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Taxonomic Assessment of *Acetes indicus* H. Milne Edwards, 1830 (Crustacea, Decapoda, Sergestoidea) as Revealed from Molecular and Morphological Analyses: Re-validation of *A. spiniger* Hansen, 1919 and Designation of a New Species

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Abstract The shallow water planktonic shrimp *Acetes indicus* H. Milne Edwards, 1830 (Crustacea: Decapoda: Sergestoidea) was established on the basis of specimens obtained from the Ganges Delta, and is the type species of the genus *Acetes*. This shrimp is important as one of the major products for small-scale coastal fisheries across tropical eastern Asia. The results of mitochondrial DNA analyses from individuals across South and South-East Asia have revealed the existence of two genetically separate major clades, one of which could be further divided into two sub-clades, leading to three reciprocally monophyletic clades (Bangladesh, South-East Asia, and eastern Indian Ocean clades). Morphological analysis agreed with the results of genetic analyses by showing minor, but consistent differences between the three clades, demonstrating that they are isolated reproductive units. This finding has raised a concern about the true identity of *A. indicus*. The type(s) of *A. indicus* were not found in the most possible holding institution, Muséum national d'Histoire naturelle, Paris (MHHN). Specimens from Bangladesh, possible topotypic materials sampled at different times and locations, were regarded the representative of *A. indicus.* Accordingly, a new species, *Acetes omorii* (≈ Omori's large form), is proposed to accommodate the sister clade occurring in South-East Asia. Moreover, *Acetes spiniger* Hansen, 1919, once regarded a synonym of *A. indicus*, is herein re-validated to accommodate the Indian Ocean population (≈ Omori's small form).

Key words: Mitochondrial DNA, taxonomy, genetic divergence, *Acetes omorii* sp. nov., coastal waters, estuary, Ganges Delta.

Introduction

Acetes indicus is a shallow water planktonic shrimp species established by H. Milne Edwards in the year 1830 on the basis of specimens collected from the Ganges Delta, with this species being the type species of the genus *Acetes* H. Milne Edwards, 1830.

Nearly a century after H. Milne Edwards' paper (1830), Hansen (1919) reported *Acetes spiniger* from the waters off Rangoon (= Yangon), Burma (= Myanmar) as well as Surabaya, Indonesia and Indo-Chinese Sea (= South China Sea). Due to its close similarity with *A. indicus*, several researchers thought that *A. spiniger* should be a junior synonym of *A. indicus* (*e.g.*, Burkenroad, 1934; Pathansali, 1966).

Omori (1975) made the first worldwide review of *Acetes*, and regarded *A. spiniger* to be a synonym of *A. indicus*. However, he also noted the existence of two morphological forms among individuals attributable to *A. indicus*; *i.e.*, the "small form" largely present in the Indo-Burmese area and the "large form" occurring mainly in South-East Asian waters (see also Pathan and Jalihal, 1997). Although Omori (1975) had a little doubt about the taxonomic status of these morphological forms, he nevertheless concluded that they might be ontogenetic variations. Most researchers have since accepted this synonymy (Ravindranath, 1980; Pérez Farfante and Kensley, 1997: De Grave and Fransen, 2011; Vereshchaka *et al.*, 2016). There were, however, exceptions, such as Pathan and Jalihal (1997), whom insisted that these morphological variations may represent the differences at species rank.

Recently, Wong *et al.* (2017) reported the presence of individuals separated by a deep genetic gap in *A. indicus* off the west coast of Peninsular Malaysia. At about the same time, we obtained a similar result from our studies of genetic population structure and diversification of *Acetes* shrimps in the Indo-West Pacific (*e.g.*, Hardianto *et al.*, 2022b). The results of further analyses have demonstrated that *A. indicus* is a species complex, involving several cryptic species.

This finding had raised a taxonomic concern about which clade the type material(s) of *A. indicus* should be referred to. Omori (1975) noted that the type of *A. indicus* might be deposited in the Muséum national d'Histoire naturelle, Paris (MNHN). Despite our attempts to have access to the type material(s), including a direct survey of collections in that institute, we were not able to find it. The type was probably lost or destroyed during the historical time and, most likely, no longer extant (staff members in the institute, pers. comm. in September 2018).

Examinations of materials from the Ganges Delta could be the second best choice to clarify the problem. Following this line of thought, we were able to obtain notable numbers of specimens from Bangladesh, part of the Ganges Delta. These materials, together with those from other localities in eastern Asia, were examined by incorporating genetic and morphological analyses.

To date, the extent of *A. indicus* is known to be distributed across tropical eastern Asia (Omori, 1975; Tirmizi and Ghani, 1982), and it has long been exploited for small-scale fisheries in the region (Omori, 1975; Holthuis, 1980; Xiao and Greenwood, 1993). Better understanding for the entity and genetic backgrounds of wild stocks would be substantial to achieve their sustainable use as well as for conservation.

Thus, our study addressed to clarify the identity of *A. indicus* based on samples gathered from broad areas in South and South-East Asia.

Vereshchaka and his colleagues proposed a new taxonomic scheme in *Acetes*, by combining *Peisos* Burkenroad, 1945 into the genus *Acetes*, and the Sergestidae was split into four families, including Acetidae (Vereshchaka *et al.*, 2016; Vereshchaka, 2017). Our preliminary analysis of DNA has elucidated a slight possibility of alternative schemes for a part of its taxonomic categories (Imai *et al.*, unpublished data). Regardless of its validity, such kind of studies are beyond the scope of this article.

Materials and Methods

The material dealt with in this study has been collected during our research activities conducted under bi-lateral research projects between Japanese institutions/researchers (with official research permissions at each country: research pass reference numbers; BVP/PLI//14011/34885 from Malaysia; 456/E5/E5.4/SIP/2019 from Indonesia; ID 2011/005 from Thailand) and/or academic institutions and its counterparts overseas. Thus the materials used in this study have been acquired regally. It came from various sources as remarked in the "Material examined" sections in the taxonomic accounts; direct sampling in the field, fishery catches, and/or commercial products at local markets. Specimens were fixed and stored in >70% ethanol, if not mentioned otherwise.

DNA analysis

Shrimp specimens attributable to *A. indicus* collected from 12 localities in South-East and South Asia were chosen for DNA analyses. The mitochondrial 16S and COI genes, which were widely used in this kind of studies, were conducted to evaluate the genetic differences among the populations (Vera-Silva and Mantelatto, 2022). Total genomic DNA was extracted from approximately 10 mg muscle tissue of specimens fixed in ethanol using the proteinase K, phenol-chloroform and diethyl ether with TNES-8M urea buffer (Imai *et al.*, 2004). The partial mitochondrial 16S ribosomal RNA and cytochrome oxidase subunit I (COI) genes were amplified for phylogenetic analysis using the combination primer 16sar-L (5′-CGCCTGTTTATCAAAAAC AT-3′) and 16sbr-H (5′-CCGGTTTGAACTCAG ATCACGT-3′) for 16S rRNA (Palumbi *et al.* 1991), and LCO1490 (5′-GGTCAACAAATCATA AAGATATTGG-3′) and HCO2198 (5′-TAAACT TCAGGGTGACCAAAA AATCA-3′) for COI gene (Folmer *et al.*, 1994).

Polymerase Chain Reaction (PCR) were performed in EmeraldAmp PCR master mix (Takara Bio). PCR conditions were conformed to Imai *et al.* (2004) and Wong *et al.* (2017). The nucleotide sequences were determined using the ABI 3730xl DNA analyzer (Applied Biosystems). All sequence data were aligned, manually edited, and compared using MEGA ver. X (Kumar *et al.*, 2018). We calculated Kimura's two-parameter (K2P) distance with 1,000 bootstrap replications, analysed the pairwise genetic difference, nucleotide composition and constructed phylogenetic tree by the Maximum Likelihood (ML) and Neighbor Joining (NJ) methods using MEGA. We also constructed the phylogenetic tree by the Bayesian Inference (BI) method using BEAST ver. 2.4.2 (Bouckaert *et al.*, 2014). Haplotype network analyses between the species were also constructed by the analysis of minimum spanning network (MSN) using PopART (Leigh and Bryant, 2015). The sequences obtained in this research were deposited in the DNA Data Bank of Japan (DDBJ) under Accession Numbers LC682346 to LC682362 for 16S rRNA, and LC804564 to LC804580 for COI genes.

