**Remarks.** - *Scylla olivacea* can be separated from its congeners using the characters presented in Tables 4 and 5, and Figs 7 and 8. This is the species that has most often been identified as *Scylla serrata* by recent workers following the papers of Estampador (1949a) and Serène (1952).

*Scylla olivacea* (Herbst, 1796) has been overlooked as an available name for a *Scylla* species. It was described from “Ostindien” (East Indies) which was considered to extend from the east coast of India to the Indo-Malaysian region. While the description is insufficient to recognise the species, Herbst provided a colour plate (Pl. 38, fig. 3) which clearly shows that the cheliped has no spines on the outer margin of the carpus, or on the disto-dorsal margin of the palm. Further the absence of polygonal patterning, and the rusty-red colour on the legs and claws are also typical of only one species. The frontal spines are more pointed than are normal for this species but the majority of characters support our decision. The Herbst collection is held in the Museum für Naturkunde, Berlin, but as Prof. Dr. H.-E. Gruner has written to us “about half of the material he described is missing since the Museum bought the collection. Unfortunately, I could not find the type specimen of *Cancer olivaceus* Herbst, 1796. I have checked the species list and the collection as well, without success. The type material of this species is lost.” Therefore we here designate a neotype male (QM W20895) collected from Kupang, Indonesia, which can be considered to be within the range of the “Ostindien” type locality.

The syntype series of *Portunus tranquebaricus* Fabricius, 1798, contains one specimen of *Scylla olivacea* (ZMUC CRU1880), collected from the Indian Ocean, by D. Daldorff.

**Habitat.** - Associated with mangrove forests and coastlines inundated with reduced salinity seawater during the wet season. In Australia, distribution is limited to embayments where salinity is reduced e.g. Albatross Bay, off Weipa, north-western Queensland, and King Sound, Derby, Western Australia.

**Distribution.** - Samples have been positively identified for this study from the Indian Ocean: King Sound, Western Australia; Phuket, Thailand; Karachi, Pakistan. From the Pacific Ocean: Panay Is., Mindanao Is., Negros Is., Philippines; From the South China Sea: Bangkok, Thailand; Singapore; Vietnam; Sarawak, Malaysia; Beihai, southern China; Kaohsiung, southern Taiwan. From the Arafura Sea: Kupang, Timor, Indonesia; Weipa, Gulf of Carpentaria.

A moderately widespread species of *Scylla*, *S. olivacea* is commonly found from the South China Sea, but also occurs in specific locations across the Indo-West Pacific. It is often associated with *S. tranquebarica*.

