Macrobrachium ngankeeae, a new species of freshwater shrimp (Crustacea: Decapoda: Palaemonidae) from Papua Barat Province, Indonesia

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Abstract

A new freshwater prawn, *Macrobrachium ngankeeae* **n. sp.**, is described from two rivers in the Kaimana Regency on the southern coast of Papua Barat Province, Indonesia. The new species belongs to the *Macrobrachium placidulum* (De Man, 1892) species-group, but can be easily distinguished from the other members of this group by having fewer postorbital teeth and the epigastric tooth placed more anteriorly, with a relatively shorter epigastric length, i.e. 0.23–0.27 of the carapace length (*vs*. 0.24–0.55 in the other species). Other distinguishing morphological characters and a molecular analysis of the new species are discussed. A key to the species of the *M. placidulum* species-group is provided.

Key words: Taxonomy, Palaemonidae, new taxon, freshwater prawn, Indonesia, New Guinea, Southeast Asia

Introduction

In one of the most important early studies on the decapod fauna of the Indo-Malayan archipelago, De Man (1892) described three closely related freshwater prawn species from Indonesia, namely *Macrobrachium lepidactyloides* (De Man, 1892), *M. placidum* (De Man, 1892) and *M. placidulum* (De Man, 1892). Recently, Saeki *et al*. (2018) commented on the taxonomy and the morphology of the *M. placidulum* species-group focusing on the Ryukyu Archipelago, providing distinguishing morphological characters for *M. lepidactyloides*, *M. placidum*, *M. placidulum*, *M. feunteuni* Keith & Vigneux, 2002, an endemic species from the Marquesas archipelago (French Polynesia), and an unidentified species reported as *Macrobrachium* sp. According to these authors, species of the *M. placidulum* group are characterized by the distinctly asymmetric male second pereiopods and the fingers of the minor cheliped chela widely gaping and covered by dense setae. The chela or (and) the last three pereiopods of adult males of the *M. placidulum* species group are densely armed with very characteristic squamiform setae, which appear to represent a synapomorphy for this group.

In 2010, the Lengguru-Kaimana Scientific Expedition, a biodiversity survey in Papua Barat Province, was conducted by the Lembaga Ilmu Pengetahuan Indonesia (LIPI) [present: Badan Riset dan Inovasi Nasional (BRIN) = National Research and Innovation Agency], Institut de Recherche pour le Développement (IRD), Akademi Perikanan Sorong (APSOR), the Muséum National d'Histoire Naturelle, Paris (MNHN), Badan Penelitian dan Pengembangan Kelautan dan Perikanan (BALITBANGKP) and Dinas Kelautan dan Perikanan Kaimana (DKP-Kaimana). During this expedition, several specimens of an unidentified species clearly belonging to the *M. placidulum* species group were collected in the southern part of the Papua Barat Province. The purpose of this study is to describe this new species, providing its morphological and molecular identity.

Materials and methods

Sample collection, preparation and identification

Specimens were collected from several rivers in the southern part of the Papua Barat (= West Papua) Province, particularly in the Kaimana Regency. The prawns were caught by using an electro-shocker (portable Dekka 3000 electric device, Dekka Ltd, Germany) (Lamarque *et al*. 1975). The live specimens were photographed in the field with an Olympus TG-4 camera and

later preserved in 75–95% ethanol. Drawings were made using the digital inking method (Coleman 2006) with Adobe Illustrator (CS6). The material examined is deposited in the Museum Zoologicum Bogoriense, Bogor (MZB), Indonesia, and in the Muséum National d'Histoire Naturelle, Paris (MNHN), France. Spine terminology follows Short (2004). Indonesian words used in the text are Ds. or Desa for village; and Sg. or Sungai for river / stream. Other abbreviations used in the text include: asl, above sea level; cl, carapace length (measured from the postorbital margin to the posterior margin of the carapace); E, east; S, south; N, north; W, west; R., river; vs, versus; I., island; Is., islands.