Morphological analysis

In the sampled materials at each site, adults and/or adolescent specimens of both males and females, if available, were chosen for detailed morphological analyses.

Carapace length (cl) used to indicate the shrimp size is the length between the orbital to the postero-dorsal margins. Measurements were made using a micrometer installed on an ocular eyepiece of a stereo-microscope. Terminology basically followed Omori (1975).

The specimens used in this study are deposited in the Tsukuba Research Departments, National Museum of Nature and Science, Tokyo (NSMT) at Tsukuba, Japan, and Fisheries Research Institute (FRI), Kampung Acheh, Malaysia.

Results

Molecular analyses

A total of 481 bp segment of 16S and 509 bp of COI of *A. indicus* s.l. gathered from several localities across South and South-East Asia were amplified and aligned, together with two other relatives within the genus (*Acetes chinensis* Hansen, 1919 and *Acetes serrulatus* Krøyer, 1859) as out group taxa (Table 1).

Nucleotide composition of each clade/species is shown in Tables 2 and 3. The pairwise genetic difference with the K2P distance, based on the 16S and COI genes, of three clades is as shown in Table 4. With regard to each clade, there are sufficient differences among the clade from off Kuala Selangor and that from South-East Asia to separate them as distinct species.

The phylogenetic trees of the 16S and COI markers reconstructed using ML, NJ and BI analyses (Fig. 1a, b) clearly differentiated three different clades, although the South-East Asian clade formed a sub-ordinate clade with that of Bangladesh.

The haplotype networks based on the 16S and COI haplotypes showed that these clades assigned at different species were separated by 18–40 and 38–44 steps, respectively, which is consistent with large genetic distances among them (Fig. 2a, b), demonstrating that these three clades are sufficient to recongnise as genetically isolated populations.

Morphological analyses

In our examination, no clear differences in the structure of the male genital organ (petasma) could be detected between the three genetic clades, although in the past, it has been used as the most reliable marker to define species of *Acetes* (*e.g.*, Omori, 1975). Instead, several minor but consistent differences were observed such as the structure of the lower antennular flagellum of males, the form of the female genital area and/or the relative length of the antennal scale. Thus,

Table 1. Specimens of *Acetes indicus* species group, including two congeners, used for mitochondrial DNA analyses.

Taxon	Sampling locality	Sampling date	Number of Specimens (individuals)	Haplotype	GenBank accession number		Museum deposition number
					16S rRNA	COI	
Acetes indicus H. Milne Edwards, 1830	Bangladesh (Chiringa)	19 Aug 2018	2	CIR-1	LC682346	LC804564	NSMT-Cr 31613
				CIR-2	LC682347	LC804565	NSMT-Cr 31614
	Bangladesh (Kumira-Sandwip Ship Ghat)	Dec 2018	3	KUM-1	LC682348	LC804566	NSMT-Cr 31617
				KUM-2	LC682349	LC804567	NSMT-Cr 31618
					LC682349	LC804567	NSMT-Cr 31619
Acetes spiniger Hansen, 1919	Malaysia (Kuala Selangor)	23 Sept 2012	2	SEL-1	LC682350	LC804568	NSMT-Cr 31638
				SEL-2	LC682351	LC804569	NSMT-Cr 31639
Acetes omorii Hanamura, Imai & Hardianto sp. nov.	Malaysia (Matang Mangrove)	25 Nov 2008	2	PER-1	LC682352	LC804570	NSMT-Cr 31624
				PER-2	LC682353	LC804571	NSMT-Cr 31625
	Thailand (Samut Prakan)	June 2016	1	THA-1	LC682356	LC804574	NSMT-Cr 31636
	Indonesia (Setarap Estuary, South Kalimantan)	19 Sept 2019	4	SET-1	LC682354	LC804572	NSMT-Cr 31632
					LC682354	LC804572	NSMT-Cr 31633
					LC682354	LC804572	NSMT-Cr 31634
				SET-2	LC682355	LC804573	NSMT-Cr 31635
Out of groups							
Acetes chinensis Hansen, 1919	China (Fujian)		2	FUJ-1	LC682357	LC804575	
				FUJ-2	LC682358	LC804576	
	China (Zhoushan)		2	ZHO-1	LC682359	LC804577	
				ZHO-2	LC682360	LC804578	
Acetes serrulatus (Kröyer, 1855)	Indonesia (Kubu Raya, North Kalimantan)		2	KUB-1	LC682362	LC804579	
				KUB-2	LC682362	LC804580	

Note: Individuals with the same accession numbers indicate that they have the same haplotype.

Table 2. Base composition (%) of 16S rRNA gene amplified for species of *Acetes indicus* species group and two congeneric species.

Species name	First codon				Second codon				Third codon				Overall			
	T	C	A	G	T	C	A	G	T	C	A	G	T	C	A	G
Acetes indicus	29	32.3	22.4	16.1	49	5.6	34.4	11.3	13	20	44.4	23.1	30.1	19.3	33.7	16.8
Acetes omorii sp. nov	29	32.3	21.1	17.4	51	3.1	33.8	11.9	13	20	44.4	23.1	31	18.5	33.1	17.5
Acetes spiniger	29	32.3	23.6	15.5	51	2.5	37.5	8.8	13	19.4	44.4	23.8	30.8	18.1	35.1	16
Out of groups																
Acetes chinensis	29	32.3	19.3	19.3	43	7.5	39.4	10.6	13	19.4	44.4	23.8	28.1	19.8	34.3	17.9
Acetes serrulatus	29	31.7	22.4	16.8	49	3.1	39.4	8.1	13	19.4	44.4	23.8	30.4	18.1	35.3	16.2
Overall	29	32.2	21.8	17	48.6	4.4	36.9	10.1	13	19.6	44.4	23.5	30.1	18.8	34.3	16.9

Table 3. Base composition (%) of COI gene amplified for species of *Acetes indicus* species group and two congeneric species.

Species name	First codon				Second codon				Third codon				Overall			
	T	C	A	G	T	C	A	G	T	C	A	G	T	C	A	G
Acetes indicus	29	33.5	22.4	15.3	48	7.6	33.5	11.2	12	20.7	43.2	24.3	29.5	20.6	33.0	16.9
Acetes omorii sp. nov	29	33.5	21.2	16.5	52	2.9	33.5	11.8	12	20.7	43.2	24.3	30.8	19.1	32.6	17.5
Acetes spiniger	29	33.5	23.5	14.7	52	2.4	37.6	8.2	12	20.1	43.2	24.9	30.6	18.7	34.8	15.9
Out of groups																
Acetes chinensis	29	33.5	19.4	18.2	43	7.1	38.8	11.2	12	20.1	43.2	24.9	27.9	20.2	33.8	18.1
Acetes serrulatus	29	32.9	22.4	15.9	51	2.9	38.2	8.2	12	20.1	43.2	24.9	30.5	18.7	34.6	16.3
Overall	29	33.4	21.8	16.1	49	4.6	36.4	10.1	12	20.4	43.2	24.6	39.9	19.4	33.8	16.9

Table 4. Estimation of number of nucleotide substitutions in mitochondrial DNA 16S rRNA (below the diagonal) and COI (above the diagonal) genes based on K2P defined between *Acetes indicus* species group and its congeners (*A. chinensis* and *A. serrulatus*).

	Acetes indicus	*Acetes omorii*	*Acetes spiniger*	*Acetes chinensis*	*Acetes serrulatus*
Acetes indicus		0.10	0.13	0.14	0.13
Acetes omorii sp. nov	0.04		0.12	0.16	0.12
Acetes spiniger	0.10	0.09		0.16	0.13
Acetes chinensis	0.15	0.15	0.16		0.14
Acetes serrulatus	0.12	0.13	0.13	0.14	

each clade or species can be defined by a single major feature or a combination of them (see Table 5 and "taxonomic accounts").

The results of our analyses demonstrated that large-sized inshore specimens were almost identical to Omori's "large form" while relatively smaller-sized individuals from offshore waters corresponded to Omori's "small form". Thus, specimens identical to the "large form" have been captured from several localities across South-East Asia. In contrast, specimens referred to the "small form" have been found from offshore waters on the west coast of Peninsular Malaysia to Goa, through Burma (= Myanmar).