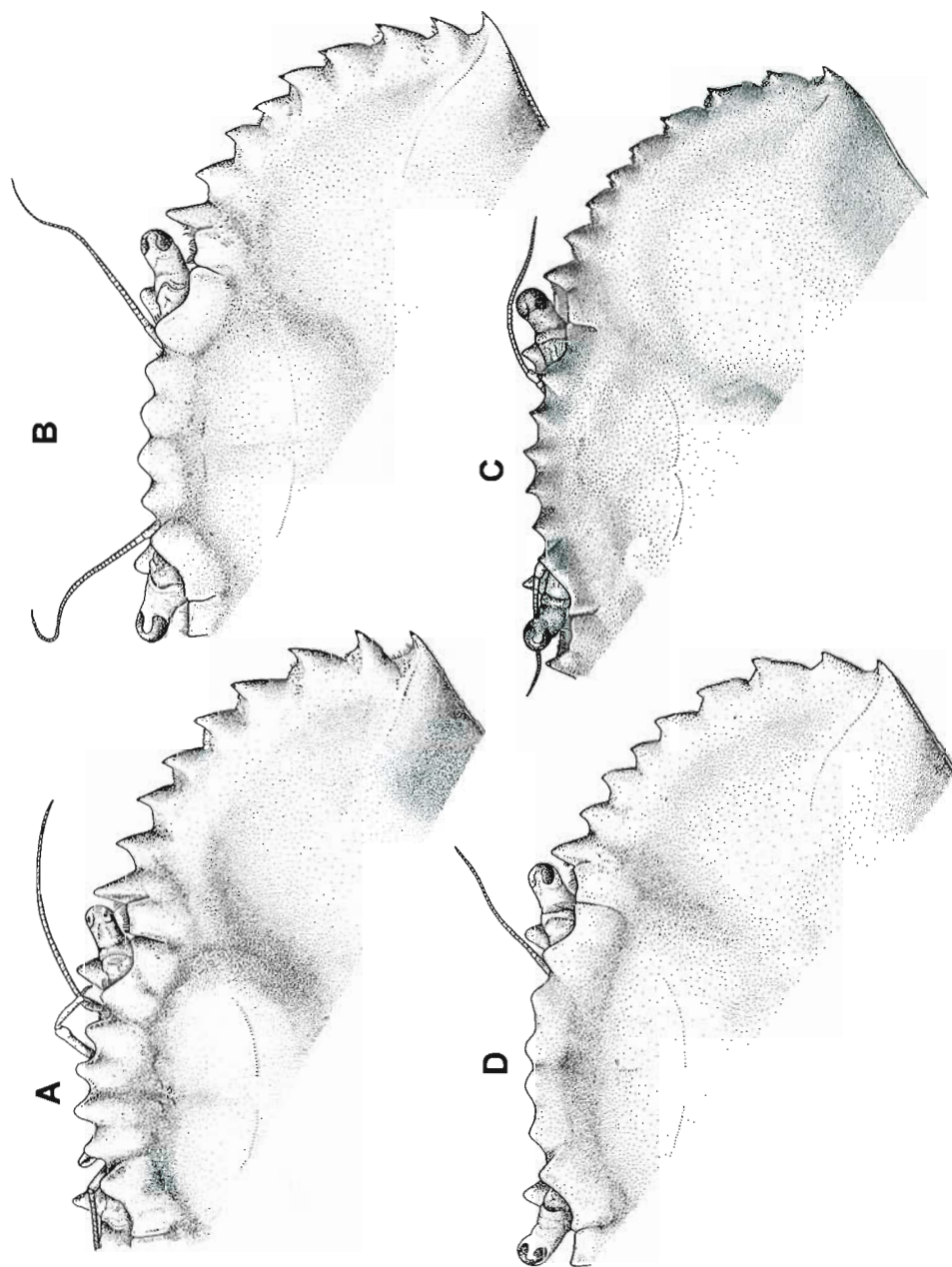


Fig. 7. Drawings of part carapace of *Scylla* species showing diagnostic taxonomic features: (A) *S. serrata* - QM W20917, male, 153.0 mm CW; (B) *S. iraniuebarica* - QM W20914, male, 120.5 mm CW; (C) *S. paramamosain* - QM W22174, male, 118.3 mm CW; (D) *S. olivacea* - QM W20895, male, 112.7 CW.