DNA extraction, amplification and sequencing

The total DNA was extracted from a tissue sample taken from the last two pairs of the shrimps' pleopods. The 16S mitochondrial rRNA was amplified by ball PCR (Illustra Hot Start Mix Ready-to-go Protocol), using the primers 16Sa-L (CGCCTGTTTATCAAAAACAT) and 16Sb-H (CTCCGGTTTGAACTCAGATCA) from Palumbi (1996) using a Biorad C1000 Touch Thermal Cycler thermocycler and the following protocol: initial denaturation of 5 min at 94°C, 40 cycles of 30 s denaturation at 94°C, 1 min 30 s hybridization at 56°C, 1 min elongation at 72°C, and a final elongation step of 7 min at 75°C. The PCR products were visualized by 1.5% agarose gel electrophoresis. The positive PCR products were sequenced in both directions using the Sanger method by the laboratory © Eurofins France. Chromatograms were then verified and cleaned by eye using MEGA v7.0.26 software (Kumar *et al*. 2016).

Molecular analyses

DNA sequences were aligned using MEGA X software with Muscle algorithm (Edgar 2004). Using Bayesian information criterion in jModelTest (Guindon & Gascuel 2003; Darriba *et al*. 2012) we retained the GTR + G + I model. Best-scoring ML trees were estimated using RAxML HPC2 v.8.2.10 (Stamatakis 2014) and best-scoring Bayesian Inference (BI) trees were estimated using MrBayes v.3.2.7 (Ronquist & Huelsenbeck 2003), both methods implemented in CIPRES with the previously determined model, running for 10,000,000 generations, a sampling frequency of 2,000 and a burn in of 10%. Support for nodes was determined using posterior probabilities calculated by MrBayes implemented in the Cyber Infrastructure for Phylogenetic Research (CIPRES) portal v.3.1. (Miller *et al*. 2010; https://www.phylo.org/). One hundred independent searches, each starting from distinct

random trees, were conducted. Robustness of the nodes was assessed using non-parametric bootstrapping (Felsenstein 1985) with 1,000 bootstrap replicates.

RESULTS

Molecular results

(Fig. 1)

A total of 13 sequences belonging to five species of the *Macrobrachium placidulum* species-group were obtained (plus one sequence retrieved from GenBank for the outgroup). Each species was recovered as a distinct clade. *Macrobrachium feunteuni* (Fig. 1: clade A), was sister to the remainder, with *M. placidum* (Fig. 1: clade B) and *M. placidulum* (Fig. 1: clade C) forming a clades as sister to a moderately supported clade (PP = 0.98; B = 82) clade comprised of the new species (Fig. 1: clade D) and *M. lepidactyloides* (Fig. 1: clade E).

Morphological results

The morphological analysis of the specimens (see below) corroborated our molecular results, giving a strong support for recognition of the specimens from Papua Barat as belonging to an undescribed species.

Taxonomy

Family Palaemonidae Rafinesque, 1815

***Macrobrachium* Spence Bate, 1868**

***Macrobrachium ngankeeae* n. sp.**

(Figs. 2, 3A)

Type material. INDONESIA. Holotype: male (cl 11.3 mm) (MZB Cru 5350) (DNA: MC1226), Papua Barat Province, Kaimana Regency, Buruway District, Ds. Karawawi, Sg. Kunafa, 04°03.260’S 133°4.742’E, 0–30 m asl, coll. P. Keith, P. Gaucher, G. Ségura, 14 October 2010. Paratypes: 1 male (cl 8.2 mm) (MNHN-IU-11859) (DNA: MC1227), same data same as for holotype; 1 male (cl 9.7 mm) (MZB Cru 5351), 1 ovigerous female (cl 8.7 mm) (MNHN-IU-2017-9340), Papua Barat Province, Kaimana Regency, Buruway District,

Ds. Karawawi, Sg. Kunafa, 77 m asl, coll. P. Keith, P. Gaucher, G. Ségura, 15 October 2010; 1 male (cl 9.7 mm) (MNHN-IU-2016-11856), 1 female (cl 9.1 mm) (MZB Cru 5352) (DNA: MC1225), Papua Barat Province, Kaimana Regency, Teluk Etna District, Ds. Kayu Merah, Sg. Kayu Merah, 03°53.290'S 134°28.655'E, coll. P. Keith, P. Gaucher, G. Ségura, 22 October 2010.