Although males from Bangladesh exhibit a close morphological similarity to those of the South-East Asia, it slightly but noticeably differed from the latter. In the male lower antennular flagellum, specimens from Bangladesh usually had a slightly narrower basal trunk (= basal three segments) as compared with specimens from South-East Asia, and the first and second segments of its trunk part showed to have a markedly oblique conjunction as against to a rather weak oblique joint in its closest relative. Moreover, the structure of the female genital part clearly differed between the two populations by having a broad and shallow longitudinal sulcus in the Bangladeshi population instead of a narrowly deep groove in the South-East one (Figs 4i, j *vs* 6c, d; Table 5).

In the present genetic analyses, a relatively

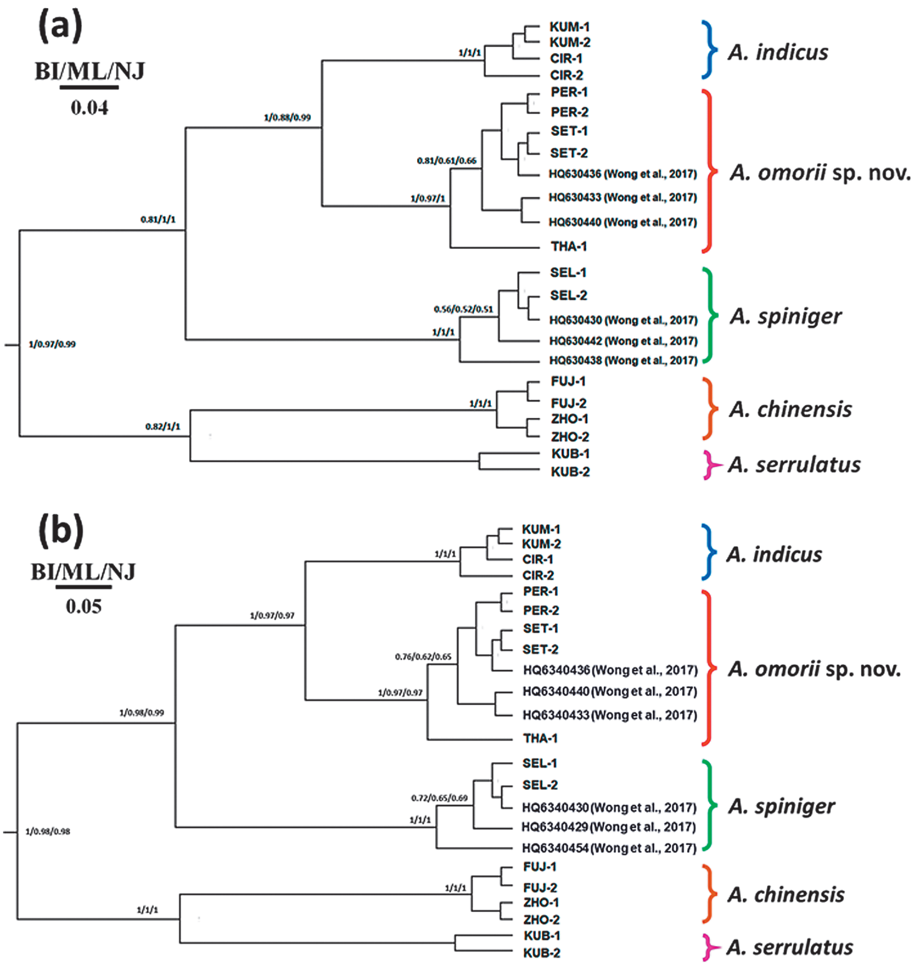

Fig. 1. Bayesian inference trees of *Acetes indicus*, *A. omorii* sp. nov., and *A. spiniger* with the outgroups of other congeneric species based on the mitochondrial 16S (a) and mitochondrial COI (b) markers. Values at the nodes are Bayesian posterior probabilities/Maximum Likelihood/Neighbor Joining support values. For the haplotype abbreviations, see Table 1.

closer relationship was detected between populations from South-East Asian regions and Bangladesh, forming sub-ordinate populations, while morphological analyses showed noticeable differences between them, indicating that they are distinct genetic units, and the population from Bangladesh was considered, at least at this time, the best representative of *A. indicus*.

Discussion

Molecular characteristics

Wong *et al.* (2017) reported the presence of two different genetic clades in *A. indicus* off the west coast of Malay Peninsula (Perak and Malacca Straits), but they did not proceed with further studies on this matter. In the same period, we also had a similar result for this species. Moreover, the phylogenetic analysis inferred from the 16S sequences using NJ, ML and BI, which incorporated sequence data based on fur-

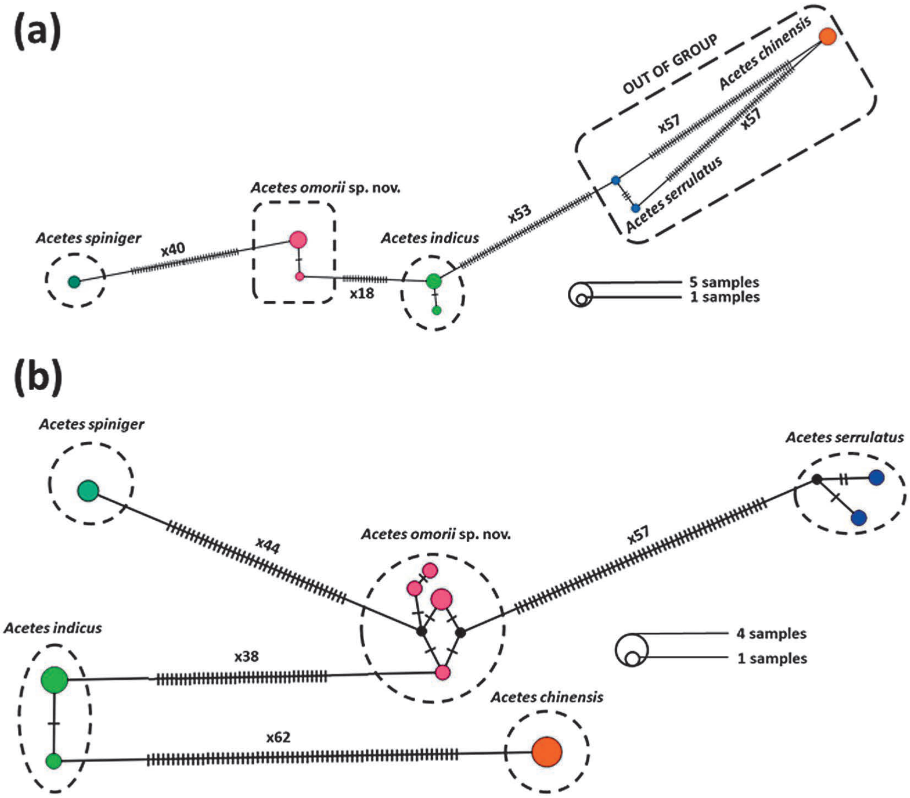

Fig. 2. Haplotype network (implemented in PopART) of the *Acetes indicus*, *A. omorii* sp. nov., and *A. spiniger* based on the mitochondrial 16S (a) and mitochondrial COI (b) markers using minimum spanning network (MSN) analysis with outgroups of congeneric species. Circles with different colours represent different species.

ther samples across South and South-East Asia, have elucidated the presence of three distinct clades within the current concept of *A. indicus* (Fig. 1). All clades were monophyletic and supported by high bootstrap values and posterior probabilities, demonstrating that *A. indicus* is a complex, involving three different populations. Nucleotide composition indicated that the studied species of *Acetes* have a high A + T content and positional biases (Tables 2, 3).

The aligned 16S sequences revealed the genetic distances between each clade ranges from 0.04–0.10 (Table 4). Similarly, the aligned COI sequences revealed the genetic distances ranges from 0.10–0.13, which also support genetic isolations between the clades (Table 4). These values obtained from both genetic markers, ranging from 0.04–0.13, are worthy to recognize them as distinct species as has been detected among species and/or cryptic species of several decapod crustaceans (Keenan *et al.*, 1998; Shih *et al.*, 2013; Bilgin *et al.*, 2014; Shih, 2015; Udayasuriyan *et al.*, 2017; Shih and Poupin, 2020).

The haplotype network also showed the distinctions of three clades, spanning respectively by 18–40 and 38–44 steps in the 16S and COI, which are consistent with the large genetic distances between the three populations (Fig. 2). Such deep haplotype network gaps may indicate species divergence as has been observed in the fiddler crab *Austruca perplexa* (H. Milne Edwards, 1852) from Moreton Bay, Australia, showing more than 50 steps differences with its congeners (Hardianto *et al.*, 2022a) and *Gelasimus variegatus* Heller, 1862 from the Bay of Bengal, having 40–42 steps differences with oth-

Table 5. Comparison of morphology between three species in relation to the genetic clades within *Acetes indicus* species group.

