

THE GIANT FRESHWATER PRAWNS OF THE *MACROBRACHIUM ROSENBERGII* SPECIES GROUP (CRUSTACEA: DECAPODA: CARIDEA: PALAEMONIDAE)

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ABSTRACT. – The present study of the giant freshwater prawns, *Macrobrachium rosenbergii* species group, examined a large series of wild-caught specimens from most of its known distribution. The results confirm that what has been called *M. rosenbergii* actually belongs to two separate species, easily-separated by a number of diagnostic adult morphological characters. *Macrobrachium rosenbergii* (de Man, 1879) sensu stricto occurs in Australia, Papua New Guinea, eastern Indonesia (east of Huxley's Line including Bali) and the Philippines (including Palawan). The second species, which is actually the one more widely fished and extensively cultured in America, Asia and Africa, is here identified as *M. dacqueti* (Sunier, 1925), and occurs throughout South and Southeast Asia, as well as Indochina. This latter species is one of the most commercially important crustaceans in the world.

KEY WORDS. – Taxonomy, Crustacea, Caridea, Palaemonidae, *Macrobrachium rosenbergii*.

INTRODUCTION

The giant freshwater prawn, previously known as *Macrobrachium rosenbergii* (de Man, 1879), is the largest known palaemonid in the world. Males can reach up to 320 mm in total body length, whilst females can grow up to 250 mm (Cowles, 1914; Holthuis, 1950, 2000). They are one of the most commercially important crustaceans, being widely fished and reared in ponds and rice fields throughout its natural distribution and beyond (see New, 2000). The modern aquaculture of the species began in the early 1960s through the work of Shao-Wen Ling, a Food and Agriculture Organization (FAO) expert, when he and his collaborators discovered that the larvae of *M. rosenbergii* needed brackish water for survival (Ling & Merican, 1961; Ling, 1977; Ling & Costello, 1979). Takuji Fujimura and his team at the Anuenue Fisheries Research Center in Honolulu, Hawaii, successfully used this information to commercialize the culture of this prawn in 1965 (New, 2000). Today, it is widely cultured all over the world. In the last decade, average *M. rosenbergii* production rose by some 9–35.48% in quantity and 19.68–24.5% in value. In 1993, the overall production was 17,164 tonnes, worth US\$ 116,799,000 and in 2005 it reached 205,033 tonnes with a net value of US\$ 896,263,000 (FAO, 2007). Giant freshwater prawn farming

is thus a major contributor to global aquaculture, both in terms of quantity and value.

Due in no small part to its commercial value, there has been extensive research on what has been widely called *M. rosenbergii*, ranging from fisheries, aquaculture, taxonomy, morphology, development, anatomy, physiology, biochemistry, ecology to even social behavior (see Holthuis, 2000). These include numerous MSc and PhD projects from all over the world (see Karplus et al., 2000). A search of the *Web of Science* from 2000 to 2005 revealed an average of 29 scientific papers published each year and in 2006 there were 69 scientific articles published relating to its culture, on aspects such as nutrition, disease control, physiology and biochemistry. There are many more papers on these and other topics related to this prawn not formally captured in the various indexing services in regional journals, local publications and “grey” literature. This is especially so since the species is widely fished, reared and studied in many less advanced and poorly-developed countries in Asia.

In contrast to this wealth of biological information, there have been some problems with the nomenclature of the species. Mention of a giant freshwater prawn species was first published in Rumphius' (1705: Pl. 1 Fig. B) *D'Amboinsche*

Rariteitkamer. The figure was actually not provided by Rumphius himself but was later added to his manuscript by the editor of Rumphius' book who wanted the book more richly illustrated (Holthuis, 1959, 2000; Beekman, 1999). The figure was referred to by Fabricius as *Astacus carcinus* in 1793, and *Palaemon carcinus* in 1798. The latter name was adopted for the next one and a half centuries. However, Sunier (1925) challenged this nomenclature. He showed that Linnaeus' (1758) description of *Cancer carcinus* (with the name of the genus changed to *Astacus* and *Palaemon* by Fabricius in 1793 and 1798, respectively), was solely based on American material and he therefore proposed the new specific name *dacqueti* for the Indo-West Pacific species (Sunier, 1925). In 1950, Sunier's views were confirmed (Holthuis, 1950), except that it was pointed out that the name *Palaemon rosenbergii* de Man, 1879, for the Indo-West Pacific species, is actually older than *P. dacqueti* Sunier, 1925 and that the specific name *rosenbergii* had to be used for the present species (see Holthuis, 2000, for more details of the nomenclatural history).

The name *Macrobrachium rosenbergii* (de Man, 1879) has 15 associated synonyms, and over the years, there has been some debate as to whether it is just one species. The current opinion, following the revision of the genus by Holthuis (1950), is that there is only one wide-ranging species. Johnson (1960, 1973), however, recognized two subspecies of *M. rosenbergii* based on their morphology. The western subspecies, which occurs on the Asian mainland and Malaysia, was identified as *M. rosenbergii schenkeli* Johnson, 1973, with the eastern subspecies called *M. rosenbergii rosenbergii* (de Man, 1879). Morphometric and allozyme work in the 1970s and 1980s supported this conclusion (see Hedgecock et al., 1979; Lindenfelser, 1984); with recent studies on mitochondrial DNA and microsatellites further corroborating this (de Bruyn et al., 2004a; Chand et al., 2005). In particular, Chand et al.'s (2005) microsatellite work showed a sharp division between the western and the eastern populations. Holthuis (1995), however, commented that if two subspecies were to be recognized, the correct name for the western subspecies would be *M. rosenbergii dacqueti* (Sunier, 1925), with the name of the eastern subspecies remaining as *M. rosenbergii rosenbergii* (de Man, 1879). While the biochemical signals may be strong for the recognition of two "populations", the morphological basis for justifying this has been "relatively weaker". The characters that had been used by morphologists to separate the two "populations" (e.g. see Johnson, 1960, 1973; Lindenfelser, 1984) are generally regarded as subtle at best and not always reliable. As such, workers have been reluctant or very cautious to regard them as separate species or even subspecies. Only recently have some taxonomists (e.g. Cai & Ng, 2001, 2002; Wowor & Choy, 2001; Cai et al., 2003) started to again recognize two subspecies in the so-called *M. rosenbergii* species group. Wowor & Ng (2001) in a meeting, presented evidence that a suite of reliable adult characters could in fact easily separate the two "populations" and proposed to recognize them as two separate species. However, up to now only an abstract was published (Wowor & Ng, 2001) and the main part of this work has remained unpublished. The present paper presents

the morphometric data and detailed analyses which argue for the recognition of two species of what has been traditionally called "*Macrobrachium rosenbergii*".

MATERIALS AND METHODS

A total of 373 specimens of the *Macrobrachium rosenbergii* species group were examined, including fresh ones from the field as well as natural history museum material. All are wild-caught specimens from much of its natural distribution. We have intentionally excluded cultured individuals unless we are certain they are based on wild stock from a known provenance. The aim of the present study is to ascertain the differences between the presently accepted two subspecies, *M. r. rosenbergii* and *M. r. dacqueti*, and to see if they should be recognised as species, using a suite of morphometric measurements and the multivariate method of Multiple Discriminant Analysis (MDA). In the taxonomy section, the description of *M. rosenbergii* is based on two adult male specimens of 54.9–62.2 mm CL and the diagnosis of *M. dacqueti* is based on three adult male specimens of 67.3–75.5 mm CL.

The material examined are deposited in Naturalis, Nationaal Natuurhistorisch Museum [formerly Rijksmuseum van Natuurlijke Historie (RMNH)], Leiden, The Netherlands; Naturhistorisches Museum Basel (NHMB), Basel, Switzerland; Natural History Museum (NHM), London, United Kingdom; the American Museum of Natural History (AMNH), New York and National Museum of Natural History, Smithsonian Institution (USNM), Washington D.C., U.S.A.; Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, National University of Singapore (NUS), Singapore; University of San Carlos (USCC), Cebu, Philippines; Division of Zoology, Research Center for Biology, Indonesian Institute of Sciences [formerly Museum Zoologicum Bogoriense (MZB)], Cibinong, Indonesia; Queensland Museum (QM), Brisbane; South Australian Museum (SAM), Adelaide; Northern Territory Museum of Arts and Sciences (NTM), Darwin; and Australian Museum (AM), Sydney, Australia. The abbreviations used are CL for carapace length; T4 for thoracic sternite 4; Is. for island; Ck. for creek; R. for river; and Rd. for road.

MORPHOMETRICS

Morphologically defining characters for each species were determined by MDA mainly based on the distinguishing features as described by Johnson (1973) (see below). For MDA (SPSS version 7), 151 complete prawn samples were used. Samples with a broken rostrum or missing both second pereiopods were recorded as missing data and were omitted from the analysis.

The following discrete characters were recorded: sex, number of dorsal and ventral teeth of the rostrum (DORTEETH and VENTTEETH), the relative position of the tip of the rostrum to the distal margin of the scaphocerite (ROSTREACH), the

height of the base of the rostrum (ROSTBASE), and the type and the presence or absence of spines on the second pereiopod (P2). Additionally, five continuous characters were measured with vernier calipers to the nearest 0.05 mm: carapace length (distance between the postorbital margin to the posterior median margin of the carapace); rostral length (distance between the tip of the rostrum and the postorbital margin); dactylus length of the second pereiopod (distance between the tip and the pivot at the dactylus-propodus joint); palm length of the second pereiopod (distance between the insertion on the dactylus and the margin at the chela-carpus joint); and carpus length of the second pereiopod (distance between the proximal and the distal margin of the carpus).

The characters were size standardized through the creation of three ratios, i.e. dactylus length/palm length (DAC/PLM), carpus length/palm length (CARP/PLM) and rostrum length/carapace length (RL/CL). Male samples with CL 52.0 mm or larger and female samples with CL 45.0 mm or larger were treated as adult, and males with CL less than 52.0 mm and females with CL less than 45.0 mm were categorized as young. All young specimens do not have fully developed second pereiopods, i.e. with especially the spines are still small and weak or have not yet developed.

The MDA analysis produces linear combinations of variables (roots) that maximize differences among a priori defined groups (in this case species), with the hit ratio (percentage correctly classified) providing a goodness of fit measure. All variables were entered simultaneously in all MDA analyses and the relative contributions of each variable were assessed on the basis of the discriminant loadings (De Grave & Diaz, 2001).

RESULTS

A continuous variable, the ratio between dactylus and palm lengths, was found not to exhibit any variation between adults of both taxa, and therefore it was excluded from further analysis. This character was used by Johnson (1973) to separate two supposed subspecies.

Two Multiple Discriminant Analyses were run; one on adults only (both sexes combined) and one on males only (adults and young specimens combined). MDA analysis on adults only (Fig. 1) shows that Root 1 separates *Macrobrachium r. rosenbergii* from *M. r. dacqueti*, and the first root accounted for all variance. Examination of the structure matrix (Table 1) reveals that three variables are highly loaded on the first root: P2, ROSTBASE and VENTEEETH. A classification matrix indicates that overall 100% of a priori grouped cases were correctly classified, with within-group classifications being: *M. r. rosenbergii* 100% and *M. r. dacqueti* 100%. The MDA analysis on males only also reveals the same structure in the data set. *Macrobrachium r. rosenbergii* is separated from *M. r. dacqueti* along Root 1, except for a single specimen of *M. r. dacqueti*, which was classified as *M. r. rosenbergii* (Fig. 2). The structure matrix shows that three variables are associated with the first root: ROSTBASE,

VENTEEETH and DORTEETH (Table 2). A classification matrix indicates that overall 99.3% of a priori grouped cases were correctly classified, with within-group classifications being: *M. r. rosenbergii* 100% and *M. r. dacqueti* 98.5%. A single young male *M. r. dacqueti* specimen was classified as *M. r. rosenbergii* by the analysis. The above morphometric analyses clearly demonstrate that the two "subspecies" are in fact two morphologically different taxa and should be recognized as distinct species, i.e. *M. rosenbergii* and *M. dacqueti*.