Type locality. Kunafa river, 04°03.260'S 133°4.742'E, Kaimana Regency, Papua Barat Province, Indonesia.

Comparative material. See Supplementary material 1.

Diagnosis. Small-sized species with subcylindrical body form. Rostrum short, reaching end of second article to end of third article of antennular peduncle; dorsal margin slightly convex, rostral formula: 3–4+6–8/2–3, dorsal teeth equidistantly spaced; first tooth at 0.23–0.27 of carapace length (measured from anterior end). Carapace glabrous. Ocular beak moderately developed. Third maxilliped with exopod shorter than ischiomerus. Second pereiopods robust, rather long, dissimilar in shape, unequal in size, covered with squamiform setae. Major second pereiopod chela with compressed palm, without setae on cutting edge of fingers, dentate on opposable margins, slightly gaping, fingers shorter than palm, distal part of dactylus and pollex each with double row of tubercles. Cutting edges of minor second pereiopod chela gaping, densely covered with long stiff setae concealing surface, fingers as long as to longer than palm. Carpus conical, shorter than chela, shorter than palm, slightly shorter than merus. Third, fourth and fifth pereiopods glabrous, with few scattered short stiff setae. T4 with median process. Preanal carina well developed. Uropods glabrous, exopod with mobile mesial spine as long as distolateral tooth. Developed eggs small, maximum size 0.6 by 0.5 mm, ovoid, numerous.

Description of holotype and paratypes (latter in parenthesis)

Carapace glabrous. Rostrum short, 0.36 cl (0.37–0.43 cl in paratypes), reaching end of second article to end of third article of antennular peduncle (Fig. 2i); moderately slender, maximum depth 0.75 times as maximal dorsoventral diameter of cornea; lateral carina well developed, continuing almost to rostral tip; dorsal carina convex, bent downwards in front of orbit, with tip directed anteriorly, armed with 10 (10–12) equidistantly spaced teeth, interspaces setose, 3 (3–4) teeth completely postorbital, first postorbital tooth on anterior 0.27 (0.23–0.26) of carapace; ventral carina convex, with 2 (2–3) teeth, proximal-most tooth located at about distal one-third of rostral length. Inferior orbit margin moderately produced, obtuse; post-antennular carapace margin evenly rounded. Antennal spine sharp, slender,

continuing posteriorly as short ridge, situated below lower orbital angle; hepatic spine smaller, situated behind and below antennal spine.

Ocular beak moderately developed without expanded lateral tip. Cornea well developed, 0.20 cl (0.19–0.22), well pigmented. Epistome (Fig. 2f), bilobed, separated by wide, rather shallow depression anteriorly, lobes with rounded anterior margin.

Antennular peduncle 0.45 (0.43–0.51) times as long as carapace. Basal article of peduncle with sharply pointed stylocerite (Fig. 2i), reaching mid-length of second article of peduncle. Scaphocerite (Fig. 2g, i), stout, reaching beyond rostrum, 0.47 (0.48–0.51) of carapace length, 2.53 (2.04–2.80) as long as maximal width maximum breadth, lamina distinctly tapering from widest point to anterior margin, lateral margin straight, mesial margin concave, distolateral tooth reaching end of lamella. Third maxilliped with exopod shorter than ischiomerus. Mouthparts typical of the genus.

First pereiopods slender, equal in length and similar in form (Fig. 2d), 1.14 cl (1.06–1.33) of carapace length, exceeding scaphocerite by chela and distal half of carpus; fingers 0.77 (0.59–0.66) times as long as palm, carpus 1.26 (1.13–1.53) times length of chela, 1.14 (1.00–1.34) as long as merus; scattered, short, stiff setae present on chela; scattered, long, stiff setae present on proximal half of merus, and on mesial margin of ischium and basis; other surfaces glabrous.