Character items	*A. indicus* H. Milne-Edwards, 1830	*A. omorii* sp. nov. (≈ Omori's" large form")	*A. spiniger* Hansen, 1919 (= Omori's "small form")
Body size	Largest male 5.6 mm, largest female 8.0 mm from Bangladesh	Largest male 7.5 mm, largest female 10.0 mm, both from Kalimantan, Indonesia	Largest male 4.8 mm, largest female 6.4 mm, both from off Goa, India
Antennule: peduncle (Male)	Third segment 0.81–0.97 times as long as combined length of first and second ones	Third segment 0.70–0.86 times as long as combined length of first and second ones	Third segment 0.90–1.10 times as long as combined length of first and second ones
lower flagellum	first segment of trunk 3 or more times as long as second, noticeably narrowing around mid-length and, these segments forming greatly oblique conjunction; fourth segment of main branch 1.0–1.5 times as long as combined length of second and third segments, with 9 or 10 setal-spines on its entire margin	Firstl segment of trunk utmost 2 times as long as second, not noticeably narrowing around mid-length, these segments forming nearly vertical or weakly oblique junction; fourth segment of main branch 1.2–1.5 times as long as combined length of second and third segments, with 9 or 10 setal-spines on its entire margin	first segment of trunk sub-equal length to second, not noticeably narrowing around mid-length, these segments forming vertical or weakly oblique junction; fourth segment of main branch 0.5–0.7 times as long as combined length of second and third segments, with 4–6 setal-spines on its anterior 2/3–1/2 margin
(Female) peduncle	Third segment about half as long as combined length of first and second segments (0.50–0.55 x)	Third segment slightly less than half as long as combined length of first and second segments (0.40–0.46 x)	Third segment against combined length of first and second segments (0.35–0.47 x)
Antenna (Male)	Antennal scale 0.0.75–0.80 as long as carapace, over-reaching anterior end of second segment of antennular peduncle	Antennal scale 0.70–0.79 times as long as carapace, over-reaching anterior end of second segment of antennular peduncle	Antennal scale 0.70–0.81 times as long as carapace, barely reaching anterior end of second segment of antennular peduncle
Genital area (Female)	Posterior part of third and anterior part of fourth thoracic sternites with rather wide and shallow longitudinal channels, swellings not pronounced	Posterior part of third and anterior part of fourth thoracic sternites with narrow longitudinal channels, swellings high and well pronounced	Posterior part of third and anterior part of fourth thoracic sternites with rather wide and shallow longitudinal channels, swellings moderately pronounced
Distribution	Recorded from Ganges Delta	Recorded from Malacca Strait to Kalimantan and Gulf of Thailand	Recorded from Malacca Strait to India

ers (Shih *et al.* 2019).

Morphological characteristics

Omori (1975) examined a part of the syntypes of *A. spiniger* from off Rangoon, Burma (= Yangon, Myanmar), as well as four additional specimens from Green Island in Burma, saying that they contained eight specimens, represented by five "large" and three "small forms". He also noted that the two forms were found at several areas of South-East Asian coastal waters, although we were able to confirm the presence of Omori's "large form" in the Pacific sector of South-East Asia alone (Fig. 3). Further confirmation is in need in future studies.

Besides, the form of the male lower flagellum illustrated by Omori (1975; fig. 15d) under his "small form" agreed well with that of *A. spiniger* by Hansen (1919; fig. 5a, c). In general, male genital organs have been used as a key character, like in most dendrobranchiate prawns, to identify species under the genus *Acetes*. In addition, the form of the female genital part presented by Hansen (1919: fig. 5f) shows a resemblance to *A. spiniger* (Fig. 7g in the present study) rather than that of the "large form" (Omori, 1975; fig. 15b, c). Thus, it is safe to think that *A. spiniger* could be a valid species of the Malay-Indian region's population, which basically corresponds with Omori's "small form" (= "Indo-Burmese form"

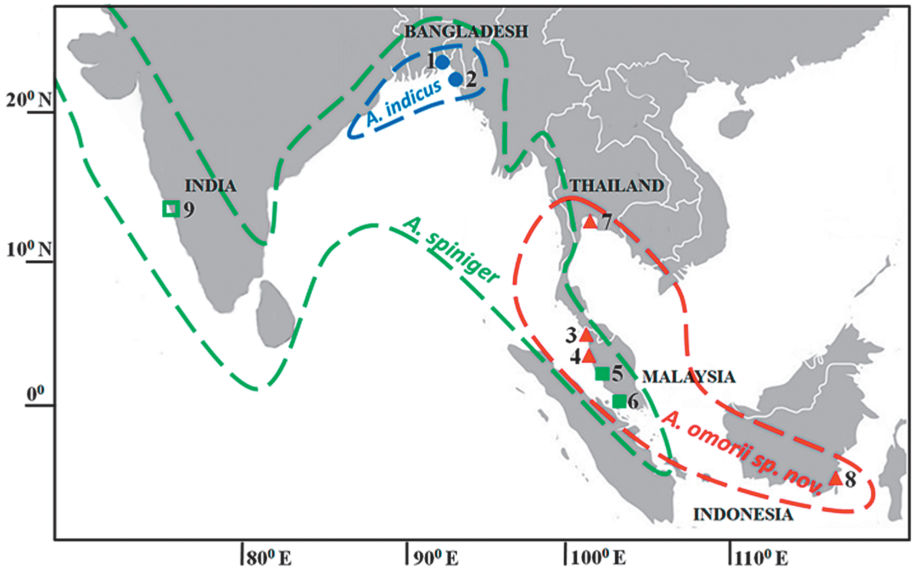

Fig. 3. Map showing sampling localities and distribution ranges of *Acetes indicus*, *A. omorii* sp. nov. and *A. spiniger* recognised in this study with certainty: blue solid circles (nos. 1–2) for *A. indicus*, green solid squares and open square (museum vouchered specimens) for *A. spiniger*, and red solid triangles for *A. omorii* sp. nov. Numerals indicating sampling locations: 1, Chiringa; 2, Kumira-Sandwip Ship Ghat; 3, Merbok Mangrove; 4; Matang Mangrove, 5; Kuala Selangor; 6, Malacca; 7, Samut Prakan; 8, Setarap Estuary, South Kalimantan; and 9, Goa.

in Pathan and Jalihal (1997). Similar specimens have been reported from the coastal waters of the eastern Indian Ocean (*e.g.*, Omori, 1975; Ravindranath, 1980; Pathan and Jalihal, 1997; this study).

Although the exact entity of the whole syntypes remained unsolved to date, *A. spiniger* might be best represented by the male specimen illustrated by Omori (1975), which was collected from off Rangoon (= Omori's "small form")

Accordingly, the South-East Asian population (= Omori's "large form"), forming a third taxon within the "*A. indicus*" species complex, was considered new and named *A. omorii* herein (see Table 5).

Consequently, our current recognition about the entity of this species group is documented as follows.

Taxonomic accounts

Genus ***Acetes*** H. Milne Edwards, 1830

Acetes indicus H. Milne Edwards, 1830

(Fig. 4)

Acetes indicus H. Milne Edwards, 1830: 351, pl. 11, figs 1–9.
?*Acetes indicus*: Kemp, 1917: 47, fig. 2a (in part)

Material examined. Bangladesh. *Chiringa (= Chakari)*: *Cox's Market Bazar*, 8 males (cl ca 3.5–5.0 mm), 19 females (cl ca 4.5–8.0 mm), 19 Aug 2018, coll. Kanak (formalin to 70% ethanol) (NSMT-Cr 31611); 5 males (cl ca 4.0–4.5 mm), 29 females (cl ca 4.5–8.0 mm), data same as precedent (ethanol) (NSMT-Cr 31612); 2 specimens used for DNA analysis, data same as previous (NSMT-Cr 31613, 31614): *Sitakunda Fish Market*, *Kumira-Sandwip Ship Ghat*: 9 females (cl 6.0–6.5 mm), 22°30.157′N, 91°41.324′E, Dec 2018, coll. Md Rakel-Ul Islam (NSMT-Cr