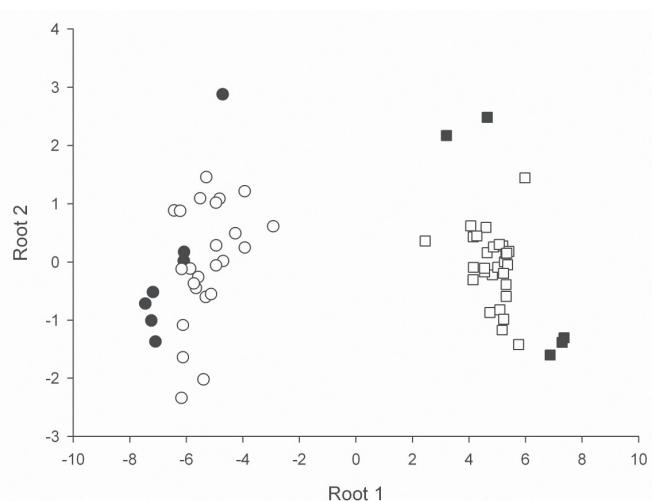


Fig. 1. Scatterplot of MDA scores (first root) for the two supposed subspecies, adults only. Symbols: *Macrobrachium rosenbergii* females (filled circle), *M. r. rosenbergii* males (empty circle), *M. r. dacqueti* females (filled square) and *M. r. dacqueti* males (empty square). Eigenvalue = 28.709; Wilks's λ = 0.034; χ^2 = 200.095, df = 8, $p < 0.0001$.

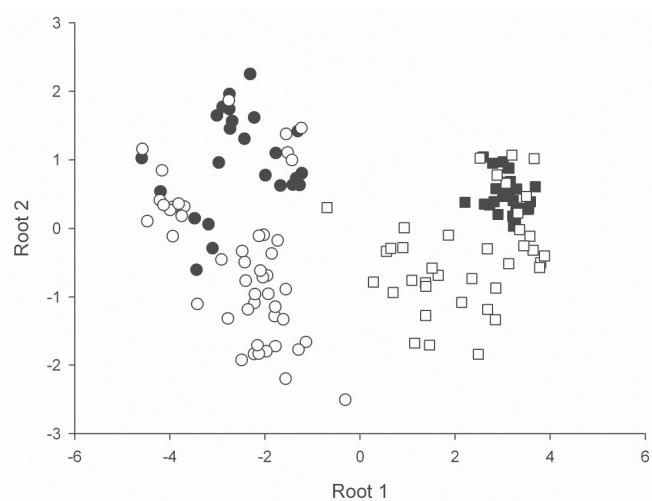


Fig. 2. Scatterplot of MDA scores (first root) for the two supposed subspecies, males only. Symbols: *Macrobrachium rosenbergii* adult males (filled circle), *M. r. rosenbergii* young males (empty circle), *M. r. dacqueti* adult males (filled square) and *M. r. dacqueti* young males (empty square). Eigenvalue = 6.587; Wilks's λ = 0.132; χ^2 = 267.485, df = 8, $p < 0.0001$.

Table 1. Discriminant analysis on adults only. Structure of discriminant loadings. All variables entered simultaneously.

	P2	ROSTBASE	VENTEETH	RL/CL	DORTEETH	ROSTREACH	CARP/PLM
Root 1	0.495	0.388	0.265	0.146	0.124	-0.118	-0.006

Table 2. Discriminant analysis on males only. Structure of discriminant loadings. All variables entered simultaneously.

	ROSTBASE	VENTEETH	DORTEETH	P2	ROSTREACH	RL/CL	CARP/PLM	DAC/PLM
Root 1	0.551	0.449	0.247	0.149	-0.136	0.045	0.035	-0.030

TAXONOMY

PALAEMONIDAE Rafinesque, 1815

Macrobrachium Bate, 1868

Macrobrachium rosenbergii (de Man, 1879)

(Figs. 3, 5A, 6A–B, 7A, 8, 10)

Palaemon Rosenbergii de Man, 1879: 167.

Palaemon carcinus – von Martens, 1868: 34 (part); de Man, 1879: 165 (part); Miers, 1880: 382 (part); Thallwitz, 1892: 7, 15; Schenkel, 1902: 504; Cowles, 1914: 3, Pl. 1, Fig. 1 (not *Cancer carcinus* Linnaeus, 1758).

Palaemon carcinus var. *rosenbergii* – Ortmann, 1891: 701.

Palaemon (Eupalaemon) carcinus – de Man, 1892: 421 (part); 1902: 475, 763 (part); Nobili, 1899: 236; Roux, 1928: 219 (not *Cancer carcinus* Linnaeus, 1758).

Palaemon (Eupalaemon) Rosenbergi – Nobili, 1899: 236.

Palaemon spinipes Schenkel, 1902: 501, Pl. 9, Fig. 7 (not *Palaemon spinipes* Desmarest, 1817).

Palaemon (Eupalaemon) carcinus var. *rosenbergi* – Roux, 1917: 595; 1921: 587; 1923: 4; 1927: 321; 1933: 344.

Macrobrachium rosenbergii – Holthuis, 1950: 111, Fig. 25 (part); Johnson, 1960: 261 (part); Hedgecock et al., 1979: 873 (part); Lindenfelser, 1984: 195 (part); Chace & Bruce, 1993: 36, Fig. 15; Mather & de Bruyn, 2003: 4 (part); de Bruyn et al., 2004a: 251 (part); 2004b: 3515; Short, 2004: 44, Figs. 16–18, 36L, M; Chand et al., 2005: 308.

Macrobrachium rosenbergi (sic) – Riek, 1951: 361, Fig. 12.

Macrobrachium rosenbergii rosenbergii – Johnson, 1973: 277; Holthuis, 1995: 148; 2000: 16, Fig. 2.2; Cai & Ng, 2001: 674.

Material examined. – Type material: *Palaemon Rosenbergii* de Man, 1879: holotype, ovigerous female (68.0 mm CL) (RMNH D 1097), Andai, New Guinea [Papua], Indonesia, coll. C. B. H. von Rosenberg, 2 Jun. 1869, Feb.–May. 1870. *Palaemon spinipes* Schenkel, 1902: holotype, male (74.4 mm CL) (NHMB 10a), Kema, Celebes [Sulawesi], Indonesia, coll. P. & F. Sarasin, 1901.

Other material – **Indonesia:** Sulawesi: 1 male (20.5 mm CL) (RMNH D 6644), Cenrana R.; 1 male (90.4 mm CL) (RMNH D 6347), Makassar; Papua: 10 males (16.5–36.0 mm CL), 11 females (10.4–33.9 mm CL), 1 ovigerous female (32.7 mm CL) (MZB), Ajkwa R., Timika; 16 males (19.0–62.2 mm CL), 18 females (29.2–41.2 mm CL), 20 ovigerous females (29.0–41.3 mm CL) (MZB), Ajkwa R., Timika; Bali: 2 males (18.2–62.6 mm CL) (NHM 1880.6); Sumba: 1 male (19.6 mm CL) (RMNH D 30657), Rende R., E. Sumba; Halmahera: 1 female (25.0 mm CL) (USNM 211084), Kao Bay. **Philippines:** 1 male (64.9 mm CL)

(NHM 1872.7); Mindanao: 1 male (81.3 mm CL) (USNM 53871), Zamboanga R.; 1 ovigerous female (42.6 mm CL) (USNM 53868), Rio Grande R.; Luzon: 1 male (83.7 mm CL), 2 ovigerous females (42.4–56.2 mm CL) (USNM), Manila; 1 male (42.5 mm CL), 1 ovigerous female (43.6 mm CL) (USNM 54613), Manila; 3 males (22.9–32.4 mm CL) (USNM 429), Manila; 1 male (75.1 mm CL), 1 female (55.6 mm CL) (USNM 441), Montalban R., San Mateo, Rizal; 1 male (52.8 mm CL), 1 ovigerous female (42.8 mm CL) (ZRC 1999.082), Southern Luzon; Panay: 2 males (33.4–70.7 mm CL), 1 female (52.3 mm CL), 3 ovigerous females (57.4–59.0 mm CL) (USNM), Jaro R.; 1 male (66.4 mm CL) (USNM 105626), Jaro R.; 1 ovigerous female (45.7 mm CL) (USNM), Jaro R.; 4 ovigerous females (49.2–55.3 mm CL) (USNM), Jaro R.; 1 male (41.9 mm CL) (USNM), Iloilo; 1 ovigerous female (52.3 mm CL) (USNM), Iloilo; Palawan: 2 females (31.9–34.1 mm CL) (NHM 1894.7.4.1–2); Bohol: 1 male (104.0 mm CL) (ZRC 2000.2407), Loboc R.; Samar: 1 male (75.0 mm CL) (USCC), Northern Samar. **Papua New Guinea:** 1 male (64.7 mm CL) (USNM 170364), Fly R.; 1 male (18.2 mm CL) (AMNH 11339), Fly R.; 1 female (39.9 mm CL) (USNM 141316), Lake Kamu R.; 1 female (29.3 mm CL) (QM W21966), Bersback R. **Australia:** Northern Territory: 1 male (53.7 mm CL), 1 female (44.6 mm CL) (USNM 151033), Darwin; 1 male (53.7 mm CL) (NHM 1858.97), Northern Australian Expedition; 1 male (41.1 mm CL) (NTM Cr005529), Daly R., Claravale; 8 males (46.3–59.4 mm CL) (NTM Cr005849), Coppermine Billabong, Daly R.; 1 female (24.8 mm CL) (QM W25412), Adelaide R.; 1 male (16.4 mm CL) (NTM Cr007395), Jim Jim Ck., Kakadu; 2 females (11.0–13.3 mm CL) (NTM Cr006792), Blyth R.; 4 males (45.6–64.7 mm CL), 2 females (37.4–41.5 mm CL) (QM W19663), Roper R.; 1 male (59.6 mm CL) (AM P42536), McArthur R.; 5 males (45.1–74.0 mm CL) (AM P42538), Ryans Bend; Queensland: 1 male (13.4 mm CL) (QM W12614), Gregory R., Riversleigh Stn.; 1 male (17.5 mm CL) (QM W15163), Leichardt R., crossing near Nardoo Stn.; 1 male (55.6 mm CL) (QM W15311), Norman R., Normanton; 1 female (42.3 mm CL) (QM W7251), Norman Ck., Normanton Rd.; 1 male (22.5 mm CL) (QM W6676), mouth of Norman R.; 1 male (31.0 mm), 3 females (15.5–46.9 mm CL) (QM W14937), Walker Ck. near Normanton; 1 male (45.0 mm CL) (QM W16398), Lynd R.; 2 males (65.4–71.2 mm CL) (QM W7892), Mt. Molloy; 1 male (60.4 mm CL) (QM W5434), Spear Ck. near Mt. Molloy; 1 male (70.3 mm CL) (QM W3063), Rifle Ck. near Mt. Molloy; 1 male (83.3 mm CL) (QM W16487), Mitchell R.; 1 female (16.4 mm CL) (QM W11967), Mitchell R.; 1 female (27.1 mm CL) (QM W16399), Palmer R.; 1 male (38.4 mm CL) (QM W24879), Walsh R.; 1 male (35.1 mm CL) (AMNH 11340), Archer R.; 2 females (23.1–24.3 mm CL) (QM W11976), Archer R.; 2 females (20.6–21.6 mm CL) (QM W16393), Archer R.; 1 male (65.5 mm CL) (QM W9714), Coconut Ck. north of Aurukun, Cape York; 1 male (38.3 mm CL) (QM W12870), Coen R.; 1 male (47.4 mm CL) (ZRC 1999.627), Wenlock R.; 2 males (12.7–21.5 mm CL), 2 females (17.6–20.2 mm CL) (QM W16848), Wenlock R.; 1 male (38.9 mm CL) (QM W16622), Wenlock R.; 3 males

(27.5–49.2 mm CL), 2 females (31.9–35.0 mm CL) (QM W16701), Dulhunty R. at telegraph line crossing; 1 female (39.5 mm CL) (QM W24289), north of Weipa; 1 male (20.1 mm CL) (QM W22243), Olive R.; 1 male (45.0 mm CL) (QM W16397), East Normanby R., SW of Cooktown; 1 male (21.1 mm CL), 3 females (19.1–26.3 mm CL) (QM W16623), Normanby R., Orange Plain Waterhole; 1 male (34.6 mm CL) (QM W3993), Hann R.; 1 male (71.0 mm CL) (QM W16621), Hann R., Peninsula Developmental Rd.; 2 males (23.6–44.4 mm CL), 4 females (25.8–34.4 mm CL) (QM W22028), McIvor R., Isabella-McIvor Rd. crossing.

Diagnosis. – Rostrum long when young, relatively shorter with age, basal crest low to moderately low, sinuous. Rostral formula: 2-3/8-14 (mode 12)/6-15 (mode 9). Second pereiopod long, subcylindrical with carpus extending beyond scaphocerite, carpus longer than merus, similar in form, equal in size, covered by large and small spines except dactylus which is covered by pubescence. T4 armed, post T4 with ridge. Preanal carina present. Mobile mesial spine of exopod of uropod smaller than distolateral tooth. Eggs small, numerous.