Second pereiopods dissimilar in shape and size, robust, covered with squamiform and mammiliform setae, larger and more developed in adult sub-dominant and dominant males than in females.

Male major cheliped (Fig. 2a): chela 1.12 (0.83–1.17) of carapace length, 2.70 (1.37–2.83) as long as maximal width, lateral and mesial margins convex; palm compressed, ventral, outer and dorsal margins with flexible, squamiform setae, mesial margin with blunt, stiff, mammiliform setae, setae on mesial margin larger than those on other margins; fingers (Fig. 2b) 0.69 (0.63–0.79) times length of palm, slightly gaping, with unguiculate tip; dactylus with 3 teeth, increasing in size, at proximal half, followed by unarmed edge ending in a triangular tooth at about two-third from proximal, remaining distal part of dactylus with row of small tubercles on each mesial and lateral cutting edge, margins of dactylus with 2 (2) and 1 (2) tubercles, respectively; cutting edge of pollex with similar armature as that of dactylus], 4 teeth at about one-third proximal, largest one most distal, 1 triangular tooth at about half-length of pollex, remaining distal part of pollex with row of small tubercles on each mesial and lateral cutting edge, margins of pollex with 3 (3) and 1 (3) tubercles respectively; palm noticeably longer than maximal width of carpus and merus; chela 2.25 (2.09–2.5) times length

of carpus; carpus 0.75 (0.68–0.86) times length of palm, conical, length twice as long (1.69–2.16 times as long), 1.09 (0.92–1.23) times length of merus, merus 1.25 (1.13–1.52) times length of ischium.

Male minor cheliped (Fig. 2c, numbers in parenthesis refer to minor cheliped of paratype male, cl 9.7 mm) 0.93 (0.92) as long as major cheliped; chela with margins slightly convex to almost straight; palm cylindrical, lateral margin with few scattered, small, flexible squamiform setae, shorter than those on major chela, mesial margin with minute, blunt, stiff, mammiliform setae, dorsal and ventral margins glabrous (armed with squamiform setae in / on all articles in paratype male, cl 9.7 mm), fingers as long as palm, not gaping, both cutting edges with few tufts of stiff setae (1.49 times length of palm, gaping, both cutting edges with numerous tufts of stiff setae); proximal portion of dactylus with 3 small teeth, proximal portion of pollex with 4 small teeth; palm 4.20 (1.41) times as long as wide; carpus 0.60 (0.49) times length of palm, conical, 2.11 (1.83) times as long as wide, 0.30 (0.39) times as long as chela, 0.63 (0.84) times length of merus, merus 1.25 (1.53) times as long as ischium.

Female major cheliped with ventral, lateral and dorsal margins densely covered with flexible, squamiform setae, mesial margin with blunt, stiff, mammiliform setae, setae of mesial margin larger than those on other margins; chela 0.86 of carapace length; fingers 0.74 times length of palm, not gaping, with unguiculate tip; cutting edge of dactylus with 3 teeth increasing in size distally; cutting edge of pollex with 5 teeth increasing in size distally; palm cylindrical, length 1.76 times of width; carpus long, conical, 0.88 times length of palm, 2.26 as long as wide, 0.88 times length of chela, as long as merus; merus 1.61 times length of ischium.

Female minor cheliped with same setae organization as major cheliped; chela about as long as chela of major cheliped; fingers 0.70–0.85 times length of palm, both cutting edges densely covered with tufts of stiff setae, unarmed; palm cylindrical, 2.59–2.63 times as long as wide; carpus 0.80–0.87 times length of palm, long, conical or subcylindrical, 2.69–2.81 times as long as wide, 0.47 times length of chela, 0.49 times length of merus , merus 1.16–1.23 times as long as ischium.