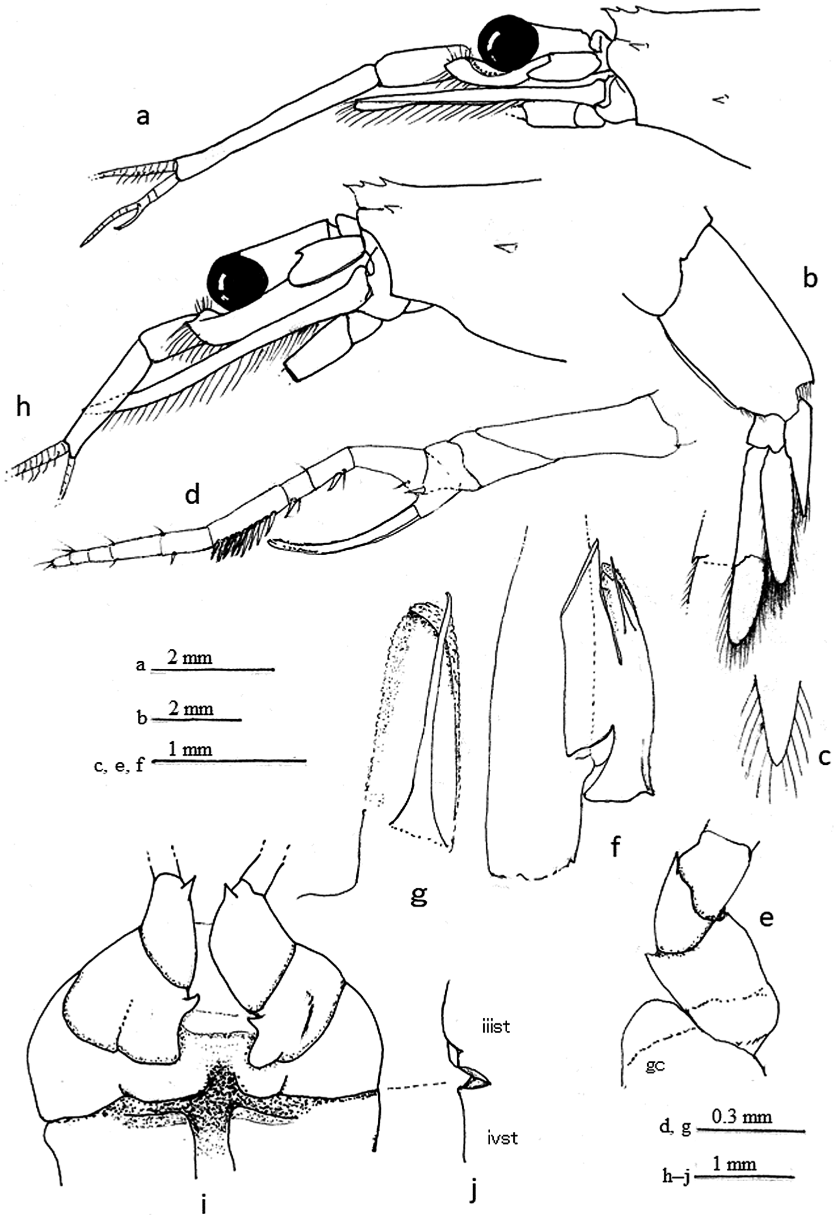

Fig. 4. *Acetes indicus* H. Milne Edwards, 1830. (a–g) male (cl 5.6 mm) from Kumia-Sandwip Ship Ghat Bangladesh, and (h–j) female (cl 7.3 mm) from same locality (NSMT-Cr 31616): a, anterior part of cephalothorax, lateral; b, posterior part of abdomen, lateral; c, posterior part of telson, dorsal; d, left lower antennular flagellum; e, basal segments of third pereopod and genital coxa, ventral; f, right petasma, posterior; g, same, capitulum; h, anterior part of cephalothorax, lateral; i, basal segments of third pereopod and third and fourth abdominal sternites, ventral; j, lateral profile showing channels and sternites between third and fourth thoracic somites. Abbreviations: gc, genital coxa; iiist and ivst, third and fourth thoracic sternites, respectively.

31615); 35 males (cl 4.3–5.6 mm), 37 females (cl 4.0–7.0 mm), Feb 2019, other data same as precedent (NSMT-Cr 31616); 3 specimens used for DNA analysis, data same as precedent (NSMT-Cr 31617–31619): 25 males (cl 4.6–6.0 mm), 9 females (cl 6.0–7.6 mm), commercial catch, Feb

2019, coll. Md Rakel-Ul Islam (NSMT-Cr 31620).

Description. *Male.* Rostrum (Fig. 4a, h) typical of Asian members of genus in having sub-triangular plate raised slightly from dorsal margin of carapace, having sharply pointed terminal tooth and small anterior tooth in addition to somewhat larger posterior tooth on its dorsal margin. Carapace smooth on surface, except for post-orbital and hepatic teeth.

Abdomen with first somite possessing procurved sharp tooth present at median part of ventral sternite between right and left pleopods. Sixth somite (Fig. 4b) twice length of fifth, postero-dorsal part ending in small postero-median tooth, no red spot on postero-ventral part. Telson (Fig. 4b, c) 0.7 times as long as sixth abdominal somite, with narrowly rounded or sub-triangular distal end.

Eye (Fig. 4a) with well pigmented cornea, latter wider than eye-stalk.

Antennule noticeably elongate in mature males, particularly in third segment of peduncle, 0.81–0.97 times as long as combined length of first and second segments; lower flagellum (Fig. 4a, d) modified into clasping organ, commonly composed of 12 segments, infrequently 13 or 14 segments; first segment of trunk rather long, noticeably narrowing at mid-length, three times or more as long as its narrowest part, forming distinct oblique conjunction with second one; major clasping spine moderately stout, reaching mid-length of fourth segment of main branch, bearing 2 incompletely aligned rows of minute serrated denticles, and also microscopically small clasping spine near base of major one; first segment of main branch with single basal setal-spine, and with or without single distal setal-spine, second and third segments each with single distal and/or sub-distal setal-spine, fourth segment 1.0–1.5 times as long as combined length of second and third segments, bearing usually 9 or 10 setal-spines on its entire margin, fifth segment with 1–3 setal spines.

Antennal scale (Fig. 4a) 0.75–0.80 times as long as carapace, slightly but distinctly extending beyond anterior margin of second segment of antennular peduncle.

External maxilliped and pereopods varying in length depending on body size. Third maxilliped in larger males extending as far as anterior end of antennular peduncle, distal segment three-fourths times as long as penultimate. First pereopod in larger males extending as far as cornea. Second pereopod in larger males reaching as far as anterior end of antennal scale. Third pereopod (Fig. 4e) in larger males extending anterior end of antennular peduncle, distinct sharp tooth present at disto-mesial part of basis and anteriorly curving projection on inner margin of coxa. Genital coxa (Fig. 4e) often with slender or sub-acute distal part in lateral aspect, while sub-rectangular or obtusely rounded in ventral aspect, with truncate or widely sinuous anterior part.

Petasma (Fig. 4f, g) with blunt and distally rounded capitulum bearing numerous hooks along lateral surfaces as well as distal part; processus ventralis slender, extending as far as distal margin of capitulum; no trace of pars astringen. Appendix masculina with 2 or 3 short hooks distally.

Endopod (Fig. 4b) of uropod with 1–6 irregularly-shaped red-spots in fresh materials: exopod with small tooth on lateral margin, demarcating non-ciliated and ciliated parts, latter about 0.6 times as long as former.

Female. Usually larger than males.

Antennule (Fig. 4h) not elongated as in males, first segment longest, and third segments 0.50–0.55 times as long as combined length of first and second segments; no examined females with intact lower flagellum.

Antennal scale (Fig. 4h) 0.71–0.74 times as long as carapace, extending to mid-length to distal one-third of third segment of antennular peduncle.

Third and fourth thoracic sternite having a somewhat shallow and wide longitudinal groove, not conspicuously narrowing anteriorly, median swelling low and not pronounced (Fig. 4i, j).

Body size. Largest male recorded from Bangladesh cl 5.6 mm, female 8.0 mm.

Type locality. Ganges Delta.

Remarks. As mentioned above, our study evidently showed that the current concept of *Acetes indicus* is a species complex, which may have derived a consequence of cryptic speciation from a common ancestor, leading to the existence of three extant species (see Figs 1, 2; Tables 2, 3). Among them, the population collected from the coastal waters of Bangladesh was regarded the representative of *A. indicus.*

Besides, Pathan and Jalihal (1997) mentioned that the materials reported by Kemp (1917) contains both the large and small forms. We suspect that his materials may have included some specimens of the typical *A. indicu*s because the illustration of the male lower antennular flagellum (Kemp 1917, fig. 2a) seems similar to this species rather than its South-East Asian congener.