Description. – Rostrum: Long (1.37–1.45 times CL in young males of 25.4–27.0 mm times CL with tip distinctly extending beyond distal end of scaphocerite), becoming shorter with age (0.59–0.73 times CL in fully adult males of 65 mm times CL and larger, with tip not extending beyond distal end of scaphocerite but extending beyond end of third segment of antennular peduncle); moderately deep, maximum depth slightly more than maximum dorsoventral diameter of cornea; lateral carina well developed, continuing to about proximal half; basal crest low to moderately low, sinuous; teeth above orbit more closely spaced than those on carapace and distal half of rostrum, teeth on distal half of rostrum most widely spread, armed with 8–14 teeth (mode 12) including 1 or 2 apical teeth, 2 or 3 teeth completely postorbital, postorbital

teeth on anterior 0.24–0.30 of carapace; ventral carina with 6–15 teeth (mode 9), first tooth located at about proximal one-third or one-fourth.

General cephalon: ocular cornea well developed, 0.10–0.11 times CL (0.15–0.17 times CL in other specimens). Inferior orbital margin moderately produced, generally angular, with postantennular carapace margin concave or straight in developed specimens, sometimes obtuse, slightly angular above and rounded below in younger specimens. Antennal spine sharp, slender, continuing posteriorly as a ridge, situated below lower orbital angle; hepatic spine smaller, situated behind and below antennal spine; branchiostegal suture running from hepatic spine to carapace margin. Carapace spinulate. Ocular beak well developed with expanded lateral tip. Epistome completely bilobed, lobes with blunt rounded margin. Scaphocerite stout, 0.67–0.68 times CL, length 2.76–2.82 times maximum breath, lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at inner angle, lateral margin slightly concave, distolateral tooth failing to reach end of lamella. Third maxilliped with ultimate segment reaching beyond antennal peduncle; ultimate shorter than penultimate, 0.75 as long as penultimate; exopod shorter than ischiomerus.

First pereiopods: Slender, exceeding scaphocerite by distal one-third of carpus; fingers about as long as palm; carpus 2.30–2.39 times chela length, 1.32–1.33 times merus length; a row of short stiff setae present along inner margin of ischium and basis.

Second pereiopods: similar in shape, equal in size, long, slender; carpus of cheliped extending beyond end of scaphocerite. Cheliped: large spines and spinules abundant on all segments except dactylus; dactylus thickly covered by pubescence; chela 2.02–2.03 times CL, length 12.37–14.09 times width, outer and inner margins straight, upper and lower margins rounded; palm subcylindrical, about equal to maximum merus width, width 1.02–1.10 times depth, outer and upper margins more densely covered with smaller spines than inner and lower margins, spinules of equal size cover all surfaces; fingers 0.61–0.74 times palm length, not gaping, cutting edges with well-developed teeth, teeth obscured by pubescence, dactylus with 2 large teeth on proximal 0.3, subequally distributed, pollex with 1 large tooth at distal and 2 smaller teeth towards articulation of fingers distributed along proximal one-fifth, teeth unequally distributed along cutting edges; fingers uncinate at tip; carpus 1.07–1.11 times palm length, subcylindrical, length 6.91–7.11 times distal width, 0.64–0.67 times chela length, 1.33 times merus length; merus not inflated, slightly tapered, 1.41–1.46 times ischium length; ischium tapered with a median groove along upper margin, spines and spinules relatively less dense.

Third pereiopods: large spines, spinules and few scattered rather long stiff setae present on all segments; entire dactylus extend beyond scaphocerite; dactylus stout, curved, fringed with dorsolateral setae, ventral carina obsolete; propodus length 12.47–13.77 times longer than wide; 11 ventral spines distributed along length of propodus, 2 distal most spines paired; carpus 0.44–0.48 times propodus length;

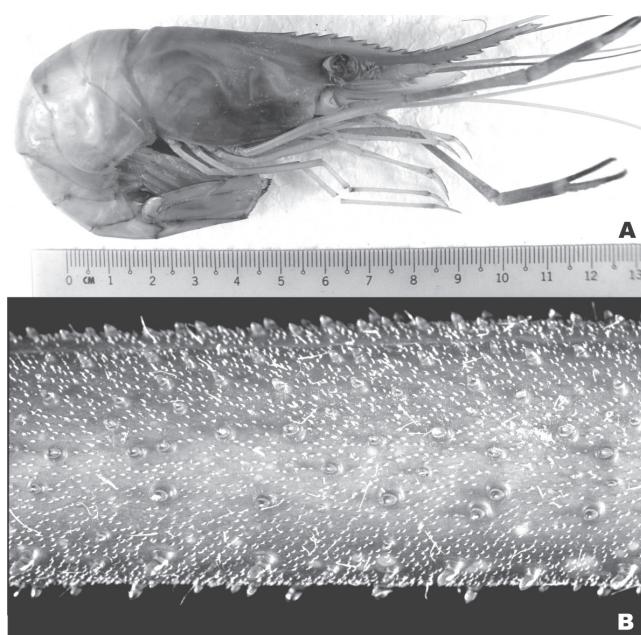


Fig. 3. *Macrobrachium rosenbergii* (de Man, 1879): A, ovigerous female 39.10 mm CL, lateral view (MZB); B, male 83.30 mm CL, close up, carpus of second pereiopod (QM W 16487).

merus 1.07–1.13 times propodus length, 2.32–2.38 times ischium length.

Fourth pereiopods: entire dactylus extending beyond scaphocerite; large spines, spinules and few scattered rather long stiff setae present on all segments; propodus with 14 ventral spines, 2 distal-most spines paired; merus 2.39–2.52 times ischium length.

Fifth pereiopods: entire dactylus extend beyond scaphocerite; large spines, spinules and few scattered rather long stiff setae present on all segments; 15 ventral spines distributed along length of propodus; merus 0.94–1.07 times as long as propodus, 2.47–2.61 times longer than ischium.

Thoracic sternum: T4 with small triangular median process, posterior submedian plate low with bluntly rounded tips, notch shallow and wide; T8 with moderately separated anterolateral lobes, without median process. Abdomen: smooth, glabrous. Male abdominal sternites: first 2 abdominal sternites each with medium-sized triangular median process, third abdominal sternite without median process. Inter-uropodal sclerite: well developed, elevated as longitudinal preanal carina, carina small, smaller than posterolateral teeth of sixth abdominal somite. Telson: moderate, stout, glabrous, 3.97–4.32 times median width, lateral margins straight, convergent, 2 pairs of dorsal spines present, posterior subventral margin straight with sharp median point, median projection overreaching inner pair of posterior spines. Uropods: with acute distolateral tooth, mobile mesial spine distinctly smaller than distolateral tooth, exopod 1.95–2.04 times longer than broad.

Remarks. – This species was described by de Man (1879) on the basis of a large ovigerous female from Andai, New Guinea [present day Papua, Indonesia]. However, Ortmann (1891) regarded *P. rosenbergii* as only a variety of *Palaemon carcinus* Linnaeus, 1758, as characterized by Fabricius (1798), an action which was subsequently followed by de Man himself (1892). Cowles (1914) later provided a detailed description and figures of specimens from the Philippines as *P. carcinus*. This name was widely used in the early literature. In his paper, however, Cowles (1914) commented that whilst the Philippine form of *P. carcinus* closely resembles *P. rosenbergii* de Man, 1879, it shows certain distinct and constant differences from the Indian form, which he regarded as the typical form of *P. carcinus*. The differences he referred to were mainly related to the structure of the rostrum.

Holthuis (1950) also regarded *Macrobrachium rosenbergii* (de Man, 1879) as identical with *Palaemon carcinus* of Fabricius (1798) but used de Man's name, as *P. carcinus* sensu Fabricius (1798) was not the same as *Cancer carcinus* Linnaeus (1758). Holthuis (1950) elaborated in detail the clear differences between *M. carcinus* (Linnaeus, 1758) from West Atlantic and *M. rosenbergii* (de Man, 1879) from the Indo-West Pacific region.

Schenkel (1902) described *Palaemon spinipes* from Kema, Minahassa, northern Sulawesi. According to Holthuis

(1995), Schenkel's species is likely to belong to the eastern subspecies although he did not specifically assign it to either taxon. Subsequently, Cai & Ng (2001) treated *P. spinipes* under the synonymy of *M. rosenbergii* in the broad sense. Re-examination of the type specimen shows it fits well with the characters of *M. rosenbergii* de Man, 1879 *sensu stricto*. Therefore, *P. spinipes* Schenkel, 1902 should be regarded as a synonym of *M. rosenbergii*.

We have also observed geographic variation within the Australian populations during this study but this was not reported by Hedgecock et al. (1979) and Lindenfelser (1984). Overall, the morphology of the Australian populations is conservative but is clearly different from *M. dacqueti* from the west of Huxley's Line. The morphology of the northeastern Australian population is more similar to those from New Guinea and the Philippines, while the northwestern population has a relatively much shorter rostrum and lower rostral formula (8–12 teeth on the dorsal margin and 5–8 teeth on the ventral margin). Short (2004) also noted that the *M. rosenbergii* of mid-northern Australia exhibited an intermediate form between the northeastern and northwestern Australian population on the basis of the maximum length of the developed ova being 0.6–0.7 mm (New Guinea and Philippines form), 0.9 mm (mid-northern Australia form) to 1.3 mm (northwest Australian form). The status of all Australia populations will need to be dealt with in a separate study using more material from more parts of Australia. For the moment, however, we provisionally consider all Australian populations as *M. rosenbergii* *sensu stricto*.

Distribution. – East of Huxley's Line, from the Philippines including Palawan Island, Lesser Sunda Islands, New Guinea and northern region of Australia.

Macrobrachium dacqueti (Sunier, 1925)

(Figs. 4, 5B–C, 6, 7B, 9, 10)

Cancer (Astacus) carcinus – Herbst, 1792: 58, Pl. 28, Fig. 1 (not *Cancer carcinus* Linnaeus, 1758).

Astacus carcinus – Fabricius, 1793: 479 (part) (not *Cancer carcinus* Linnaeus, 1758).

Palaemon carcinus – Fabricius, 1798: 402 (part); Olivier, 1811: 659; von Martens, 1868: 34 (part); de Man, 1879: 165 (part); 1888: 280; 1897: 766; 1908: 224, Pl. 19, Fig. 5; Miers, 1880: 382 (part); Ortmann, 1891: 700, Pl. 47, Fig. 1; Henderson, 1893: 340, 441; Lanchester, 1901: 565; Henderson & Matthai, 1910: 281, Pl. 15, Fig. 1a-g; Kemp, 1918: 255; Menon, 1938: 292, Figs. 21-23; Tiwari, 1955: 232 (not *Cancer carcinus* Linnaeus, 1758).

Palemon carcinus – H. Milne Edwards, 1837: 395 (not *Cancer carcinus* Linnaeus, 1758).

Palaemon (Eupalaemon) carcinus – de Man, 1892: 421 (part); 1898: 137; 1902: 475, 763 (part); Nobili, 1900: 480; Roux, 1932: 564, 568; Boone, 1935: 154, Pl. 39 (not *Cancer carcinus* Linnaeus, 1758).

Palaemon whitei (Guérin-Meneville MS) Sharp, 1893: 122 (nomen nudum).

Palaemon d'Acqueti Sunier, 1925: 117.

Macrobrachium carcinus – Suvatti, 1937: 49 (not *Cancer carcinus* Linnaeus, 1758).

Macrobrachium rosenbergii – Holthuis, 1950: 111, Fig. 25 (part); 1959: 67, 98; Johnson, 1960: 261 (part); 1961: 56; Ling & Merican, 1961: 55; Sandifer & Smith, 1979: 56; Tombes & Foster, 1979: 179; Hedgecock et al., 1979: 873 (part); Lindenfelser, 1984: 195 (part); Hiramatsu et al., 1985: 150; Liu et al., 1990: 104; Ng, 1990: 197; 1994: 75; 1997: 269; Ng & Choy, 1990: 15; Choy, 1991: 126, 138, Pl. 9; Barki et al., 1991a: 252; 1991b: 145; 1997: 81; Naiyanetr, 1998: 33; Dang & Ho, 2001: 33, Fig. 12; Mather & de Bruyn, 2003: 4 (part); de Bruyn et al., 2004: 251 (part); Wowor et al., 2004: 346, Fig. 8; de Bruyn et al., 2005: 370 (not *Palaemon rosenbergii* de Man, 1879).

Macrobrachium roseenbergii (sic) – Maccagno & Cucchiari, 1957: 355, Fig. 44 (not *Palaemon rosenbergii* de Man, 1879).