Third pereiopod glabrous, with few scattered short stiff setae on all articles; dactylus stout, curved, fringed with setae on dorsolateral surface; propodus 3.12–3.67 times length of dactylus, 6.59–6.77 times as long as wide, with 5–7 spinules along ventral margin of propodus, 2 distal-most spinules paired; carpus 0.53–0.59 times length of propodus; merus 1.02–1.05 times length of propodus, 1.89–2.43 times length of ischium. Fifth pereiopod (Fig. 2e) glabrous, with few scattered, short, stiff setae on all articles; dactylus stout, curved;

propodus with a ventrolateral row of setae at distal end, 7.93 (8.34–8.46) times as long as wide, 4.23 (3.63–4.29) times as long as dactylus, with 5–6 spinules along ventral margin of propodus; carpus 0.52 (0.57–0.59) times as long as propodus; merus 0.80 (0.77–1.00) times as long as propodus, 1.72 (1.59–2.48) times as long as ischium.

Thoracic sternite 4 with small median process, with distinct submedian plate; thoracic sternite 8 with contagious anterolateral lobes (in fully developed male), with large shallow conical median process.

Pleon smooth, glabrous; sixth pleonite 1.34 (1.30–1.65) times as long as fifth pleonite. Pleonites of first 2 male sternites each with triangular median process, sloping about 70°; sternite of pleonite 3 unarmed. Inter-uropodal sclerite well developed as large, longitudinal, preanal carina.

Telson (Fig. 2h) elongate, 1.46 (1.28–1.88) times as long as sixth pleonite, 3.13 (2.44–3.06) times length of median width; lateral margins straight, convergent posteriorly; dorsal surface with 2 pairs of spines; posterior margin triangular, with large rounded median margin overreached by mesial pair of posterior spines, latter 2.7 longer than lateral pair of spines; 9–13 pairs of long, plumose, subventral setae present between mesial pair spines.

Pleopods not especially modified. Endopod of male first pleopod kidney-shaped, with concave mesial margin and convex lateral margin, apex rounded, reaching 0.29–0.41 times total length of endopod . Male second pleopod with appendix masculina long, slender, reaching 0.59 times length of endopod, with numerous simple, stiff setae on anterior margin; appendix interna reaching 0.51 of appendix masculina. Uropods glabrous; exopod with movable spine as long as or longer than distolateral tooth.

Ovigerous female with numerous, oval-shaped, small-sized eggs (diameter 0.62–0.52 mm × 0.42–0.48 mm).

Life color. Mainly translucent grey, with mottled pattern of gold-white and darker spots scattered especially on cephalothorax and walking legs; pleon, telson and uropods translucent (Fig. 3A).

Etymology. The late Ng Ngan Kee (14 April 1966–5 July 2022) was a leading taxonomist of brachyuran crabs, especially the family Varunidae. She was a good friend and

ex-lab mate of the third author (DW), and a very kindhearted person, who always gave her hands whenever people needed her help. The present new species, *Macrobrachium ngankeeae* **n. sp.**, is dedicated to her memory. The specific epithet refers to her first combined name, Ngan Kee, the name by which most of N. K. Ng's colleagues and friends addressed her.

Remarks. Genetic analyses (Fig. 1) and morphological analyses show that *Macrobrachium ngankeeae* sp. nov. belongs to the *M. placidulum* species-group *sensu* Saeki *et al*. (2018). Keith & Vigneux (2002) mentioned that *M. feunteuni* resembles *M. lepidactyloides* and both species were also discussed by Saeki *et al.* (2018). Therefore, in the present study, both *M. ngankeeae* **n. sp.** and *M. feunteuni* are included in the *M. placidulum* species-group.

Morphological comparisons confirmed that *M. ngankeeae* sp. nov. belongs to the *M. placidulum* species-group due to the second pereiopods being unequal in length and dissimilar in shape and the presence of squamiform setae on the walking legs.