Unfortunately, the sampling sites in this study were restricted to the eastern extremity of the Ganges Delta. Thus, a broad area of the northern coasts of the Gulf of Bengal was left un-surveyed, and future studies are strongly in need to clarify the nature of this species group in that region. The designation of a neotype, therefore, was not recommended until more detailed information are available from the region.

Distribution. Specimens attributable to *Acetes indicus* were found only from the coastal waters of Bangladesh (Fig. 3).

Acetes omorii Hanamura, Imai and Hardianto sp. nov.

(Figs 5, 6)

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Acetes indicus; Omori, 1975: 15 (in part; at least fig. 15c, e, i); Pérez Farfante and Kensley, 1997: 187, figs 128–130 (not H. Milne Edwards, 1830).
?Acetes indicus: Kemp 1917: 47 (in part): Boone, 1935: 101, fig. 9.

Material examined. Holotype: male (cl 5.3 mm), stn R 2, Matang Mangrove Estuary, Malaysia, sledge, 25 Nov. 2012, coll. Y. Hanamura & Faizul (NSMT-Cr 31621) (transferred from formalin to 70% ethanol). Paratypes: 1 male (4.8 mm), 3 females (cl 5.9–6.2 mm), data same as holotype (NSMT-Cr 31622) (transferred from formalin to 70% ethanol); 5 males (cl 3.5–5.3 mm), 9 females (cl 5.5–6.0 mm), 2 individuals (sex & size undetermined), sledge, 25 Nov 2008, coll. Y. Hanamura & Faizul (NSMT-Cr 31623); 2 specimens used for DNA analysis (sex and size undetermined), data same as previous (NSMT-Cr 31624, 31625); 2 males (cl 4.7, 5.5 mm), 3 females (cl 6.4–7.0 mm), stn R2, sledge, 29 Aug 2012, coll. Y. Hanamura & Faizul (FRI CR0011).

Other non-type materials. Malaysia. *Mouth of Merbok Mangrove Estuary*: 5 males (cl 4.5–5.0 mm), sledge, July 2005, coll. Y. Hanamura & Faizul (NSMT-Cr 31626): *Matang Mangrove Estuary*. 2 males (cl 4.8, 5.0 mm), 2 females (cl 5.9, 6.9 mm), sledge, 18 Aug 2005, coll. Y. Hanamura & Faizul (transferred from formalin to ethanol) (NSMT-Cr 31627): 14 males (cl 3.7–4.6 mm), 7 females (cl 3.7–6.4 mm), 3 juveniles (cl 1.5–2.3 mm), sledge, 25 Nov 2008, coll. Y. Hanamura & Faizul (NSMT-Cr 31628).

Indonesia. *Setrap River Estuary*, *Kalimantan Island*: 2 males (cl 6.5, 7.5 mm), 13 females (cl 7.0–10.0 mm), 30°48.005′S, 115°31.337′E, hand net, 19 Sept 2019, coll. E. Hardianto & H. Imai (NSMT-Cr 31631); 4 specimens used for DNA analysis (sex and size undetermined), data same as previous (NSMT-Cr 31632–31635).

Thailand. *Bam Bo Village*, *Samut Prakan (Gulf of Thailand)*: 1 male (cl 4.7 mm), commercial catch, June 2016, coll. K. Nakahara, part of appendages used for DNA analysis (NSMT-Cr 31636).

Description. *Male*. Rostrum (Fig. 5a, b) subtriangular, elevated slightly from dorsal margin of carapace, with sharply pointed terminal tooth and small anterior tooth in addition to somewhat larger posterior tooth on its dorsal margin. Carapace entirely smooth on surface, except for postorbital and hepatic teeth.

Abdomen with first somite possessing procurved sharp tooth at median part of ventral sternite between right and left pleopods. Sixth

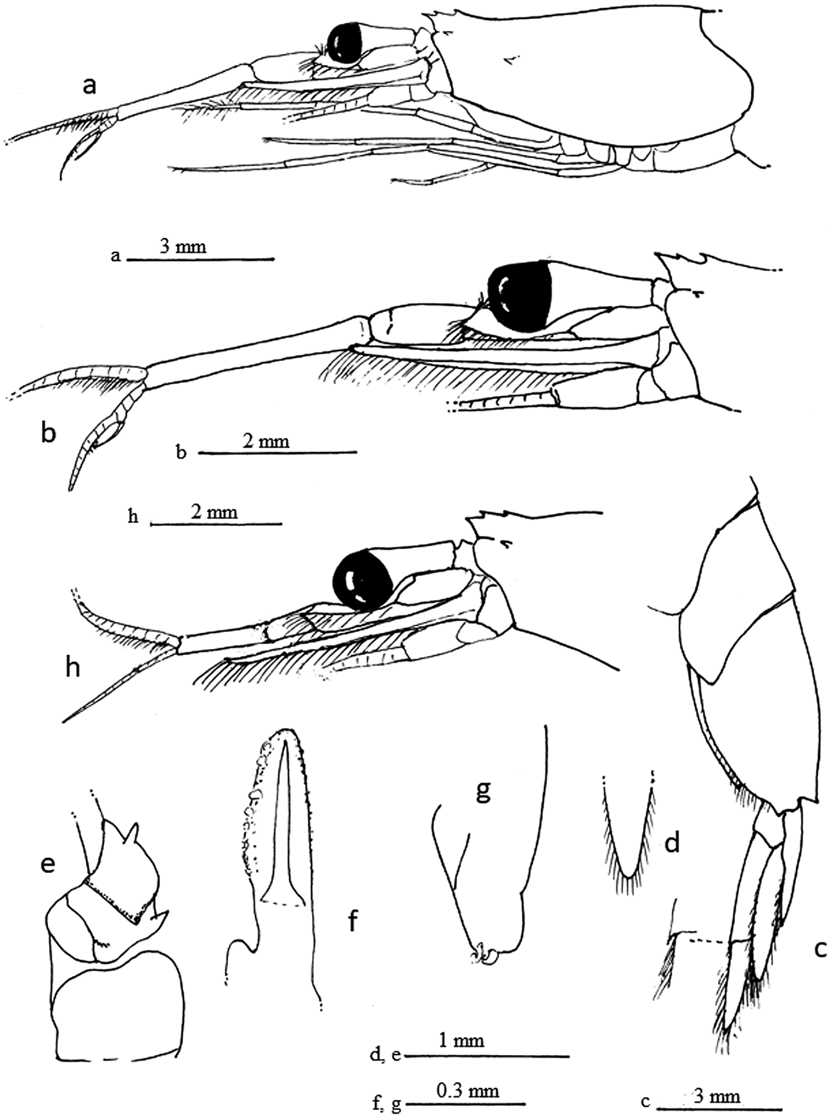

Fig. 5. *Acetes omorii* Hanamura, Imai and Hardianto sp. nov. (a–g) holotype male (cl 5.3 mm) (NSMT-Cr 31621), and (b–d) paratype female (cl 6.0 mm) from Matang Mangrove, Malaysia (NSMT-Cr 31622): a, cephalothorax, lateral; b, same, anterior part enlarged; c, right posterior part of abdomen, lateral; d, posterior part of telson, dorsal; e, basal segments of third pereopod and genital coxa; f, capitulum of petasma, posterior; g, right endopod of second pleopod, mesial; h, anterior part of body.

somite (Fig. 5c) twice length of fifth, postero-dorsal part ending in small tooth, no red spot on postero-ventral part. Telson (Fig. 5c, d) 0.7–0.8 times as long as sixth somite, posterior end narrowly rounded or sub-triangular with rounded distal part.

Eye (Fig. 5a, b) with well pigmented cornea, latter wider than eye-stalk.