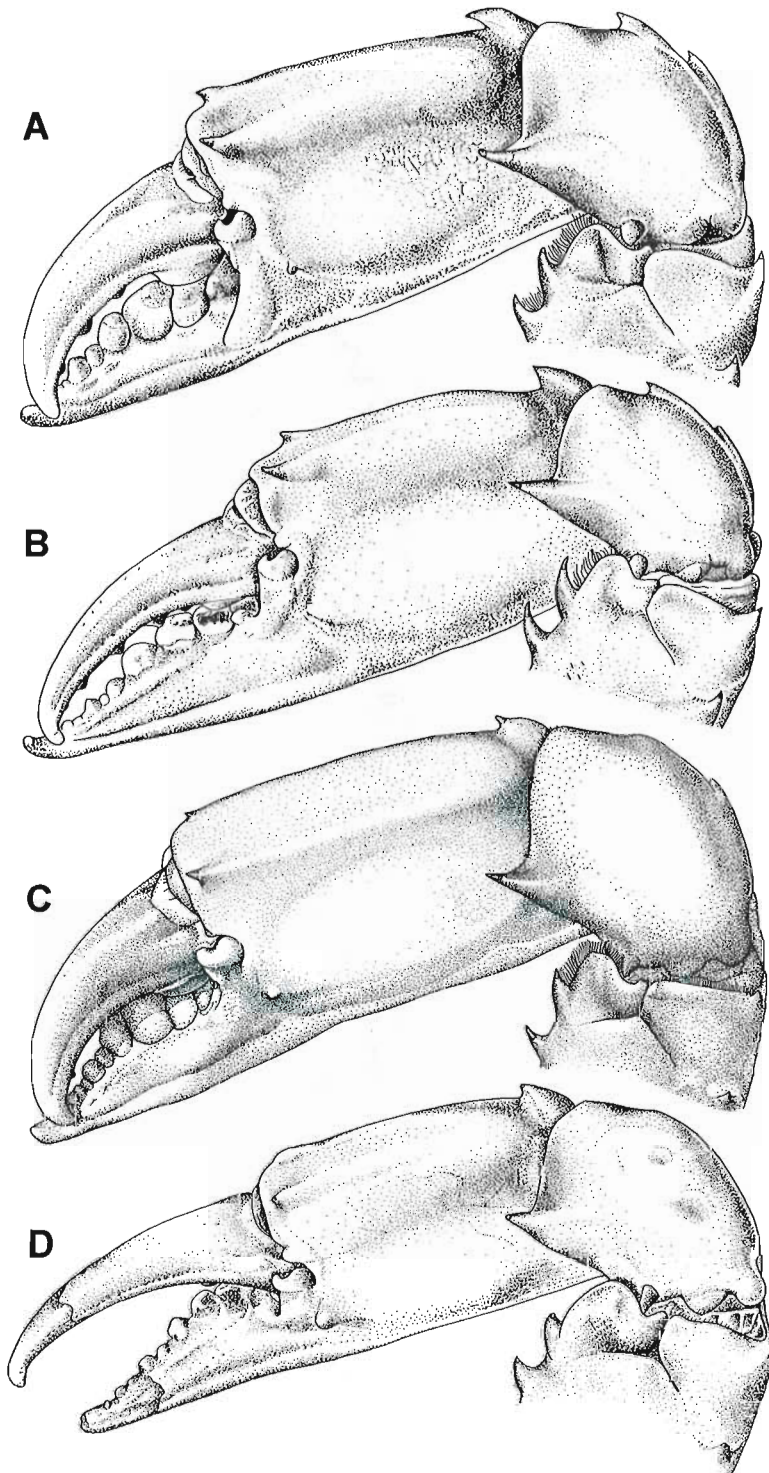


Fig. 8. Drawings of right cheliped of *Scylla* species showing diagnostic taxonomic features: (A) *S. serrata* - QM W20917, male, 153.0 mm CW; (B) *S. tranquebarica* - QM W20914, male, 120.5 mm CW; (C) *S. paramamosain* - QM W22174, male, 118.3 mm CW; (D) *S. olivacea* - QM W20895, male, 112.7 CW.