Macrobrachium rosenbergii schenkeli Johnson, 1973: 277.

Macrobrachium rosenbergii dacqueti – Holthuis, 1995: 148; 2000:

16, Fig. 2.1; Beekman, 1999: 18, Pl. 1 Fig.B, 396; Cai & Dai, 1999: 233; Wowor & Choy, 2001: 286; Cai & Ng, 2002: 78; Cai et al., 2004: 582.

Material examined. – Type material: *Palaemon d'Acquetti* Sunier, 1925: lectotype, male (74.1 mm CL, designated herein) (RMNH D 1065), Batavia [Jakarta], Java, Indonesia, coll. P. Bleeker, 1842–1860; paralectotypes, 2 ovigerous females (34.4–38.6 mm CL) (RMNH D 2437), Kampung Makassar near Batavia [Jakarta], Java, Indonesia, coll. S. F. Groen, 1861.

Other material. – **Indonesia:** Java: 3 females (13.3–30.0 mm CL) (MZB Cru.1319), Cibinua R., Banten; 3 males (44.2–86.4 mm CL) (MZB), Cikawung R., Banjar; Sumatra: 7 males (48.9–56.7), 10 females (17.9–47.6 mm CL) (USNM 67553), Musi R., Palembang; 1 male (33.9 mm CL), 1 female (36.4 mm CL) (MZB Cru.1064), Krueng Jambo, Aceh; 3 males (52.9–70.3 mm CL), 4 ovigerous females (41.9–48.7 mm CL) (ZRC 2000.2408), Batam Is.; Kalimantan: 2 males (19.5–23.5 mm CL), 3 females (20.4–26.1 mm CL), 3 ovigerous females (24.8–27.0 mm CL) (MZB Cru. 1423 & 1424), Lake Jempang; 3 males (28.9–88.9 mm CL) (MZB), Lake Semayang; 13 males (53.0–65.0 mm CL), 1 female (27.1 mm CL), 3 ovigerous females (30.8–42.6 mm CL) (ZRC 2000.2406), Tayan R.; 2 males (67.3–67.4 mm CL), 2 ovigerous females (36.6–45.3

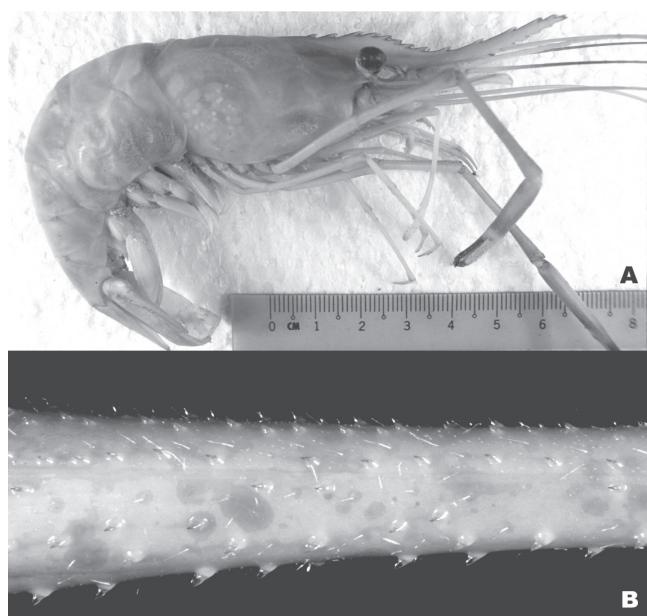


Fig. 4. *Macrobrachium dacqueti* (Sunier, 1925): A, ovigerous female 41.90 mm CL, lateral view (ZRC 2000.2408); B, male 64.15 mm CL, close up, carpus of second pereiopod (SAM C 11228).

mm CL) (ZRC 2000.2405), Sambas R.; 5 males (61.3–75.4 mm CL), 1 female (34.5 mm CL) (MZB), Sambas R.; 1 ovigerous female (34.0 mm CL) (ZRC 1995.462), Sebuku R.; 3 males (19.9–21.7 mm CL), 1 female (35.2 mm CL) (ZRC 1995.526), Tulit R., Semunad; 1 male (23.3 mm CL) (ZRC 2000.2401), Kapuas R. at Sintang; 7 males (11.7–14.8 mm CL), 3 females (11.7–13.0 mm CL) (MZB), Kapuas R. at Sintang. **Brunei Darussalam:** 2 males (69.2–80.9 mm CL), 2 ovigerous females (40.5–44.9 mm CL) (ZRC 1996.1682–1685), Bandar Seri Begawan. **Cambodia:** 3 males (70.6–74.7 mm CL) (ZRC), Tonle Sap. **Singapore:** 2 males (53.2–53.4 mm CL) (ZRC); 2 males (30.5–41.5 mm CL) (ZRC 1986.258–259), Nee Soon near Seletar Reservoir. **Malaysia:** Peninsular Malaysia: 1 male (56.5 mm CL), 1 ovigerous female (40.0 mm CL) (ZRC 2000.2402), Selangor R.; 2 males (26.8–53.6 mm CL) (NHM 1893.24), Pinang Is.; 3 males (36.2–52.6 mm CL), 1 female (34.1 mm CL) (ZRC), Taman Negara, Pahang; 2 males (32.5–41.9 mm CL), 1 female (31.3 mm CL) (ZRC), Tahan R. in Taman Negara, Pahang; 4 males (41.2–42.2 mm CL) (ZRC 1996.113–116), Tanjung Kualang, Ipoh; 4 males (20.45–47.55 mm CL) (ZRC), Ulu Sedili R., Mawai, Johor; East Malaysia: 1 female (35.8 mm CL) (NHM 1900.12.1.34), Kuching; 2 females (32.7–34.0 mm CL) (NHM), Kuching Bay; 1 male (59.6 mm CL), 1 female (24.4 mm CL) (NHM 1893.3.26.1–2), Marabah; 2 males (57.2–69.7 mm CL), 1 female (46.5 mm CL) (ZRC 2000.2404), Serian; 2 males (62.8–75.5 mm CL), 1 ovigerous female (41.6 mm CL) (ZRC 1996.1686–1688), Serian; 1 male (47.9 mm CL) (ZRC 2000.2403), Nyungan R. in Lanjak-Entimau Wildlife Sanctuary; 1 male (54.6 mm CL), 2 ovigerous females (29.3–36.5 mm CL) (MZB), Kinabatangan R. at Bukit Garam; 1 male (49.4 mm CL), 1 female (33.3 mm CL) (ZRC 1994.4200), Kinabatangan R. near Batu Puteh; 2 males (24.7–32.4 mm CL) (ZRC 1994.4218), Kinabatangan R. near Batu Puteh; 1 female (32.4 mm CL) (ZRC 1994.4209), Kinabatangan R. at jetty to Danau Girang; 3 males (31.6–42.4 mm CL), 1 ovigerous female (41.6 mm CL) (ZRC 2000.2478), Marudu R. **Thailand:** 1 male (86.7 mm CL) (USNM), Thailand; 1 male (66.0 mm CL) (USNM 21365), Trang; 1 male (54.7 mm CL) (USNM), Trang; 1 male (65.6 mm CL) (USNM 65563), Chao Phraya R.; 1 male (24.1 mm CL) (USNM 65563), Chao Phraya R.; 1 male (65.6 mm CL) (USNM 95528), Chao Phraya R.; 1 male (20.4 mm CL) (USNM 65564), Chao Phraya R. at Pak Nam; 2 males (14.6–15.3 mm CL) (USNM 65565), Bangkok; 1 female (19.0 mm CL) (USNM 65494), Bangkok; 2 males (16.5–18.7 mm CL), 5 females (18.1–21.5 mm CL) (USNM), Mae Khlong R. at Ratchaburi; 1 male (32.9 mm CL) (USNM 65491), Pasak R.; 1 female (28.4 mm CL) (USNM 65490), Chao Jet R. at Ban Pua; 1 male (19.6 mm CL), 1 female (15.4 mm CL) (USNM 65492), river at Pak Kret; 2 males (16.5–18.7 mm), 1 female (12.4 mm CL) (USNM 65493), Ranode R., outlet of a lake. **Myanmar (=Burma):** 1 male (68.4 mm CL) (NHM 1889.6.17.139), Tavoy; 1 female (33.4 mm CL) (NHM 1889.6.17.180), Tavoy; 3 males (48.4–63.9 mm CL) (NHM 1891.11.20.1–4), Tungoo. **Sri Lanka:** 1 male (67.2 mm CL) (NHM), Ceylon; 1 female (33.4 mm CL) (USNM), Mahaweli R. at Trincomalee.

Diagnosis. – Rostrum: Long (1.17–1.44 times CL in young males of 24.70–28.85 mm times CL with tip distinctly extending beyond distal end of scaphocerite), becoming relatively shorter with age (0.76–1.01 CL in fully adult males of 65 mm CL and larger with tip slightly extending beyond or reaching distal end of scaphocerite); moderately deep, maximum depth slightly more than maximum dorsoventral diameter of cornea; basal crest high to moderately high, sinuous; teeth above orbit closely spaced, teeth on distal two-thirds of rostrum widely spread, armed with 8–15 teeth (mode 13) including 1 apical tooth, 2 or 3 teeth completely

postorbital, postorbital teeth on anterior 0.25–0.28 of carapace; ventral carina with 6–16 teeth (mode 12), first tooth located at about proximal one-fifth or one-fourth.

General cephalon: ocular cornea well developed, 0.09–0.10 times CL (0.11–0.14 times CL in other specimens). Carapace spinulate. Ocular beak well developed with expanded lateral tip. Epistome completely bilobed, lobes with blunt rounded margin.

Second pereiopod: distal half of merus extend beyond end of scaphocerite. Cheliped: large spines abundant on all segments except dactylus; dactylus thickly covered by pubescence; chela 2.08–2.20 times CL, length 12.06–14.01 times width, outer and inner margins straight; palm subcylindrical, about equal to maximum merus width, width 0.94–1.02 times depth, outer and upper margins more densely covered with smaller spines than inner and lower margins; fingers 0.67–0.76 times palm length, not gaping; dactylus with 2 large teeth on proximal one-third, subequally distributed, pollex with 1 large tooth at distal and 2 smaller teeth towards articulation of fingers distributed along proximal 0.26, teeth unequally distributed along cutting edges; carpus 0.94–0.99 times palm length, subcylindrical, length 6.33–8.02 times distal width, 1.31–1.38 times merus length; merus straight, 1.29–1.38 times ischium length; ischium tapered.

Third pereiopods: medium-sized spines present on all segments; distal half of propodus extends beyond scaphocerite; dactylus stout, curved, ventral carina obsolete; propodus length 17.05–19.71 times longer than wide.

Thoracic sternum: T4 with small triangular median process, without posterior submedian plate; T8 with moderately separated anterolateral lobes, without median process. Abdomen: smooth, glabrous. Male abdominal sternites: first 2 abdominal sternites each with medium-sized triangular median process, third abdominal sternite without median process. Inter-uropodal sclerite: well developed as longitudinal preanal carina, carina small or medium-sized. Telson: moderate, stout, glabrous.

Remarks. – The first published figure of this species appeared in Rumphius (1705, *D'Amboinsche Rariteitkamer*, Pl. 1 Fig. B) under the name of “*Locusta Marina*”, but there is no text accompanying the figure. The original figure of Rumphius' *Rariteitkamer* is still extant and was republished by Beekman (1999: 18, Fig. 1B) and Holthuis (2000: 14, Fig. 2.1). The high basal crest of the rostrum of the original figure of the prawn makes it likely that this is *Macrobrachium dacqueti* which is in Rumphius Memorial Volume and was considered as *M. rosenbergii* (see Holthuis, 1959: 67).

Herbst (1792) was the first to provide a good description and illustration of *M. dacqueti* under the name *Cancer (Astacus) carcinus* Linnaeus, 1758. However, Fabricius in his accounts of *Astacus carcinus* (in 1793) and *Palaemon carcinus* (in 1798) referred only to Rumphius' Pl. 1, Fig. B. Subsequently, Fabricius (1798) transferred the Linnaean species from *Astacus* to *Palaemon*. The specific name *Palaemon carcinus*

(Fabricius, 1798) was then adopted (incorrectly) for the next 150 years until the matter was clarified by Holthuis (1950). Interestingly, the work of Herbst was overlooked by Fabricius and subsequent workers had in fact used the name *P. carcinus* (also incorrectly) for the East Indian form. The real *Macrobrachium carcinus* (Linnaeus, 1758), as pointed out by Holthuis (1950), is a wholly American species.