Antennule (Fig. 7a, b) noticeably elongate in mature males, particularly in third segment of peduncle, 0.70–0.86 times as long as combined length of first and second segments; lower flagellum (Figs 5a, b, 6a) modified into clasping organ, commonly composed of 12-segmented; first seg-

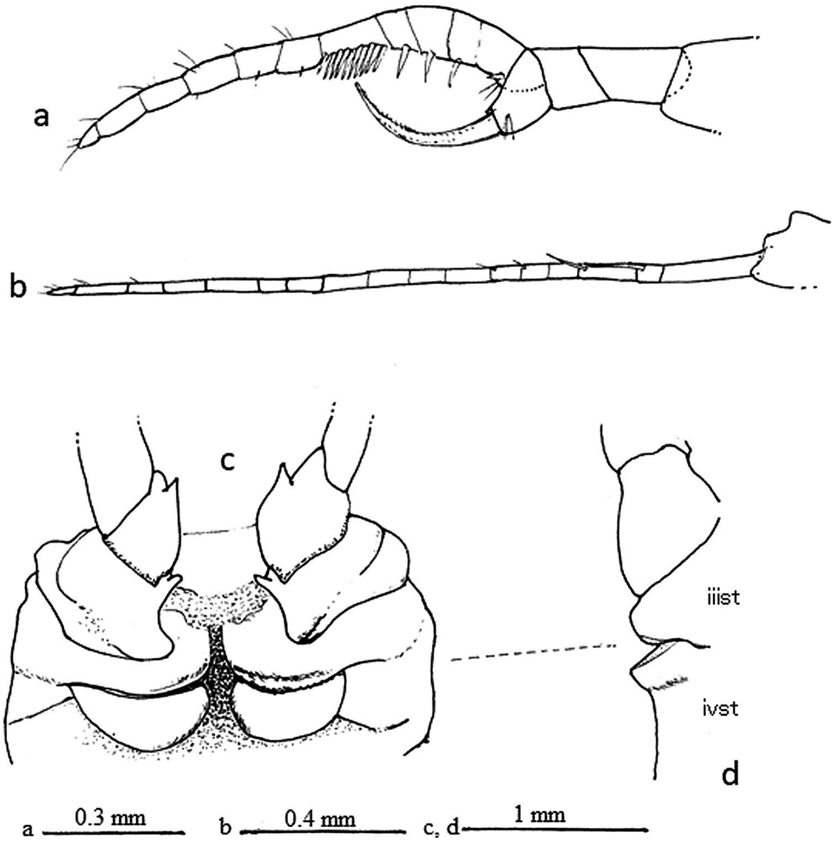

Fig. 6. *Acetes omorii* Hanamura, Imai & Hardianto sp. nov. (a) holotype male (cl 5.3 mm) (NSMT-Cr 31621), and (b–d) paratype female (cl 6.0 mm) (NSMT-Cr 31622) from Matang Mangrove, Malaysia: a, b, right lower antennular flagellum of male and female, respectively; c, basal segments of third pereopod and third and fourth abdominal sternites, ventral; d, lateral profile showing channels and sternites between third and fourth thoracic somites. Abbreviations: iiist, ivst, third and fourth thoracic sternites, respectively.

ment of trunk not noticeably long, almost uniform in width through length and utmost about twice length of its width, showing weakly oblique conjunction with second one; major clasping spine moderately stout, reaching as far as mid-length of fourth segment of main branch, with 2 aligned rows of minute serrated denticles, and rudimentary clasping spine present near base of major one; first sub-segment of main branch with single basal and single distal setal-spines, second and third each with single distal and/or sub-distal setal-spine, fourth segment 1.2–1.5 times as long as combined length of second and third segments, and usually bearing 9 or 10 setal-spines on its entire margin, fifth segment with 1–3 setal-spines.

Antennal scale (Fig. 5a) 0.70–0.79 times as long as carapace, slightly but distinctly extending beyond anterior margin of second segment of antennular peduncle.

External maxilliped and pereopods varying in length depending on body size. Third maxilliped in larger males extending as far as anterior end of antennular peduncle, distal segment about three-fourths times as long as penultimate. First pereopod in larger males extending as far as cornea. Second pereopod in larger males reaching as far as anterior end of antennal scale. Third pereopod (Fig. 5e) in larger males extending anterior end of antennular peduncle, distinct sharp tooth present at disto-mesial part of basis; coxa with anteriorly curving on its inner margin. Genital coxa (Fig. 5e) often with slender or sub-acute distal part in lateral aspect, while sub-rectangular in ventral aspect, with widely truncated or widely sinuous anterior part.

Petasma (Fig. 5f) with brunt and distally rounded capitulum bearing numerous hooks along lateral surface as well as distal part; processus ventralis slender, reaching as far as distal margin of capitulum; no trace of pars astringen, Appendix masculina (Fig. 5 g) with 2 or 3 short hooks distally.

Endopod (Fig. 5c) of uropod with 1–6 irregularly-shaped red-spots in fresh materials: exopod with small tooth on lateral margin demarcating non-ciliated and ciliated parts, latter about 0.7–0.8 times as long as former.

Female. Usually larger than males.

Antennule (Fig. 5h) not elongated as in males, first segment longest, and third segments 0.39–0.46 times as long as combined length of second and third segments; lower flagellum (Fig. 6b) as long as third segment of peduncle, constituted of 18–20 sub-segments.

Antennal scale (Fig. 5h) 0.67–0.74 times as long as carapace, extending to mid-length to distal one-third of third segment of antennular peduncle.

Third and fourth thoracic sternites forming longitudinal groove rather deep and narrow, median swelling steep and well pronounced (Fig. 6c, d).

Body size. Largest male cl 7.5 mm, female 10.0 mm, recorded from south-eastern part of Kalimantan Island, Indonesia.

Type locality. Matang Mangrove Estuary, Peninsular Malaysia.

Etymology. This species is named in honour of the late Dr. Makoto Omori (1937-2022), who first discussed the two morphological forms in *Acetes indicus*.

Remarks. Tirmizi and Ghani (1982) noted that specimens of *A. indicus* collected from Pakistan resemble Omori's large form. However, we have the impression that their morphological features appeared to be similar to *A. spiniger* rather than *A. omorii* sp. nov.

The specimens reported from Thailand by Pérez Farfante and Kensley (1997; figs 128–130) are regarded to be *A. omorii*, because the male lower antennular flagellum agrees well with that of this species.

Distribution. *Acetes omorii* sp. nov. has been collected with certainty in the coastal waters of South-East Asia, from Kalimantan Island, Indonesia to the Malacca Straits, via the Gulf of Thailand (Fig. 3). On the west coasts of Peninsular Malaysia, specimens of *A. omorii* sp. nov. were commonly captured in the inshore waters including mangrove estuaries (see also Hanamura *et al.*, 2007; under *A. indicus*).

Acetes spiniger Hansen, 1919

(Fig. 7)

Acetes spiniger Hansen, 1919; pl. 4, fig. 5a–f.
Acetes indicus: Kemp, 1917: 47 (in part); Omori, 1975: (in part; at least fig. 15a, b, d, f, g–i); Ravindranath, 1980: 255, figs 1–3; Pathan and Jalihal, 1997: 510.
?*Acetes indicus*: Tirmizi and Ghani, 1982: 44, figs 1, 2.

Material examined. Malaysia. *Off Kuala Selangor*, *Selangor (Malacca Straits)*: 31 males (cl 3.2–4.3 mm), 38 females (cl 3.3–5.8 mm), 9 juveniles and damaged specimens (cl 2.8–4.0 mm), several body parts, off-shore commercial catch, 23 Sept 2012, coll. Y. Hanamura & Faizul (NSMT-Cr 31637); 2 specimens used for DNA analysis (sex and size undetermined), data same as previous (NSMT-Cr 31638, 31639): 7 males (cl 3.5–4.4 mm), 10 females (cl 3.5–5.8 mm), 2 abdomens, data same as previous (NSMT-Cr 31640); 3 males (cl 3.7–4.0 mm), 2 females (cl 5.2, 5.8 mm), data same as previous (NSMT-Cr 31641). *Malacca*: 1 male (cl 3.8 mm), 13 females (cl 3.5–6.3 mm), fish market (dried products), 5 Aug 2005, coll. Y. Hanamura & Faizul (NSMT-Cr 31642).

India. *Off Calangule*, *Goa*; 4 males (cl 3.9–4.8 mm), 1 female (cl 6.4 mm), 1 Dec 1972, coll. C.T. Achuthanktty, id. M. Omori (NSMT-Cr 22267).