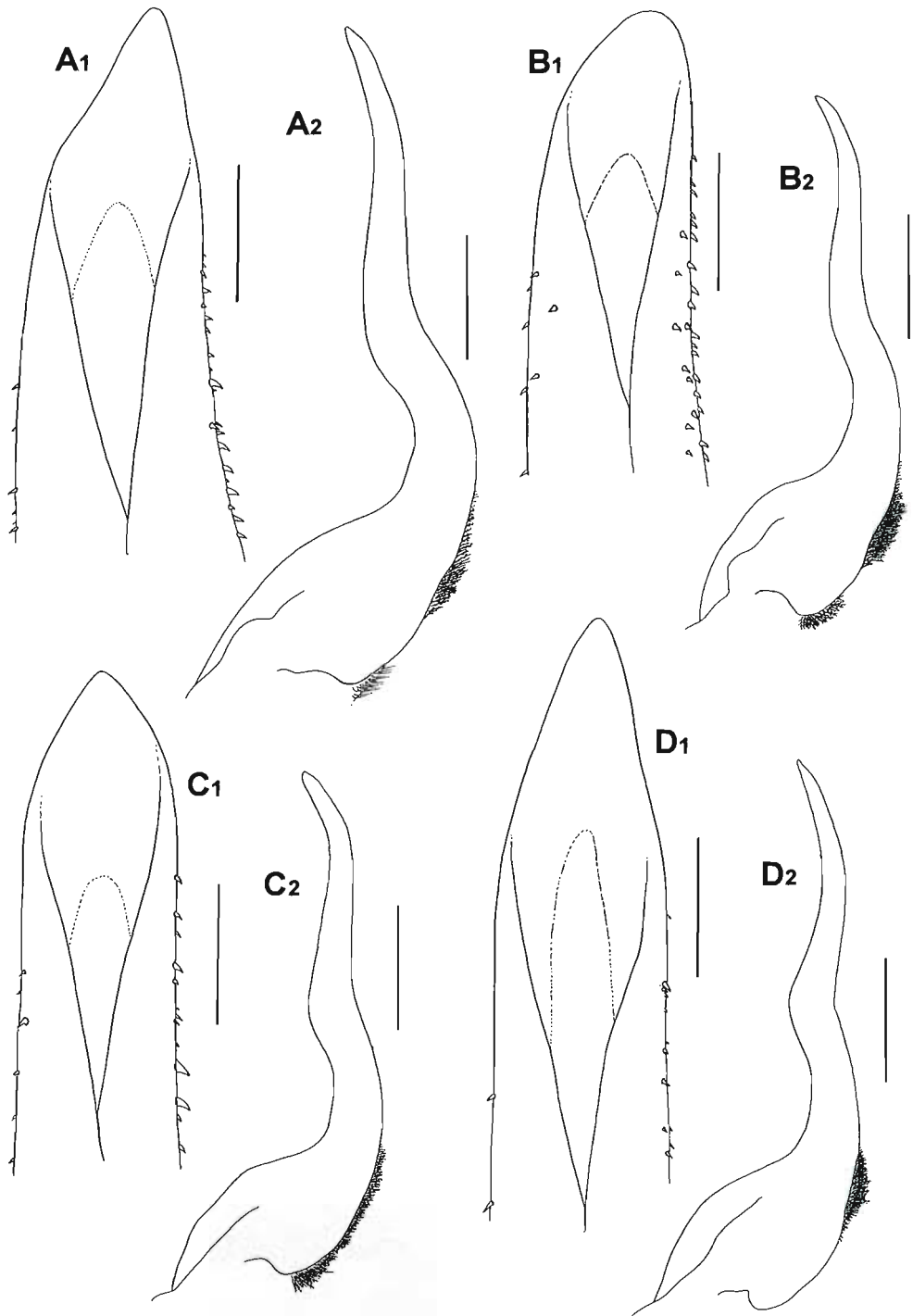


Fig. 9. Drawings of left gonopods of *Scylla* species: (A) *S. serrata* - QM W20917, male, 153.0 mm CW; (B) *S. tranquebarica* - QM W20914, male, 120.5 mm CW; (C) *S. paramamosain* - QM W22167, male, 112.1 mm CW; (D) *S. olivacea* - QM W20915, male, 121.2 CW; showing (1) detail of tip, (2) whole view. Scales: (1) = 0.5 mm; (2) = 5.0 mm.

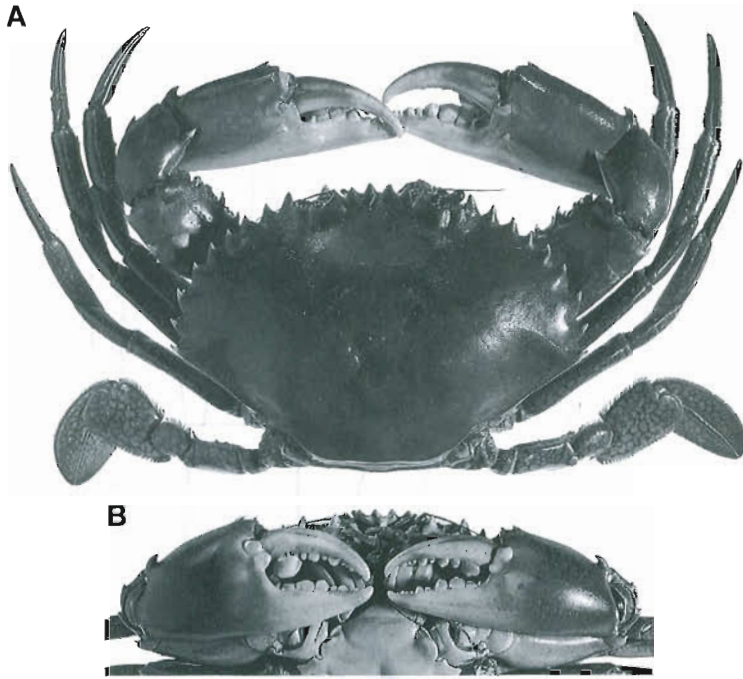


Fig. 10. Photographs of *S. serrata* - QM W20917, male, 153.0 mm CW, showing diagnostic features: (A) dorsal; (B) frontal.