Holthuis (2000: 13), who provided a taxonomic history of the last 200 years of this species, comments: “The first who challenged this nomenclature was Sunier (1925), who showed that Linnaeus' description of *Cancer carcinus* was solely based on material of the American species named *jamaicensis* by Herbst (1792). Sunier (1925) accepted the consequences of his discovery and replaced the name *jamaicensis* by *carcinus* and proposed the new specific name *dacqueti* for the Indo-West Pacific species, honoring burgomaster d'Acquet. In 1950, Sunier's views were confirmed (Holthuis, 1950), except that he pointed out that the name *Palaemon rosenbergii* de Man, 1879 for the Indo-West Pacific species is older than *P. dacqueti* Sunier, 1925, and that the specific name *rosenbergii* had to be used for the present species”.

Johnson (1973a) first recognized the differences between the two taxa, but he treated them as subspecies, including establishing a new name for the western population which he named *M. rosenbergii schenkeli*. This recognition of two subspecies was followed by Hedgecock et al. (1979), Lindenfelser (1984) and de Bruyn et al. (2004). Holthuis (1995) provided the correct nomenclature for the two subspecies, and he correctly noted that the western subspecies must be known as *M. r. dacqueti* (Sunier, 1925), if this population be recognized as a separate taxon. In the present study, *M. r. dacqueti* is regarded as a distinct species, i.e. *M. dacqueti*.

Distribution. – Asian mainland to the western border of Huxley's Line excluding Palawan, i.e. from eastern part of Pakistan, India, Sri Lanka, and southern China up to Borneo and Java.

DISCUSSION

The MDA analyses of the large morphometric data set of the *M. rosenbergii* species group showed a clear morphometric disjunction into two taxa, indicating that they are actually two distinct species, i.e. *M. rosenbergii* and *M. dacqueti*. This is supported by the MDA scores along the first root and the percentage of correctly re-classified individuals in the original groups.

The primary variables in separating *M. rosenbergii* and *M. dacqueti* as a whole were related to height of rostral base and number of teeth on ventral margin of rostrum. The basal crest of *M. rosenbergii* is always low to moderately low, while that of *M. dacqueti* is always high to moderately high (see Figs. 3A, 4A, 5). This character is not affected by age and sex, and was used by de Man (1879), Cowles (1914) and Johnson (1973). The number of ventral rostral teeth of

M. rosenbergii ranges from 6 to 15 teeth with mode 9 teeth and *M. dacqueti* has 6 to 16 ventral teeth with mode 12 teeth. Although the mode of the number of ventral rostral teeth of the two species is different, the ranges of the teeth number almost totally overlap. The same is also true for the number of dorsal rostral teeth since *M. rosenbergii* and *M. dacqueti* have 8–14 teeth (mode 12 teeth) and 8–15 teeth (mode 13 teeth), respectively. This character is therefore not very useful, and we do not agree with Cowles (1914) and Johnson (1973) in using the rostral formula as a key feature for recognizing the two taxa. Almost all large adult males and females *M. rosenbergii* of 65.0 mm CL or larger have shorter rostrums compared to those of *M. dacqueti*, i.e. the tip of the rostrum failing to reach (vs. always distinctly exceeding) the distal end of the scaphocerite (Figs. 5A–B, 9B). Only a few large adult males with carapace lengths ranging from 65.0 mm to 75.0 mm have longer rostrums in which the tip either reaches or slightly exceeds the distal end of the scaphocerite. While the tip of the rostrum clearly exceeds the end of the scaphocerite in smaller adult males of carapace length between 52.0 mm and 65.0 mm, the tip of the rostrum either reaches or clearly exceeds the end of the scaphocerite in smaller adult females of carapace length between 45.0 mm and 65.0 mm. A similar rostral pattern is also seen in the Philippine material of *M. rosenbergii* (Cowles, 1914) and other *M. rosenbergii* specimens studied by Johnson (1973) (Fig. 6). For practical purposes, using the rostral length character for distinguishing *M. rosenbergii* from *M. dacqueti* is only suitable for large adult specimens, which are not always easily obtainable from the wild. Nevertheless, the present analysis does show that the rostrum of *M. rosenbergii* grows at a slower rate than that of *M. dacqueti*.

The spination of the second pereiopods of adult specimens (males of 52.0 mm CL or larger and females of 45.0 mm CL or larger) is very useful in separating the two species and this is the first time this character has been used. All segments of the second pereiopods of adult *M. rosenbergii* are abundantly covered with spinules interspersed with widely-spaced, elevated large spines except for the dactylus and the ischium (Fig. 3B). In the case of *M. dacqueti*, the second pereiopods are covered only with widely-spaced and elevated large spines, without the spinules (Fig. 4B). Unfortunately, this reliable character is only fully developed and apparent in adult individuals of both sexes.

The carpus of the second pereiopod of both young *M. rosenbergii* and *M. dacqueti* is always distinctly longer than the palm. However, the growth rate of the carpus is not as fast as that for the palm with increasing age. In large specimens, the carpus is slightly shorter than the palm (ratio of carpus length to palm length of *M. rosenbergii* and *M. dacqueti* ranges from 0.80 to 2.87 and from 0.84 to 2.50, respectively). The ratio of dactylus length to palm length of *M. rosenbergii* and *M. dacqueti* ranges from 0.61 to 1.13 and from 0.61 to 1.00, respectively, i.e. they totally overlap. Therefore, the relative lengths of carpus to palm and dactylus to palm cannot be used to differentiate the two species even among adult males, as had been proposed by Johnson (1973).

As mentioned previously, in young *M. rosenbergii* and *M. dacqueti*, the tip of the rostrum always exceeds the distal end of the scaphocerite, and the spination on all pereiopods (except for the first pereiopods) has not developed or has not fully developed; these facts make the differences between the juvenile and young individuals of the two species more subtle. Therefore, the height of the basal crest of the rostrum and the presence or absence of the posterior submedian plate on the T4 are the only most useful morphological characters in determining juveniles of the two species, at least for all the specimens examined in the present study. The last character mentioned is particularly useful for determining the identity of preserved specimens.

In an attempt to resolve the outstanding taxonomic problems, some additional important distinguishing characters have been identified during the present study including live colouration, which are presented in Table 3. The large number of specimens of the two taxa examined over their entire native distributions and analyses done here, permit a better understanding of the variation seen in adults and young, and allow discrete adult differences to be accurately quantified for the first time.

According to Short (2004), the live colouration of Australian *M. rosenbergii* specimens differs distinctly from that of "Asian" *M. dacqueti* but is closer to the colour of the Philippines *M. rosenbergii*. We can confirm this with fresh adult material of *M. rosenbergii* we have seen from Papua (Fig. 8), being darker than *M. dacqueti* (Fig. 9) which is generally more distinctly blue. Very young *M. rosenbergii* specimens in Australian populations develop a chromatophore pattern similar to very young *M. dacqueti* specimens of Asian stock in the form of several black longitudinal stripes on the carapace, one red band in the middle of rostrum and black mottling on the abdomen, features which subsequently disappears in adults (Hiramatsu et al., 1985; Short, 2004) (Figs. 6A, B). This pattern is only visible when the very young *M. dacqueti* specimens reach 7.0 mm CL, 10.3 mm rostrum length and 25.0 body length. Thereafter, the black mottling on the abdomen disappears and in turn several reddish brown or dark orange markings appear on the pleural condyle of each segment when they reach 14.9 mm CL, 19.6 mm rostrum length and 49.4 mm body length; the red band in the middle of rostrum fades away when they reach 16.7 mm CL, 19.7 mm rostrum length and 50.0 mm body length; and the chromatophore pattern on carapace totally disappears when they reach 23.0 mm CL, 25.0 mm rostrum length and 71.0 mm body length (Fig. 6C). At this stage of their development, they have similar colour patterns to the adults (Hiramatsu et al., 1985). The same chromatophore pattern with a quite similar colour pigment is also noticeable among young *M. rosenbergii* specimens in the Philippine populations and this pattern is retained later and only becomes much less distinct when they reach 190 to 240 or 250 mm body length (Cowles, 1914) (Figs. 6A, B, 8). The young *M. rosenbergii* specimens in the Papuan population have also the same chromatophore pattern but have a different pigment colour. The Papuan specimens have brown stripes on the carapace and brown mottling on the abdomen. Similar to the

Philippine *M. rosenbergii* populations, the *M. rosenbergii* of Papuan stock retains the chromatophore pattern until they reach about 45.0 mm CL. It is therefore obvious that the chromatophore pattern exists much longer in *M. rosenbergii* than in *M. dacqueti*. Although the colours of the pigments of the chromatophores of young Philippine *M. rosenbergii* and young Papuan *M. rosenbergii* are different, the colour of the spots on pleural condyles is the same bright red (Fig. 7). In older *M. rosenbergii* males of 240 or 250 to 320 mm body length, the chromatophore pattern almost entirely disappears (Cowles, 1914) (Figs. 8A, B). However, the bright red dots on the fourth to sixth pleural condyles of *M. rosenbergii* and the dark orange spots on the fourth to sixth pleural condyles of *M. dacqueti* are retained (Fig. 7), from very young to very old individuals. This character is easily observed and it is quite practical for application in separating live specimens of both species.

Overall, the morphological characters and the results of the morphometric analyses show that the two taxa are in fact, two valid species. This hypothesis is also supported by allozyme (Lindenfelser, 1984), mitochondrial DNA (mtDNA) and microsatellite work which reveal that they have been genetically isolated for a significant evolutionary time-frame (de Bruyn et al., 2004; Chand et al., 2005).

The biology of their larvae is also different. Experiments conducted by Sarver et al. (1979) showed that larvae of Australian strain (= *M. rosenbergii*) have a shorter larval development time compared to the Anuenue stock from Hawaii which was originally from Malaysia (= *M. dacqueti*); with the post-larvae of the Australian population also being smaller in size. In rearing several "pure" strains from various populations, they only managed to get one group of Palauan larvae to develop and all efforts to rear the Philippine larvae failed (both populations belong to *M. rosenbergii* sensu stricto). This might be due to the different niches or basic biological needs of the larvae of the two species. In addition, Sarver et al. (1979) also attempted to raise hybrids between Anuenue mothers and, Australian, Palau, Philippine and Thai fathers; with all hybrids successfully reared and tested. Although the F₁ and F₂ were fertile, no exhaustive studies were done, and the strength, vigor and/or fecundity of these hybrids are not known (S. Malecha, pers. comm.). Apparently the cultivation of the hybrids is not very successful. Several attempts have been made in the past to culture native Australian *M. rosenbergii* stock with the aquaculture prerequisites of *M. dacqueti* but the activities has since stopped. This is mainly due to the relatively low yields and subsequent poor economic forecasts (Ian Ruscoe, pers. comm.). This is indirect indication that we are actually dealing with two species. One therefore needs to know more about the exact physiology of *M. rosenbergii* so success in raising this species can be guaranteed. In the Philippines, the production of post-larvae from native *M. rosenbergii* stock is very limited and the produced seed stock could not really meet the demand of local grow-out culturists. Instead, the demand for post-larvae in the Philippines is supplied by *M. dacqueti* stocks (originally from Thailand) which are being propagated in local hatcheries (M. Rowena

R. Romana-Eguia, pers. comm.). Studies by Philippine biologists on the two species (they have previously regarded them as "populations") have shown that while *M. rosenbergii* is difficult to rear while *M. dacqueti*, on the other hand is easy to keep, and has been successfully cultured there (M. Rowena R. Romana-Eguia, pers. comm.).

The only three countries which have *M. rosenbergii* sensu stricto are Australia, Philippines and Indonesia. Both Australia and Indonesia do not culture *M. rosenbergii* to any scale we are aware of, and only the Philippines does the post-larvae production for solely research purposes conducted by two local agencies, i.e. the Southeast Asian Fisheries Development Center (SEAFDEC), and Bureau of Fisheries and Aquatic Resources (BFAR).

Macrobrachium dacqueti is the only species cultured in Indonesia to meet local demand and it is not cultivated in Australia. It is also well known that most cultured populations found outside the natural range of this species can be traced to brood-stock imported to Hawaii from Malaysia (Karplus et al., 2000). Therefore, the species is known as the Giant Malaysian prawn in America (Woodley et al., 2002). Thailand also supplies parental stock to several Asian countries such as Japan (Gomez Diaz, 1987), the Philippines and Israel (A. Barki, pers. comm.). The above evidence indicates that *M. dacqueti* is the only extensively cultured species so far and not *M. rosenbergii*.