Description. *Male*. Rostrum (Fig. 7a) subtri-

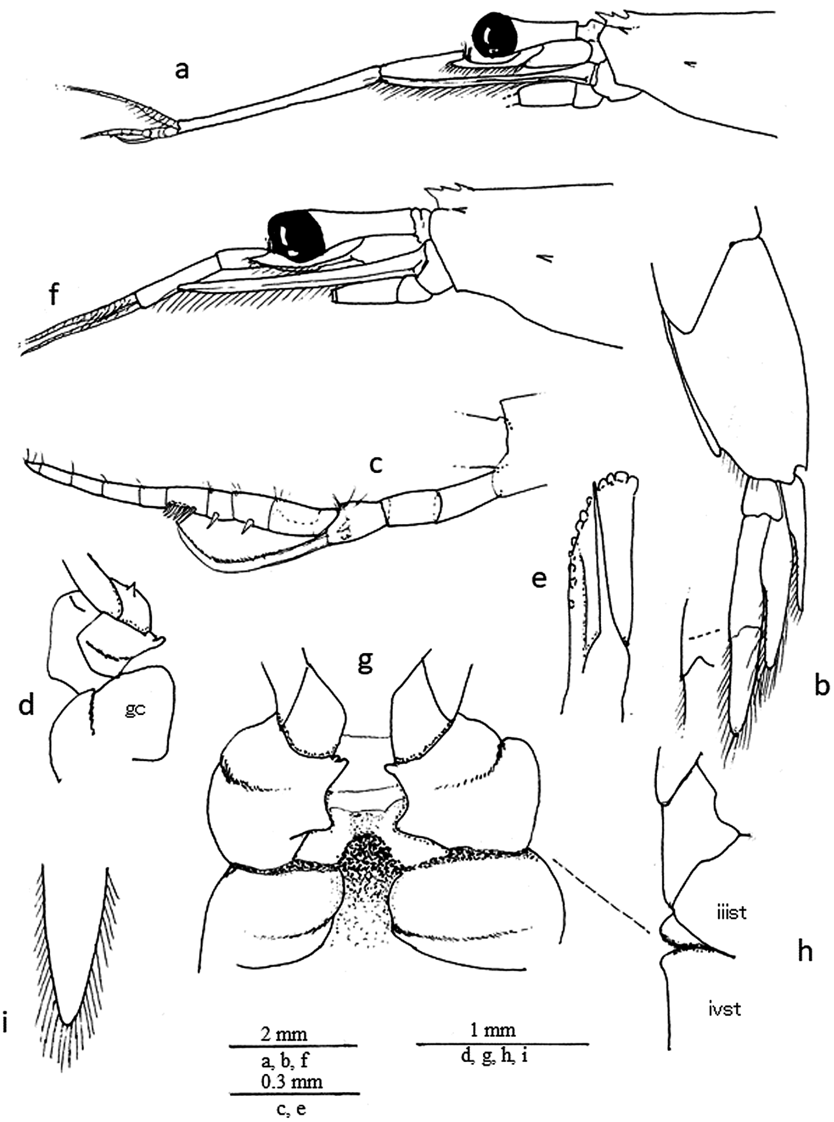

Fig. 7. *Acetes spiniger* Hansen, 1919. (a–e) male (cl 4.3 mm) and (f–i) female (cl. 5.8 mm) from off Kuala Selangor, Malaysia (NSMT-Cr 31637): a, anterior part of cephalothorax, lateral; b, posterior part of abdomen, lateral; c, right left lower antennular flagellum; d, basal segments of third pereopod and genital coxa, ventral; e, capitulum of right petasma; f, anterior part of cephalothorax, lateral; g, basal segments of third pereopod and third and fourth thoracic sternites, ventral; h, lateral profile showing channels and sternites between third and fourth thoracic somites, i, posterior part of telson, dorsal. Abbreviations: gc, genital coxa; iiist, ivst, third and fourth thoracic sternites, respectively.

angular, elevated slightly from dorsal margin of carapace, apex ending into sharp tooth, and armed dorsally with 2 teeth, posterior tooth larger than anterior one. Carapace (Fig. 9a) smooth, with small post-orbital and hepatic teeth.

Abdomen with first sternite possessing procurved sharp tooth at mid-part between right and left pleopods; sixth somite (Fig. 7b) somewhat compressed, 2.1–2.3 times as long as fifth, bearing small tooth or point at postero-median part, without red spot on postero-ventral part. Telson (Fig. 7b, i) 0.6–0.7 times as long as sixth abdominal somite, posterior part somewhat narrowing, then forming sub-triangular end.

Eye (Fig. 7a) with well pigmented cornea, latter wider than ocular peduncle in dorsal aspect.

Antennule (Fig. 7a) with elongate peduncle in adults, particularly in third segment, latter 0.92–1.10 times as long as combined length of first and second segments: lower flagellum (Fig. 7c) modified into clasping organ, most commonly with 12 sub-segments, distal part of first segment of trunk part forming nearly vertical or weak conjunction with second one; major clasping setal-spine somewhat slender, extending as far as mid-length of fourth segment of main branch, with single line of serrated denticles and rudimentary clasping spine placed near base of major spine; first segment of main branch with or without setal-spine; second and third segments with single setal-spine, fourth segment 0.5–0.7 times as long as combined length of anterior 2 segments, bearing 4–6 setal-spines on distal half.

Antennal scale (Fig. 7a) 0.70–0.81 times as long as carapace, barely reaching end of second segment of antennular peduncle but not extending beyond it, outer margin with small tooth at distal end.

Third maxilliped reaching mid-length of third segment of antennular peduncle, distal segment two-thirds times as long as penultimate segment. First pereopod shortest, falling slightly short of cornea of eye; second pereopod falling short of anterior end of antennal scale; third pereopod (Fig. 7d) longest, reaching mid-length of third segment of antennular peduncle; coxa with stout tooth or projection on distal inner margin; basis with obtuse tooth near distal inner part. Genital coxa narrowly tapering distally in lateral aspect, but widely truncated or weakly grooved in ventral aspect.

Petasma (Fig. 7e) with capitulum robust and somewhat rounded distally, bearing numerous hooks on distal and lateral surfaces; processus ventralis narrow, reaching as far as distal end of capitulum; pars astringen occasionally noticeable as weak elevation or vestigial lobule. Appendix masculina with 2 or 3 hooks on distal margin.

Uropod (Fig. 7b) with exopod bearing small but distinct tooth at distal 0.64–0.76 on lateral margin, basal part from which is naked while setose in distal part; no confident data for its number of red spots, but at least 1 or 2 spots present in preserved specimens.

Female. Usually larger in body size than males and also differing in several sexual characters.

Antennule (Fig. 7f) with first segment longest, and third segment of peduncle not elongated as in male, 0.33–0.47 times as long as combined length of second and third segments; lower flagellum simple and not modified, composed of 19 or 20 sub-segments.

Antennal scale (Fig. 7f) 0.64–0.73 times as long as carapace, reaching about basal 2/5–1/3 length of third segment of antennule peduncle.

Third maxilliped extending beyond antennular peduncle by distal and 1/2–1/3 of penultimate segment, distal segment 0.70–0.75 times as long as penultimate.

First pereopod shortest, fully reaching cornea of eye; second pereopod falling slightly short of distal end of antennular peduncle; third pereopod extending beyond antennular peduncle by length of propodus and dactylus.

Third and fourth thoracic sternites forming longitudinal groove rather wide and shallow, not conspicuously narrowing anteriorly and not swelling markedly (Fig. 7g, h)

Body size. Largest male cl 4.8 mm and female cl 6.4 mm from Goa, India.

Type locality. The type locality of this species should be off Rangoon, Burma (now Yangon, Myanmar), based on which materials Omori (1975) evidently noted the morphological traits of this species.

Remarks. Tirmizi and Ghani (1982) reported *A. indicus* from Pakistan, as a species resembling Omori's "large form" (= *A. omorii* sp. nov.). The male lower flagellum figured by these authors appeared to show an unusual form for the "*A. indicus*" species complex in having an extremely elongated first segment of the main branch as well as a relatively short clasping tooth. However, the form of the female genital area seemed similar to *A. spiniger* rather than the latter by a broad sternal groove, although future confirmation is in need for specimens occurring in Pakistan.

Distribution. This species is known with certainty in the peripheral region of the north-eastern part of the Indian Ocean, from the Malacca Straits and off Galangule, Goa, India (and probably to Pakistan). In the Malacca Straits, *A. spiniger* is commercially fished by offshore trawls. Contrary to this, *A. omorii* sp. nov. occur in great abundance in the inshore waters including mangrove estuaries, suggesting that the two closest relatives are sharing their major habitats (Fig. 3).

Acknowledgements

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