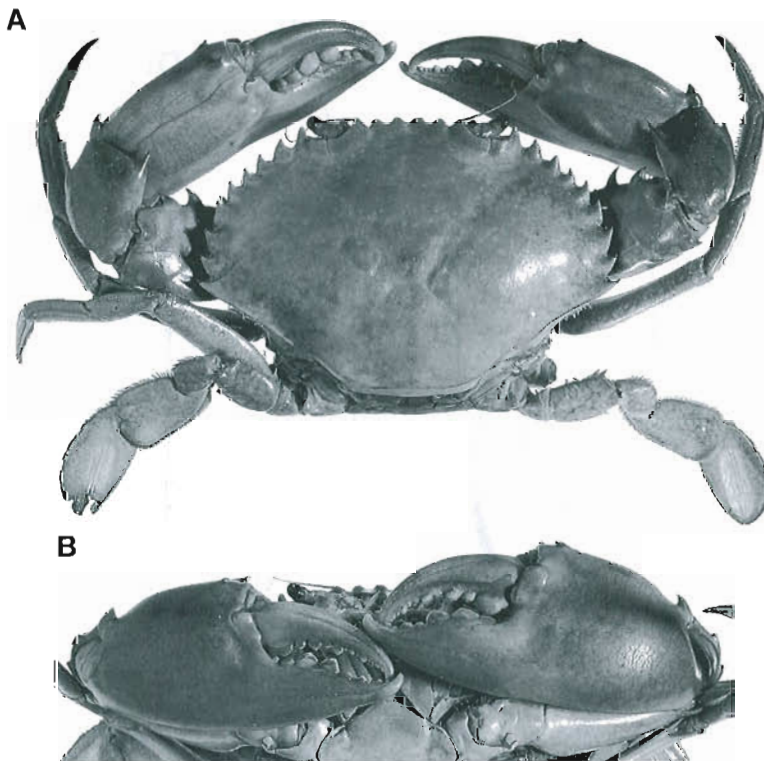


Fig. 11. Photographs of *S. tranquebarica* - QM W20914, male, 120.5 mm CW, showing diagnostic features: (A) dorsal; (B) frontal.

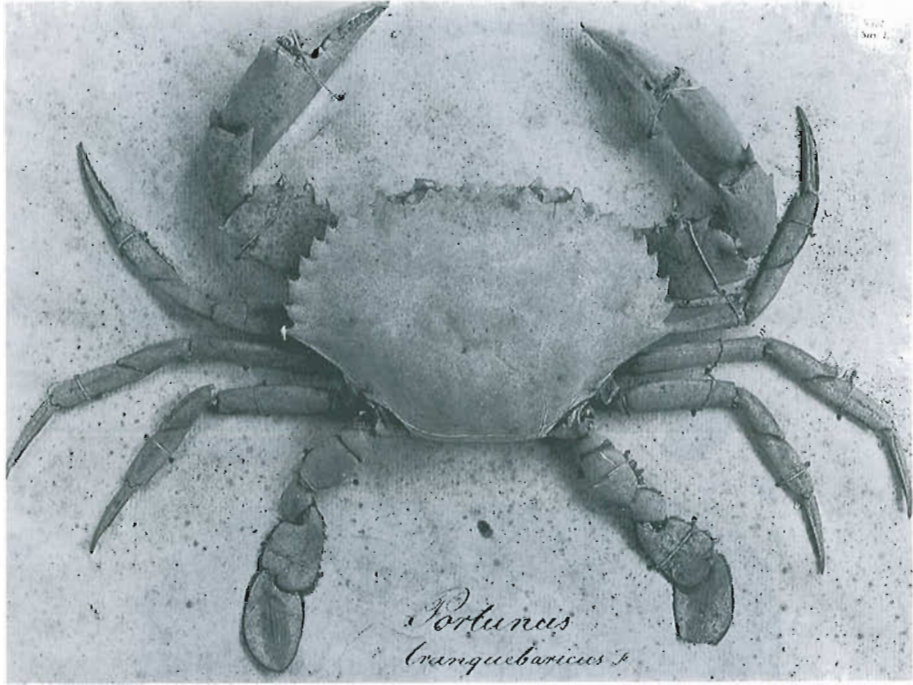


Fig. 12. Photograph of lectotype of *S. tranquebarica* Fabricius (1881). ZMUC CRU1881, female.