All the available evidence supports our contention that *M. dacqueti* (Sunier, 1925) is clearly a different species from *M. rosenbergii* (de Man, 1897). The material used and studied by the great majority of giant freshwater prawns researchers is in fact, *M. dacqueti* not *M. rosenbergii*. An incorrect name application can affect the success of the aquaculture industry since using the wrong species name can lead to the culturing of the wrong species; improvement of the wild-stock management of the different species for conservation purpose; and correct application of research results. For example, a good understanding of the taxonomy of the mud crab *Scylla* spp. (Brachyura: Portunidae) has proved important in improving mud crab aquaculture. The uncertainty of genetic relationships between economically valuable cryptic species is known to be one of the main constraints to the management of the wild fisheries and the development of aquaculture (see Keenan et al., 1998).

The most recent distributional study of these two *Macrobrachium* species (as populations) (de Bruyn et al., 2004) suggests that it follows Huxley's Line, an extension of Wallace's Line, which is a well-known biogeographical boundary that runs through Indonesia. However, the present study shows that the distribution of *M. rosenbergii* and *M. dacqueti* does not exactly conform to either Huxley's or Wallace's Line. The most westerly boundary line for *M. rosenbergii* includes Palawan in the Philippines and Bali in Indonesia (Fig. 10). Apparently their distribution is more affected by the larval dispersal factors such as high salinity tolerance combined with sea current patterns rather than tectonic history. The larvae of *M. rosenbergii* have been

successfully raised to post-larvae stage in 100% artificial seawater indicating that the species may have limited marine dispersal capability (see Sandifer & Smith, 1979). Although the larvae can survive in high saline seawater, they clearly prefer to live in less saline conditions as their survival rate is better there (Ling & Merican, 1961; Ling, 1977; Ling & Costello, 1979). This suggests the larvae prefer the brackish waters of river mouths and may stay close to their home river. There are less big rivers in islands east of Wallace's line including Palawan. Therefore, it is less easy for the larvae to migrate to the drier islands in the east and this serves as a natural barrier to dispersal. The oceanographic history of these areas, however, may also affect the distribution of the *M. rosenbergii* species group as shown by population genetic studies on the distribution of the mantis shrimp *Haptosquilla pulchella* inhabiting Indonesian reef systems, suggesting the presence of a marine equivalent of Wallace's Line (Barber et al., 2000).

The present conclusions create a serious problem for prawn biologists and aquaculturists. The species which is the best studied and has been called "*M. rosenbergii*" for decades, is in fact, *M. dacqueti*. The number of published papers referring to the *M. rosenbergii* sensu stricto in fact is very little compared to that for *M. dacqueti*. We are now preparing an application to the International Commission for Zoological

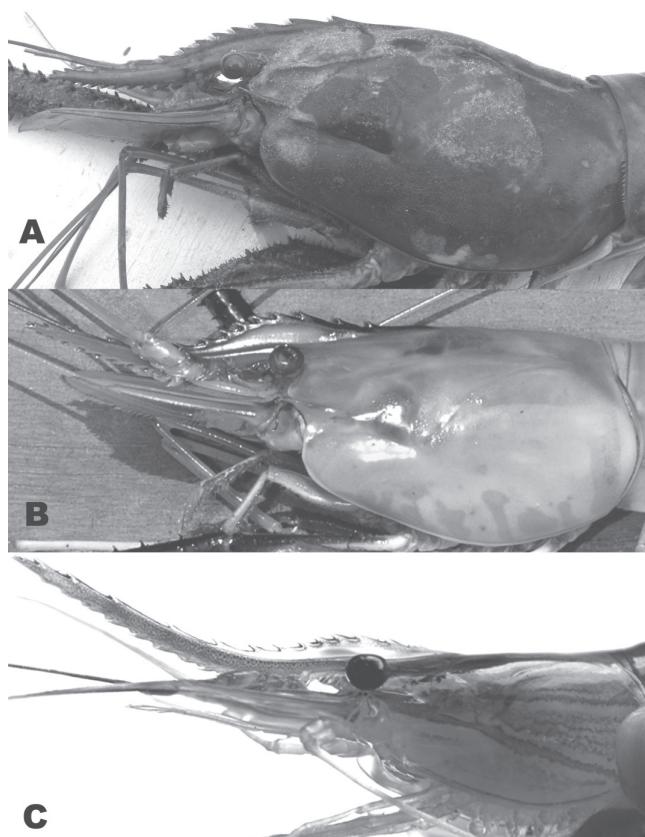


Fig. 5. Carapace: A, *Macrobrachium rosenbergii* (male 75.0 mm CL, Ajkwa R., Papua, Indonesia, not preserved); B–C, *M. dacqueti*: B, adult (male 62.60 mm CL, Jaya R., Bukit Sarang area, Bintulu, Sarawak, East Malaysia, Borneo, coll. H. H. Tan (ZRC), 20 Aug. 2005); C, young specimen from Serian, Sarawak, East Malaysia, Borneo, not preserved.

Nomenclature to have the name *Macrobrachium dacqueti* (Sunier, 1925) suppressed under *Macrobrachium rosenbergii* (De Man, 1879) by changing the holotype. An expedient solution would be to suppress the holotype of *M. rosenbergii* (De Man, 1879) and to have it replaced with the holotype of *M. dacqueti* (Sunier, 1925). This would make both names objective synonyms and retain the name *M. rosenbergii* (De Man, 1879) for the Asian species. At the same time, the Australian, Philippine and Papuan species would then have to be given a new name with a new holotype as there are no other available names. This should, however, cause far less confusion as the species in this area is only rarely utilized for research purposes. This act will conserve the name *M. rosenbergii*, familiar to most prawn biologists.

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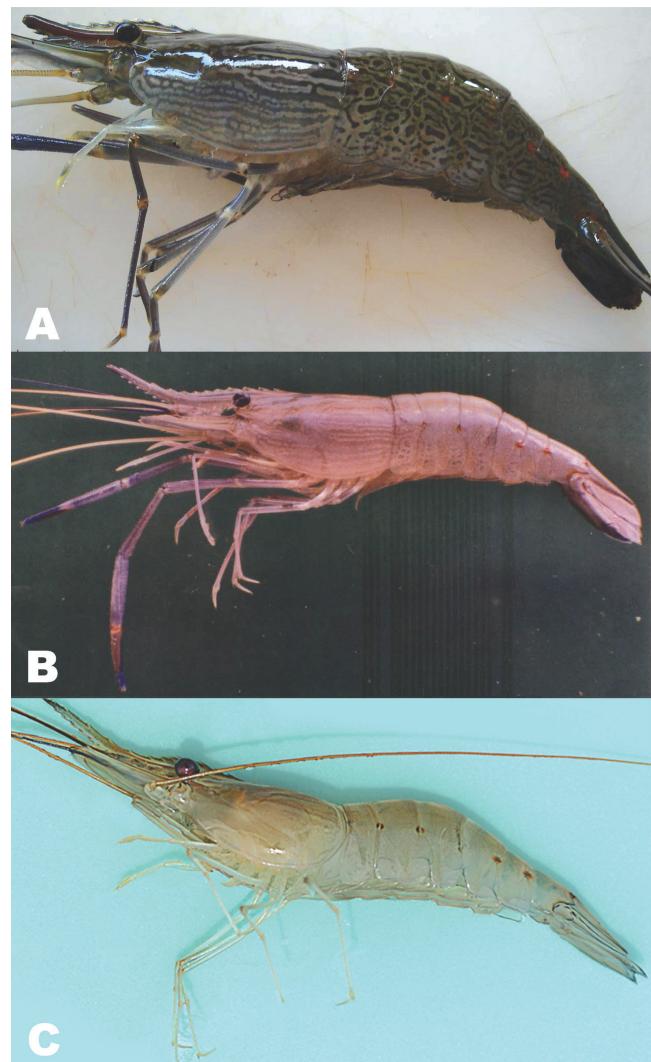


Fig. 6. Young individuals: A–B, *Macrobrachium rosenbergii*: A, 45.0 mm CL, Tambulig, Panguil Bay, Mindanao, Philippines, not preserved; B, Ajkwa R., Papua, Indonesia, not preserved; C, *M. dacqueti*, Serian, Sarawak, East Malaysia, Borneo, not preserved.

Table 3. Useful morphological characters for identifying the *Macrobrachium rosenbergii* species group.

Characters	<i>Macrobrachium rosenbergii</i>	<i>Macrobrachium dacqueti</i>
Height of basal crest	Low to moderately low	High to moderately high
2 nd Pereiopods ^{1, 2}	All segments covered with abundant spinules interspersed with widely-spaced, elevated large spines	All segments covered with widely-spaced, elevated large spines only
3 rd -5 th Pereiopods ^{1, 2}	All segments covered with abundant spinules interspersed with widely-spaced, elevated medium-sized spines	All segments covered with widely-spaced, elevated medium-sized spines only
T4	With posterior submedian plate in form of low ridge	Without posterior submedian plate
Live colouration ³	Carapace lightly brown with several brown bands; abdomen lightly brown with brown mottled pattern and bright red markings on each pleural condyle	Carapace with several black bands; several dark blue areas visible near margins of abdomen segments, telson and uropods, and reddish brown (=dark orange) markings present on each pleural condyle*
Live colouration	Carapace and abdomen uniformly olive brown to very dark brown; pleural condyle of 4 th -6 th segments with bright red markings ⁴	Carapace and abdomen uniformly translucent olive grey to grayish blue; pleural condyle of 4 th -6 th segments with dark orange markings ⁵
Live colouration ⁶	Brown in undeveloped males, bright violet in developing males, dark violet brown or black in fully developed males**	Unpigmented or pink in undeveloped males, orange in developing males, dark blue in fully developed males***

¹ males ≥ 52.0 mm CL and females ≥ 45.0 mm CL; ² except for dactylus and ischium; ³ specimens of 14.9-23.0 mm CL; ⁴ specimens of ≥ 48.0 mm CL; ⁵ specimens of > 23.0 mm CL; ⁶ Second Pereiopods; * Hiramatsu et al, 1985; ** Short, 2004; *** Ra'anana & Sagi, 1985; live colouration based on fresh *M. rosenbergii* specimens from Ajkwa R., Papua.

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LITERATURE CITED

- Barber, P. H., S. R. Palumbi, M. V. Erdmann & M. K. Moosa, 2000. Biogeography: a marine Wallace's line? *Nature*, **406**(6797): 692-693.
- Barki, A., I. Karplus & M. Goren, 1991a. The agonistic behaviour of the three male morphotypes of the freshwater prawn
- Macrobrachium rosenbergii (Crustacea, Palaemonidae). *Behaviour*, **116**(3-4): 252-277.
- Barki, A., I. Karplus & M. Goren, 1991b. Morphotype related dominance hierarchies in males of *Macrobrachium rosenbergii* (Crustacea, Palaemonidae). *Behaviour*, **117**(3-4): 145-160.
- Barki, A., S. Harpaz & I. Karplus, 1997. Contradictory asymmetries in body and weapon size, and assessment in fighting male prawns, *Macrobrachium rosenbergii*. *Aggressive Behavior*, **23**: 81-91.
- Bate, C. S., 1868. On a new genus, with four new species, of freshwater prawns. *Proceedings of the Zoological Society of London*, **1868**: 363-368, Pls. 30, 31.
- Beekman, E. M., 1999. *The Amboinese curiosity cabinet. Georgius Everhardus Rumphius*. Translated, edited, annotated, and with an introduction. Yale University Press, New Haven and London, 567 pp.
- Boone, L., 1935. Crustacea: Anumura, Macrura, Euphausiacea, Isopoda, Amphipoda and Echinodermata: Asteroidea and Echinoidea. In: Scientific Results of the World Cruise of the Yacht "Alva," 1931, William K. Vanderbilt, Commanding. *Bulletin of the Vanderbilt Marine Museum*, **6**: 1-264, Figs. 1-13, Pls. 1-96.
- Cai, Y. & A. Y. Dai, 1999. Freshwater shrimps (Crustacea: Decapoda: Caridea) from the Xishuangbanna region of Yunnan Province, southern China. *Hydrobiologia*, **400**: 211-241.
- Cai, Y., P. Naiyanetr & P. K. L. Ng, 2004. The freshwater prawns of the genus *Macrobrachium* Bate, 1868, of Thailand (Crustacea: Decapoda: Palaemonidae). *Journal of Natural History*, **38**: 581-649. (This article was published electronically in 2003, but the hard copy available only in 2004).
- Cai, Y. & P. K. L. Ng, 2001. The freshwater decapod crustaceans of Halmahera, Indonesia. *Journal of Crustacean Biology*, **21**(3): 665-695.