The following characters enable to distinguish the members of this species-group (Table 1):

- Number of post-orbital teeth on the dorsal margin of the cephalothorax (3–4 in *M. ngankeeae* sp. nov. *vs.* ≥4 for the other four species).
- Position of the first tooth in proportion of the total cephalothorax length measured from the anterior end (0.23–0.27 in *M. ngankeeae* sp. nov. *vs.* >0.29 for all except *M. feunteuni* (0.24–0.30).
- Major second pereiopod dactylus length compared to palm length: dactylus distinctly shorter than palm in *M. ngankeeae* sp. nov. and *M. placidulum* (*vs.* dactylus shorter to slightly longer than palm in *M. feuteuni* and *M. placidum, vs.* dactylus distinctly longer than palm in *M. lepidactyloides*).
- Major second pereiopod chela length compared to carpus length (chela more than 2.3 times as long as carpus in *M. ngankeeae* sp. nov., *M. lepidactyloides* (*vs.* chela less than 2.3 times as long as carpus in *M. feunteuni, M. placidulum and M. placidum*).
- Minor second pereiopod dactylus length compared to palm length (dactylus slightly shorter to longer than palm in *M. ngankeeae* sp. nov., *M. feunteuni* and *M. placidulum* vs slightly shorter to slightly longer in *M. placidum, vs.* dactylus considerably longer than palm in *M. lepidactyloides,*
- Ocular beak (prominent only in *M. ngankeeae* sp. nov.).
- Projection on the fourth thoracic sternite (present only in *M. ngankeeae* sp. nov.).

Ecology. *Macrobrachium ngankeeae* **n. sp.** inhabits moderate to fast-flowing rivers in coastal lowlands, at elevation ranging from below 5 to 30 m (Fig. 3B). The number and the size of the eggs in ovigerous females are indicative of a prolonged larval development typical for amphidromous species (Wowor *et al*. 2009).

Distribution. This new species is presently known only from the southern lowlands in Papua Barat Province, Indonesia.

***Macrobrachium feunteuni* Keith & Vigneux, 2002**

Macrobrachium feunteuni Keith & Vigneux, 2002: 130, figs 25–33.

Material examined. See Supplementary material 1.

Diagnosis. Medium-sized species with subcylindrical body form. Rostrum reaching to the middle of the third segment of the antennular peduncle, dorsal margin slightly convex, rostral formula: 5–7+3-4/1–2, Small setae present between teeth of both dorsal and ventral margins. first tooth placed 24.6–30.7 percent of the length of the cephalothorax. Carapace glabrous. Ocular beak moderately developed. Second pereiopods robust, dissimilar in shape, unequal in size. The major P2 dactylus bears proximally 3 to 4 rather large teeth, which are placed close together, distally 3 rounded tubercules. The pollex near the articulation with the propodus bears a ridge which consist of 4–8 indistinctly separated, often crenulated teeth, then after an unarmed space a large tooth, distally 8 rounded tubercules. Fingers 0.66–1.03 times as long as palm, chela 1.57–2.33 times as long as carpus. Minor 2nd pereiopod with fingers 0.85–1.55 times as long as palm. Cutting edges of minor second pereiopod gaping, densely covered with long stiff setae concealing surface. All articles covered with modified squamiform and long blunt mamilliform setae. Third, fourth and fifth pereiopods with modified squamiform setae and few scattered short stiff setae. T4 without median process. Preanal carina well developed. Uropods glabrous, exopod with mobile mesial spine longer than distolateral tooth. Developed eggs small, maximum size 0.6 × 0.5 mm, ovoid, numerous.

Distribution. So far *M. feunteuni* is is only encountered in three islands of Marquesas Islands, French Polynesia.

***Macrobrachium lepidactyloides* (de Man, 1892)**

Palaemon (Macrobrachium) lepidactyloides De Man, 1892: 497, pl. 29, fig. 51

Palaemon lepidactylus. — Cowles, 1914: 389, pl. 3, Fig. 9 [not *P. lepidactylus* Hilgendorf, 1879.]

Macrobrachium hirtimanus. — Holthuis, 1950: 245 [part], fig. 51a.

Macrobrachium lepidactyloides. — Holthuis, 1952: 210, pl. 15, fig. 2; Chace & Bruce, 1993: 32, fig. 12; Ito *et al*. 2006: 23; Chen *et al*. 2009: 234, tab. 2; Eguia *et al*. 2009: 31; Keith *et al*. 2013: 108; Saeki *et al*. 2018: 35, figs 2–4, 5A–D, 6.

Material examined. See Supplementary material 1.