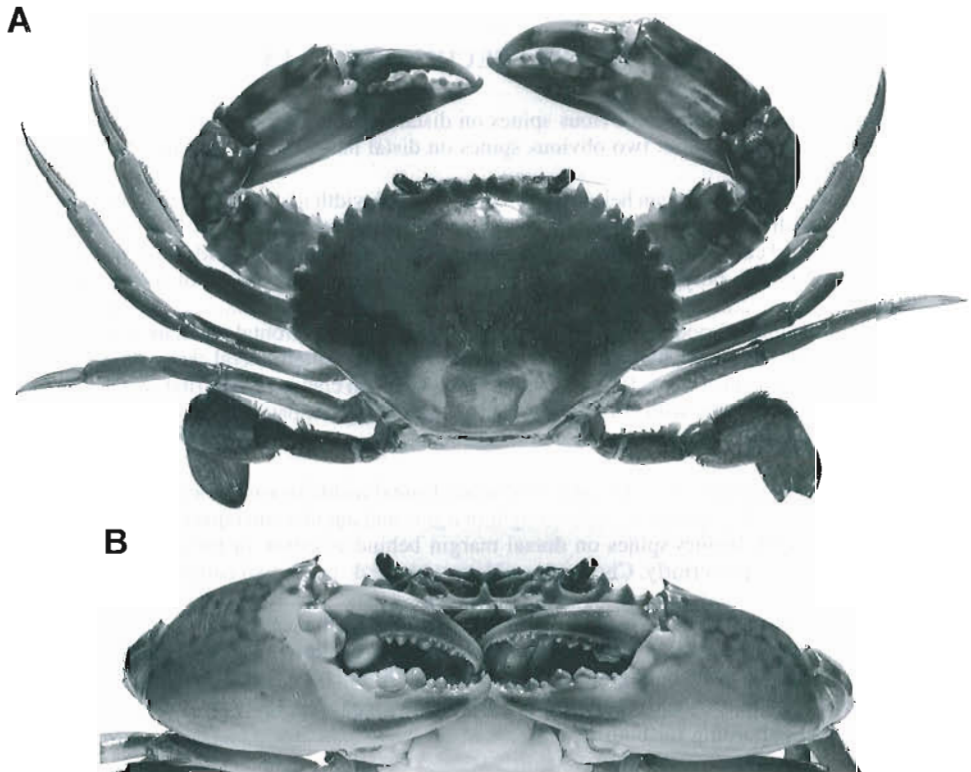


Fig. 13. Photographs of *S. paramamosain* - QM W22174, male, 118.3 mm CW, showing diagnostic features: (A) dorsal; (B) frontal.