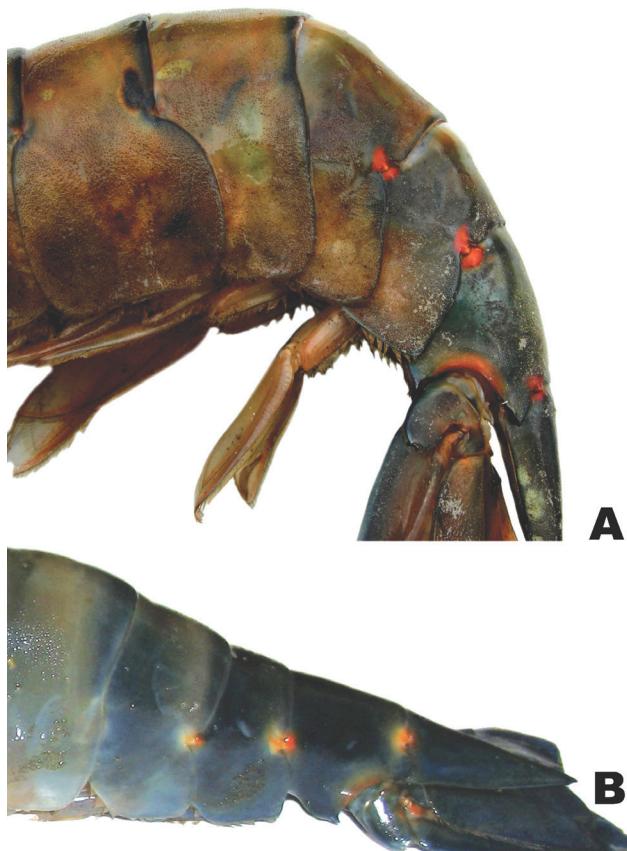


Fig. 7. Abdomen: A, *Macrobrachium rosenbergii* (male 75.0 mm CL, Ajkwa R., Papua, Indonesia, not preserved); B, *Macrobrachium dacqueti* (male 62.80 mm CL, Mahakam R., Melak, E. Kalimantan, Indonesia).

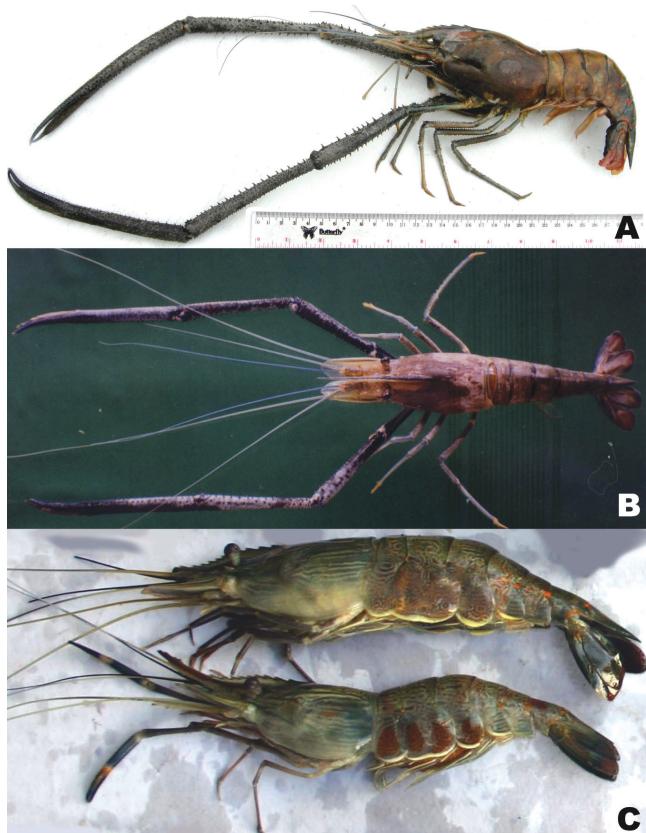


Fig. 8. *Macrobrachium rosenbergii*: A, B, 2 adult males from Ajkwa R., Papua, Indonesia, not preserved; C, 2 ovigerous females from Dinas, the Philippines, not preserved.

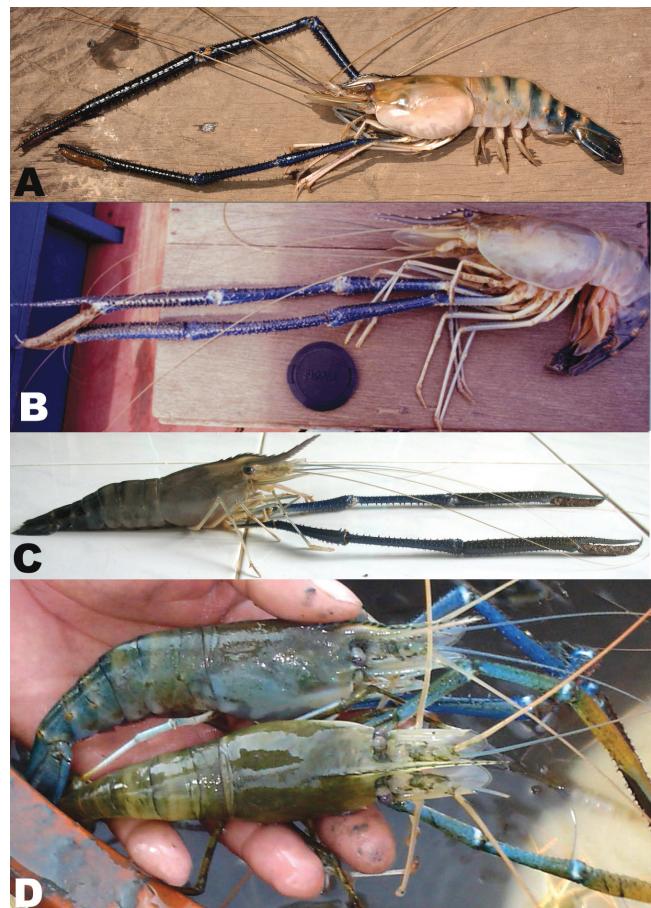


Fig. 9. *Macrobrachium dacqueti*: A, male 62.60 mm CL, Jaya R., Bintulu, Sarawak, East Malaysia, Borneo, coll. H. H. Tan (ZRC), 20 Aug. 2005; B, male 88.90 mm CL, Lake Semayang, E. Kalimantan, Indonesia, coll. D. Wowor & H. H. Tan (MZB), Nov. 1999; C, male 62.80 mm CL, Mahakam R., Melak, E. Kalimantan, Indonesia; D, 2 males, from aquaculture, Philippines, originating from Thailand, not preserved.



Fig. 10. Map of natural distribution of *Macrobrachium rosenbergii* (on the right side of dash line) and *M. dacqueti* (on the left side of dash line). Dashed line = distribution border of the two species.

- Cai, Y. & P. K. L. Ng, 2002. The freshwater palaemonid prawns (Crustacea: Decapoda: Caridea) of Myanmar. *Hydrobiologia*, **487**: 59–83.
- Chace, F. A. & A. J. Bruce, 1993. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907–1910, Part 6: Superfamily Palaemoidea. *Smithsonian Contribution to Zoology*, **543**: vii + 152 pp, Figs. 1–23.
- Chand, V., M. de Bruyn & P. B. Mather, 2005. Microsatellite loci in the eastern form of the giant freshwater prawn (*Macrobrachium rosenbergii*). *Molecular Ecology Notes*, **5**: 308–310.
- Choy, S. C., 1991. The crustacean fauna of negara Brunei Darussalam. *The Brunei Museum Journal*, **7**(3): 117–153.
- Cowles, R. P., 1914. Palaemons of the Philippine Islands. *The Philippine Journal of Science*, (D) **9**(4): 319–403, Fig. 1, Pls. 1–3.
- Dang, N. T., & T. H. Ho, 2001. *Dong vat chi Viet Nam (Fauna of Vietnam). 5. Giap xac nuoc ngot*. Science and Technics Publishing House, Hanoi, Vietnam. Pp. 9–53 (in Vietnamese).
- De Bruyn, M., J. A. Wilson & P. B. Mather, 2004a. Huxley's line demarcates extensive genetic divergence between eastern and western forms of the giant freshwater prawn, *Macrobrachium rosenbergii*. *Molecular Phylogenetics and Evolution*, **30**: 251–257.
- De Bruyn, M., J. C. Wilson & P. B. Mather, 2004b. Reconciling geography and genealogy: phylogeography of giant freshwater prawns from the Lake Carpentaria region. *Molecular Ecology*, **13**: 3515–3526.
- De Bruyn, M., E. Nugroho, Md. M. Hossain, J. C. Wilson & P. B. Mather, 2005. Phylogeographic evidence for the existence of an ancient biogeographic barrier: the Isthmus of Kra seaway. *Heredity*, **94**: 370–378.
- De Grave, S. & D. Diaz, 2001. Morphometric comparison between Mediterranean and Atlantic populations of *Pontophilus norvegicus* (Decapoda, Crangonidae). *Hydrobiologia*, **449**: 179–186.
- De Man, J. G., 1879. On some species of the genus *Palaemon* Fabr. with descriptions of two new forms. Notes from the Royal Zoological Museum of the Netherlands at Leyden, **1**(41): 165–184.
- De Man, J. G., 1888. Report on the Podophthalmous crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F.R.S., Superintendent of the Museum. *The Journal of the Linnean Society*, **22**: 1–312, Pls. 1–19.
- De Man, J. G., 1892. Decapoden des Indischen Archipels. In: Weber, M. (ed.), *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien*, **2**: 265–527, Pls. 15–29.
- De Man, J. G., 1897. Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden, 5. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, **9**: 725–790, Pls. 12–14.
- De Man, J. G., 1898. Macroura. Part I. In: The Crustaceans. Zoological Results of the Dutch Scientific Expedition to Central Borneo. *Notes from the Leyden Museum*, **20**: 137–161, Pls. 6–8.
- De Man, J. G., 1902. Die von Herrn Professor Kükenthal in Indischen Archipel gesammelten Dekapoden und Stomatopoden. In: Kükenthal, W. (ed.), *Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **25**(3): 467–929, Pls. 19–27.
- De Man, J. G., 1908. Decapod Crustacea, with an account of a small collection from brackish water near Calcutta and in the Decca district, Eastern Bengal. In: The fauna of brackish ponds at Port Canning, lower Bengal, Part X. *Records of the Indian Museum*, **2**: 211–231, 2 pls.
- Desmarest, A.-G., 1817. Crustacés fossiles. In: *Nouveau Dictionnaire d'Histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc.*, pp. 495–519.
- Fabricius, J. C., 1793. *Entomologia Systematica*, **2**: 478–487. Hafniae.
- Fabricius, J. C., 1798. *Supplementum Entomologiae Systematicae*. Hafniae, 527 pp.
- FAO, 2007. FAO Yearbook. Fishery statistics: aquaculture production 2005. www.fao.org/figis. Accessed 12 May 2007.
- Gomez Diaz, G., 1987. Influence of the parental history on the larval development of *Macrobrachium rosenbergii* (de Man). *International Journal of Invertebrate Reproduction and Development*, **12**: 45–56.
- Hedgecock, D., D. J. Stelmach, K. Nelson, M. E. Lindenfelser & S. R. Malecha, 1979. Genetic divergence and biography of natural populations of *Macrobrachium rosenbergii*. *Proceedings of the World Mariculture Society*, **10**: 873–879.
- Henderson, J. R., 1893. Contribution to Indian Carcinology. *Transactions of the Linnean Society of London*, series 2 (Zoology), **5**(1): 325–458, Pls. 36–40.
- Henderson, J. R., & G. Matthai, 1910. On certain species of *Palaemon* from South India. *Records of the Indian Museum*, **4**(4): 277–305, Pls. 15–18.
- Herbst, J. F. W., 1792. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen beschreibung ihrer verschiedenen Arten*, **2**(2): 49–78, Pls. 26–29. Berlin and Stralsund: Gottlieb August Lange.
- Holthuis, L. B., 1950. The Decapoda of the Siboga Expedition, Part X: The Palaemonidae collected by the Siboga and Snellius Expeditions, with remarks on other species, Part I: Subfamily Palaemoninae. In *Siboga-Expedition*, **39a**: 268 pp, 52 figs.
- Holthuis, L. B., 1959. 1959. Notes on Pre-Linnean carcinology (including the study of Xiphosura) of the Malay Archipelago. In: de Wit, H. C. D. (ed.), *Rumphius Memorial Volume*, pp. 63–125, Photos 7–11.
- Holthuis, L. B., 1995. Notes on Indo-West Pacific Crustacea Decapoda III to IX. *Zoologische Mededelingen*, Leiden, **69**(13): 139–151.
- Holthuis, L. B., 2000. Nomenclature and taxonomy. In: New, M. B. & W. C. Valenti (eds.), *Freshwater prawn culture: The farming of Macrobrachium rosenbergii*. Blackwell Science, London, U.K. Pp. 12–17.
- Hiramatsu, K., Y. Uno & N. Horas, 1985. Variation in chromatophore patterns on the bodies of different sizes of post-larvae to adolescent of *Macrobrachium rosenbergii* (De Man) in the laboratory (Decapoda, Natantia). *Crustaceana*, **49**(2): 150–160.
- Johnson, D. S., 1960. Sub-specific and infra-specific variation in some freshwater prawns of the Indo-Pacific region. In: Purchon, R. D. (ed.), *Proceedings of the Centenary and Bicentenary Congress of Biology*, Singapore, **1958**: 259–267.
- Johnson, D. S., 1961. A synopsis of the Decapoda Caridea and Stenopodidea of Singapore, with notes on their distribution and a key to the genera of Caridea occurring in Malayan waters. *Bulletin of the National Museum*, Singapore, **30**: 44–79, Pl. 2.