Diagnosis. Medium-sized species with subcylindrical body form. Rostrum which seldom reaching to the end of the antennular peduncle, dorsal margin slightly convex, rostral formula: 5–7+4–6/2–3, dorsal teeth unequally spaced; first tooth placed 47.3–55.0 percent of the length of the cephalothorax. Carapace glabrous. Ocular beak moderately developed. Second pereiopods robust, dissimilar in shape, unequal in size. The Major P2 dactylus bears proximally 2–3 rather large teeth, which are placed close together, distally around 10 smaller triangular teeth. The pollex, near the articulation with the propodus bears a ridge which consist of 2–3 indistinctly separated, often crenulated teeth, then after an unarmed space a large tooth, distally numerous smaller triangular teeth, more than 10. The number of these triangular teeth varies with the length of the fingers. Fingers 1.27–1.33 as long as palm, chela 2.37–2.53 as long as carpus, Minor 2nd pereiopod with fingers 1.75–2.12 times as long as palm. Cutting edges of minor second pereiopod gaping, densely covered with long stiff setae concealing surface. All articles covered with modified squamiform and long blunt mamilliform setae. Third, fourth and fifth pereiopods with modified squamiform setae and few scattered short stiff setae T4 with median process. Preanal carina well developed. Uropods glabrous, exopod with mobile mesial spine longer than distolateral tooth. Developed eggs small, maximum size 0.6 × 0.5 mm, ovoid, numerous.

Distribution. Wide-ranging in the Indo-West Pacific from eastern Indonesia, the Philippines, Taiwan and subtropical Japan to Fiji and French Polynesia.

***Macrobrachium placidulum* (De Man, 1892)**

Palaemon (Macrobrachium) placidulus De Man, 1892: 489, pl. 28, fig. 48.

Macrobrachium placidulum. — Holthuis, 1950: 253, fig. 51c; Chace & Bruce, 1993: 35, fig. 14; Chen *et al*. 2009: 234, tab. 2; Eguia *et al*. 2009: 36; Keith *et al*. 2010: 76; Keith *et al*. 2013: 112; Saeki *et al*. 2018: 42, fig. 5E–F, 7

Material examined. See Supplementary material 1.

Diagnosis. Medium-sized species with subcylindrical body form. Rostrum short reaching at most to the end of the third segment of the antennular peduncle, mostly to the middle of second segment of the antennaular peduncle, dorsal margin slightly convex, rostral formula: 4–6+5–7/2–3, dorsal teeth more widely spaced anteriorly than posteriorly; first tooth placed 29–50 percent of the length of the cephalothorax. Carapace glabrous. Ocular beak absent or very poorly developed. Second pereiopods robust, dissimilar in shape, unequal in size. The major P2 dactylus bears proximally 3–4 rather large teeth, which are well separated, distally seven smaller rounded teeth. The pollex, near the articulation with the propodus bears a ridge which consist of 7 indistinctly separated, often crenulated teeth, then after an unarmed space a large tooth, distally eightr smaller rounded teeth.. Fingers 0.55–0.72 times as long as palm, chela 1.64–2.01 times as long as carpus. Minor 2nd pereiopod with fingers 1.0–1.29 times as long as palm. Cutting edges of minor second pereiopod gaping, densely covered with long stiff setae concealing surface All articles covered with modified squamiform and mamilliform setae. Third, fourth and fifth pereiopods with modified squamiform setae and few scattered short stiff setae. T4 without median process. Preanal carina well developed. Uropods glabrous, exopod with mobile mesial spine longer than distolateral tooth. Developed eggs small, maximum size 0.6 × 0.5 mm, ovoid, numerous.

Distribution. Commonly found in the Indo-West Pacific from south coast of Java to eastern Indonesia, the Philippines, Taiwan and subtropical Japan to Palau, Vanuatu, New Caledonia, Futuna, Fiji and Samoa.

***Macrobrachium placidum* (de Man, 1892)**

Palaemon (Macrobrachium) placidus De Man, 1892: 483, pl. 28, fig. 46

Macrobrachium placidum. — Holthuis, 1950: 251, fig. 51b; Chace & Bruce, 1993: 36

Material examined. See Supplementarx material 1.