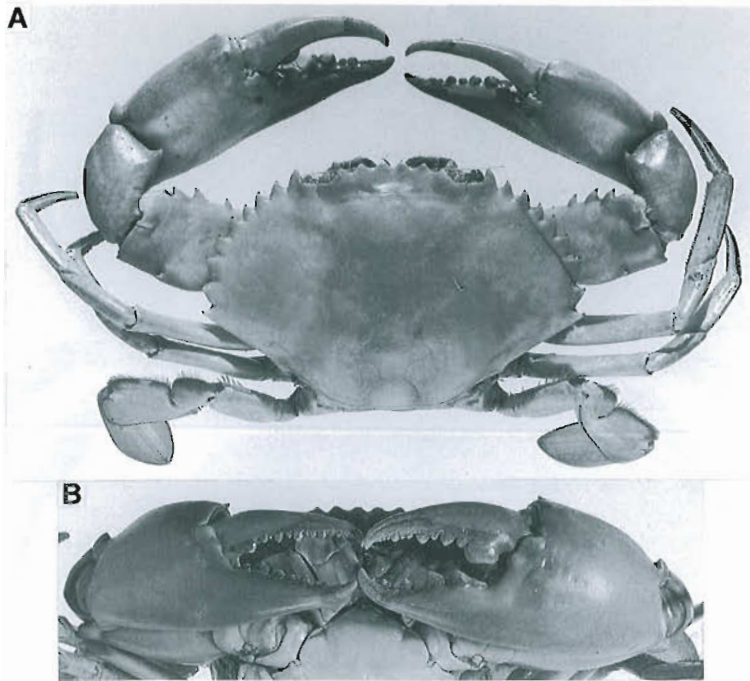


Fig. 14. Photographs of *S. olivacea* - QM W20895, male, 112.7 CW, showing diagnostic features: (A) dorsal; (B) frontal.

### KEY TO THE SPECIES OF *SCYLLA*

1. Carpus of chelipeds with two obvious spines on distal half of outer margin. .... 2
- Carpus of chelipeds without two obvious spines on distal half of outer margin. .... 3
  
2. Frontal lobe spines high (mean height c. 0.06 times frontal width measured between medial orbital sutures), bluntly pointed with tendency to concave margins and rounded interspaces. Anterolateral carapace spines narrow, with outer margin straight or slightly concave. Chelipeds and legs all with polygonal patterning for both sexes and on abdomen of female only. .... *Scylla serrata*
- Frontal lobe spines of moderate height (mean height c. 0.04 times frontal width measured between medial orbital sutures), blunted with rounded interspaces. Anterolateral carapace spines broad, with outer margin convex. Polygonal patterning weak on chelipeds and first two pairs of legs; last two pairs of legs with stronger patterning for both sexes; patterning variable on abdomen of female, absent on male. .... *Scylla tranquebarica*
  
3. Frontal lobe spines high (mean height c. 0.06 times frontal width measured between medial orbital sutures), typically triangular with straight margins and angular interspaces. Palm of cheliped with a pair of distinct spines on dorsal margin behind insertion of the dactyl, followed by ridges running posteriorly. Chelipeds and legs with weak polygonal patterning for both sexes. .... *Scylla paramamosain*
- Frontal lobe spines low (mean height c. 0.03 times frontal width measured between medial orbital sutures), rounded with shallow interspaces. Palm of cheliped usually with a pair of blunt prominences on dorsal margin behind insertion of the dactyl, inner larger than outer; may be spinous in juveniles and young adults. Chelipeds, legs and abdomen all without obvious polygonal patterning for both sexes. .... *Scylla olivacea*

## DISCUSSION

Attempts to identify *Scylla* species have led to much confusion because of the subtle morphological differences between the species. Within species variation for many important diagnostic characters is large and often overlapping between species. Ontogenetic changes also make identification of juvenile stages difficult.

Several of the most useful morphological characters for distinguishing between species have been previously used e.g. Estampador (1949a), Serène (1952), and Joel & Raj (1980), however, we have identified additional important distinguishing characters, and all are presented in a simple table (Table 5).

Table 5. Morphological characters useful in determining species identity of adult mud crabs.

Species	Frontal lobe spines		Cheliped	
	shape	height	carpus spines	propodus spines
<i>S. serrata</i>	blunt point	high	both obvious	obvious
<i>S. tranquebarica</i>	blunted	moderate	both obvious	obvious
<i>S. paramamosain</i>	triangular	moderately high	inner absent outer reduced	obvious
<i>S. olivacea</i>	rounded	low	inner absent outer reduced	reduced

The shapes of the male first gonopods are all generally similar, but there are small differences between species, with *S. olivacea* being the most distinctive. Some variation does exist however, and on its own this character is not clear enough to be easily useful. *Scylla olivacea* is remarkable for a particularly long and slender apex, and a more deeply and evenly convex inner margin over the distal half, which is more sinuous in other species. *Scylla serrata* consistently seems to have slightly concave margins on either side of the apex, whereas in *S. tranquebarica* the apex is broadly rounded, and in *S. paramamosain* the apical margins are convex as in *S. tranquebarica* but the tip is bluntly pointed. Joel & Raj (1980) stated that *S. olivacea* (as *S. serrata*) differed from *S. serrata* (as *S. tranquebarica*) by possessing chromatophores just below the apex giving a brownish-red colour; this is not apparent in our preserved specimens but may be useful in fresh material.