- Johnson, D. S., 1973. Notes on some species of the genus *Macrobrachium* (Crustacea: Decapoda: Caridea: Palaemonidae). *Journal of the Singapore National Academy of Science*, **3**(3): 273–291.
- Karplus, I., S. R. Malecha, A. Sagi, 2000. The biology and management of size variation. In: New, M. B. & W. C. Valenti (eds.), *Freshwater prawn culture: The farming of Macrobrachium rosenbergii*. Blackwell Science, London, U.K. Pp. 259–289.
- Keenan, C. P., P. J. F. Davie & D. L. Mann, 1998. A revision of the genus *Scylla* de Haan, 1833 (Crustacea: Decapoda: Brachyura: Portunidae). *Raffles Bulletin of Zoology*, **46**(1): 217–245.
- Kemp, S., 1918. Crustacea Decapoda of the Inle Lake Basin. *Records of the Indian Museum*, **14**: 81–102, Figs. 1–7, Pls. 8–10.
- Lanchester, W. F., 1901. On the crustaceans collected during the "Skeat" Expedition to the Malay Peninsula, together with a note on the genus *Actaeopsis*, Part I: Brachyura, Stomatopoda, and Macrura. *Proceedings of the Zoological Society of London*, **1901**: 534–574, Pls. 33–34.
- Lindenfels, M. E., 1984. Morphometric and allozymic congruence: evolution in the prawn *Macrobrachium rosenbergii* (Decapoda: Palaemonidae). *Systematic Zoology*, **33**: 195–204.
- Ling, S. W., 1977. *Aquaculture in Southeast Asia: A historical overview*. University of Washington Press, Seattle, USA.
- Ling, S. W. & T. J. Costello, 1979. The culture of freshwater prawns: a review. In: Pillay, T. V. R. & W. A. Dill (eds.), *Advances in Aquaculture*. Papers presented at the FAO Technical Conference on Aquaculture, 26 May–2 June 1976, Kyoto. Fishing News Books, Blackwell Science, Oxford, UK.
- Ling, S. W. & A. B. O. Merican, 1961. Notes on the life and habits of the adults and larval stages of *Macrobrachium rosenbergii* (De Man). *Proceedings of the Indo-Pacific Fisheries Council*, **9**(2): 55–60. FAO, Bangkok.
- Linnaeus, C., 1758. *Systema naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis*. Edition 10, **1**: iii + 824 pp. Holmiae.
- Liu, J. Y., X. Liang & S. Yan, 1990. A study of the Palaemoninae (Crustacea Decapoda) from China I. *Macrobrachium, Leander and Leandrites*. *Transactions of the Chinese Crustacean Society*, **2**: 102–134 (in Chinese with English abstract).
- Maccagno, T. P. & B. Cucchiari, 1957. Revisione delle Palaemoninae del Museo di Torino. *Bollettino dell'Istituto e Museo di Zoologia dell'Università di Torino*, **5**: 201–372.
- Mather, P. B. & M. de Bruyn, 2003. Genetic diversity in wild stocks of the giant freshwater prawn (*Macrobrachium rosenbergii*): implications for aquaculture and conservation. *NAGA, WorldFish Center Quarterly*, **26**(4): 4–7.
- Von Martens, E., 1868. Über einige Ostasiatische Süßwasserthiere. *Archiv für Naturgeschichte*, **34**(1): 1–64, Pl. 1.
- Menon, M. K., 1938. The early larval stages of two species of *Palaemon*. *Proceedings of the Indian Academy of Sciences*, **8B**: 288–294.
- Miers, E. J., 1880. On a collection of Crustacea from the Malaysian Region. Part III. Crustacea Anomura and Macrura (except Penaeidea). *Annals and Magazine of Natural History*, **5**(5): 370–384, Pl. 14, Figs. 6–8, Pl. 15, Figs. 1–7.
- Milne Edwards, H., 1837. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*, **2**: 1–532, Pls. 1–14. Librairie encyclopédique de Roret, Paris.
- Naiyanetr, P., 1998. *Checklist of crustacean fauna in Thailand*. Office of Environmental Policy and Planning, Bangkok, Thailand. 161 pp.
- New, M. B., 2000. History and global status of freshwater prawn farming. In: New, M. B. & W. C. Valenti (eds.), *Freshwater prawn culture: The farming of Macrobrachium rosenbergii*. Blackwell Science, London, U.K. Pp. 1–11.
- Ng, P. K. L., 1990. Freshwater crabs and prawns of Singapore. In: Chou, L. M. & P. K. L. Ng (eds.), *Essays in Zoology*. Department of Zoology, National University of Singapore, Republic of Singapore, pp. 189–204.
- Ng, P. K. L., 1994. On a collection of freshwater decapod crustaceans from the Kinabatangan river, Sabah, Malaysia, with descriptions of three new species. *Sabah Museum Journal*, **1**(2): 73–92.
- Ng, P. K. L., 1997. The conservation status of freshwater prawns and crabs in Singapore with emphasis on the nature reserves. *Proceedings of the Nature Reserves Survey Seminar: Gardens' Bulletin Singapore*, **49**(1997): 267–272.
- Ng, P. K. L. & S. C. Choy, 1990. Notes on some freshwater caridean prawn (Palaemonidae and Atyidae) from the Endau-Rompin area, Johore-Pahang, Peninsular Malaysia. *Raffles Bulletin of Zoology*, **38**(1): 11–20.
- Nobili, G., 1899. Contribuzioni alla conoscenza della fauna carcinologica della Papuasia, della Molucche e dell'Australia. *Annali del Museo Civico di Storia Naturale di Genoa*, series 2, **20**(40): 230–282.
- Nobili, G., 1900. Decapodi e Stomatopodi Indo-Malesi. *Annali del Museo Civico di Storia Naturale di Genoa*, series 2, **20**(40): 473–523.
- Olivier, A. C., 1811. Palaemon: *Palaemon*. In: Olivier, *Encyclopédie méthodique: Histoire naturelle: Insectes*, **8**: 653–667.
- Ortmann, A., 1891. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei Liu-Kiu-Inseln gesammelten und z. Z. im Strassburger Museum aufbewahrten Formen, II. Versuch einer Revision der Gattungen *Palaemon* sens. strict. und *Bithynis*. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, **5**: 693–750, Pl. 47.
- Ra'anan, Z. & A. Sagi, 1985. Alternative mating strategies in male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (De Man). *Biological Bulletin*, **169**: 592–601.
- Riek, E. F., 1951. The Australian freshwater prawns of the family Palaemonidae. *Records of the Australian Museum*, **22**(4): 358–367, Figs. 1–12.
- Roux, J., 1917. Crustacés. In: Wichmann, C. E. A. (ed.), *Expédition de 1903. Nova Guinea, Résultats de l'Expédition Scientifique Néerlandaise à la Nouvelle-Guinée*, Zoologie, **5**: 589–621, Pls. 27–28.
- Roux, J., 1921. Crustacés (Expédition de 1907, 1909 et 1912). *Nova Guinea, Résultats de l'Expédition Scientifique Néerlandaise à la Nouvelle-Guinée*, **13**, Zoologie, **4**: 585–606, Pl. 16.
- Roux, J., 1923. Crustacés d'eau douce de l'archipel Indo-Australien. *Capita Zoologica*, **2**(2): 1–22.
- Roux, J., 1927. Contribution à la faune Carcinologique d'eau douce de la Nouvelle-Guinée. *Nova Guinea, Résultats de l'Expédition Scientifique Néerlandaise à la Nouvelle-Guinée*, Zoologique, **15**: 319–350.
- Roux, J., 1928. Notes carcinologiques de l'archipel Indo-Australien. *Treubia*, **10**: 197–224.
- Roux, J., 1932. Süßwassermacruren der Deutschen Limnologischen Sunda-Expedition. *Archiv für Hydrobiologie*, supplement, **11**(67): 563–574.

- Roux, J., 1933. Note sur quelques Crustacés décapodes d'eau douce provenant de l'Australie septentrionale. *Revue Suisse de Zoologie*, **40**(24): 343–348.
- Sandifer, P. A. & T. I. J. Smith, 1979. Possible significance of variation in the larval development of Palaemonid shrimp. *Journal of Experimental Marine Biology and Ecology*, **39**: 55–64.
- Sarver, D., S. Malecha & D. Onizuka, 1979. Development and characterization of genetic stocks and their hybrids in *Macrobrachium rosenbergii*: physiological responses and larval development rates. *Proceedings of the World Mariculture Society*, **10**: 880–892.
- Schenkel, E., 1902. Beitrag zur Kenntnis der Dekapodenfauna von Celebes. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, **13**: 485–585, Pls. 7–13.
- Sharp, B., 1893. Catalogue of the Crustaceans in the Museum of the Academy of Natural Sciences of Philadelphia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1893**: 104–127.
- Short, J. W., 2004. A revision of Australian river prawns, *Macrobrachium* (Crustacea: Decapoda: Palaemonidae). *Hydrobiologia*, **525**: 1–100.
- Sunier, A. L. J., 1925. Twee mededeelingen over Palaemoniden. *Tijdschrift Nederlandsche Dierkundige Vereeniging*, **(2)** 19: cxv–cxvii.
- Suvatti, C., 1937. A check-list of aquatic fauna in Siam (excluding Fishes), pp. 1–116.
- Thallwitz, J., 1892. Decapoden-Studien, insbesondere basirt auf A. B. Meyer's sammlungen im Ostindischen Archipel, nebst einer Aufzählung der Decapoden und Stomatopoden des Dresdener Museums. *Abhandlungen und Berichte des Königlichen Zoologischen und Anthropologisch-Etnographischen Museums zu Dresden*, **1890/91**(3): 55 pp, Pl. 1.
- Tiwari, K. K., 1955. Distribution of the Indo-Burmese freshwater prawns of the genus *Palaemon* Fabr., and its bearing on the Satpura hypothesis. *Bulletin of National Institute of Sciences of India*, **7**: 230–239.
- Tombes, A. S. & M. W. Foster, 1979. Growth of appendix masculina and appendix interna in juvenile *Macrobrachium rosenbergii* (De Man) (Decapoda, Caridea). *Crustaceana*, supplement, **5**: 179–184, Pls. 1–2.
- Woodley, C. M., W. T. Slack, M. S. Peterson & W. C. Vervaeke, 2002. Occurrence of the non-indigenous giant Malaysian prawn, *Macrobrachium rosenbergii* (De Man, 1879) in Simmons Bayou, Mississippi, U. S. A. *Crustaceana*, **75**(8): 1025–1031.
- Wowor, D., Y. Cai & P. K. L. Ng, 2004. Crustacea: Decapoda, Caridea. In: Yule, C. & H. S. Yong (eds.), *Freshwater Invertebrates of the Malaysian Region*. Malaysian Academy of Sciences, pp. 337–357.
- Wowor, D. & S. C. Choy, 2001. The freshwater prawns of the genus *Macrobrachium* Bate, 1868 (Crustacea: Decapoda: Palaemonidae) from Brunei Darussalam. *Raffles Bulletin of Zoology*, **49**(2): 269–289.
- Wowor, D. & P. K. L. Ng, 2001. Identity of the Giant Prawn, *Macrobrachium rosenbergii* (de Man, 1879) (Crustacea: Decapoda: Caridea: Palaemonidae). In: *Book of Abstracts of the Fifth International Crustacean Congress, Melbourne, Australia, July 9–13, 2001*.