The confusion in identification has led to the proliferation of available names, and this in turn has led to the inconsistent use of names between authors. By carefully addressing the nomenclatural problems, we hope that future researchers will be able to build on a consistent and stable nomenclatural base.

The high degree of morphological similarity between the species suggests relatively recent speciation, with distribution rather than competition as the primary evolutionary mechanism. Competition often results in specialisation and obvious morphological change reflecting subtle shifts in diet and habitat, a classic example being Darwin's finches (Dobzhansky et al., 1977), whereas speciation through allopatry often produces less distinctive morphological changes.

The present distribution of the different *Scylla* species, when associated with information on reproductive behaviour, strongly suggests that each species may have different salinity optima for larval growth and survival. The widespread oceanic distribution of *S. serrata* is unmatched

by the other species. *S. serrata* is dominant in oceans where surface salinity is greater than 34 ppt. In the Red Sea, where only *S. serrata* occurs, salinities rise as high as 40 ppt (Lewis & Campbell, 1967). It is known that ovigerous females of this species can migrate considerable distances into oceanic waters, up to 95 km offshore, to hatch eggs (Brown, 1993; Hill, 1994).

The main distributions of the three other species centre on the South China Sea and Bay of Bengal. The areas where these species are found have salinities less than 33 ppt during the northern hemisphere summer (Lewis & Campbell, 1967). In certain locations, different *Scylla* species dominate the catch. Along the continental coast of the South China Sea, at Xiamen, China, and the Mekong Delta, *S. paramamosain* is the most common species, as it is along the northern coast of Central Java (C. Keenan, pers. obs.). The other *Scylla* species can be found sympatric with *S. paramamosain*, however they are uncommon or confined to specific habitats. The South China Sea coast is characterised by intermediate offshore salinities (32-34 ppt), whereas *S. tranquebarica* and *S. olivacea* are most common when salinity falls below 31 ppt, for example around Singapore and along the Sarawak coast of Kalimantan. In Australia, the known distribution of *S. olivacea* is limited to a few embayments where salinity is reduced for extended periods during the monsoon period; Albatross Bay, off Weipa, NW Cape York and King Sound, Western Australia. The Andaman, South China and Java Seas, the centre of distribution for *S. paramamosain*, *S. tranquebarica* and *S. olivacea*, would have experienced long periods of relative isolation from the surrounding oceans during periods of low sea level, up to 150 m below present levels, over the past 5 million years. Freshwater inflow into these seas, combined with restricted connections with the surrounding oceans would have resulted in reduced salinities for significant periods, and fewer opportunities for larval dispersal. Under these conditions, strong selection for survival at the reduced salinities would have occurred. Even in the present high sea-level environment, water exchange is extremely limited, producing consistent salinity differences between these seas and the surrounding oceans.

Another intriguing aspect of the life cycle of *Scylla* species, that reinforces the idea that speciation has occurred only recently, is the similar timing of annual offshore migrations of ovigerous female crabs of different species. Offshore migrations have been reported from many areas (Brown, 1993); for *S. serrata* these take place from September to November (Hill, 1994), prior to the wet season in Australia (January - March), and slightly later (October to December) in the cooler waters of South Africa (Hill, 1974). In Australia juvenile crabs first appear on the shore around January (Keenan, pers. obs.). Very similar timings of maturation, migration and spawning are found for the other three *Scylla* species. Two species of mud crab from Suratthani, Gulf of Thailand, most likely *S. tranquebarica* and *S. olivacea*, mature in July-August and migrate offshore during September (Khaonuna & Ratanachote, 1994). Similarly, fishers from the Mekong Delta report (Keenan, unpub.) that *S. paramamosain* migrates offshore around September - October, and juveniles return in January after the monsoon. Therefore, all four species have similar timing of their reproductive cycle regardless of the hemisphere in which they are found. These are however generalisations based on data from a restricted geographic range. Minor differences of about two months have been observed for sympatric species in Pulicat Lake, India (Joel & Raj, 1980). Further research, based on sound taxonomic identification is required to establish precise details of the life-cycle of each species throughout its range. This paper should assist such studies through the clarification of the species status and taxonomic nomenclature.

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