Diagnosis. Medium-sized species with subcylindrical body form. Rostrum short reaching at most to the end of the third segment of the antennular peduncle, mostly to the middle of second segment of the antennular peduncle, dorsal margin slightly convex, rostral formula: 5–7 +4–6/2–4, dorsal teeth more widely spaced anteriorly than posteriorly; first tooth placed 41–50 percent of the length of the cephalothorax. Carapace glabrous. Ocular beak moderately developed. Second pereiopods robust, dissimilar in shape, unequal in size. Second pereiopods robust, rather long, dissimilar in shape, unequal in size. The major P2 dactylus bears proximally 3 rather large teeth, which are placed close together, then a large tooth followed distally by around 10 smaller triangular teeth. The pollex, near the articulation with the propodus bears a ridge which consist of 4 teeth indistinctly separated, often crenulated teeth, then after an unarmed space a large tooth, distally numerous smaller triangular teeth, more than 10. The number of these triangular teeth varies with the length of the fingers. Fingers 0.82–1.02 as long as palm, chela 1.82–2.18 as long as carpus. Minor 2nd pereiopod with fingers 0.85–1.1 times as long as palm. Cutting edges of minor second pereiopod gaping, densely covered with long stiff setae concealing surface All articles covered with modified squamiform and mamilliform setae. Third, fourth and fifth pereiopods with modified squamiform setae and few scattered short stiff setae. T4 without median process. Preanal carina well developed. Uropods glabrous, exopod with mobile mesial spine longer than distolateral tooth. Developed eggs small, maximum size 0.6 × 0.5 mm, ovoid, numerous.

Distribution. West coast of Sumatra, south coast of Java and southern Sulawesi in Indonesia. This species is recorded for the first time from Catanduanes Island, Philippines.

General discussion

Macrobrachium ngankeeae **n. sp.** belongs, both genetically and morphologically, to the *M. placidulum* species group (Fig. 1). According to Saeki *et al*. (2018), this species group is characterized by males having distinctly asymmetric second pereiopods and the minor chela fingers widely gaping and densely furnished by setae. The present study suggests that the *M. placidulum* group also has several more specific characters, such as the rostrum with at least three teeth behind the orbit; the second pereiopods covered by squamiform setae on the dorsal, lateral and ventral margins, and by mamilliform setae on the mesial margin; the

preanal carina present and very prominent; the movable spine of the uropodal exopod longer than the distolateral tooth; and ovigerous females with numerous, small-sized, oval eggs, indicating an extended larval development.

All members of the *M. placidulum* group are found in the lower to middle course of lowland rivers, where they prefer well-oxygenated zones with strong current. Some specific morphological characters of this species group are related to their adaptation to the habitat (de Mazancourt *et al*. unpub.). For instance, the short and relatively slender rostrum results in less friction in a strong water current (Felgenhauer & Abele, 1983). The squamiform setae, which are present at least on the second cheliped and first walking leg, may represent a hydrodynamic adaptation for swimming in fast flowing environment. Their robust body and stout second chelipeds, with a short and conical carpus, allow them to remain stable in fast-flowing water areas. Each of the last three pairs of pereiopods terminate in a stout and have a curved, claw-shaped dactylus, which probably helps the shrimps to have a tighter grip onto the substrate and thus not being swept away by the strong river current. All members of this species group also have a well-developed preanal carina, which is a common feature in moderate to fast flowing dwellers, such as *M. gracilirostre* (Miers) and *M. lar* (Fabricius) (pers. obs.).

The number and size of the eggs (developing embryos) suggest that all members of the *M. placidulum* species group are amphidromous species with an extended larval development. The larvae are planktonic and have to develop in a saline environment in estuaries or in the open sea (Wowor *et al*. 2009). The number of the larval development stages, their duration, and the range of salinity tolerance are characteristic for each species (Shokita 1985; Ito *et al*. 2006), whereas the sea current pattern significantly contributes to species dispersal (Irving *et al*. 2017). As an example, the amphidromous *M. latimanus* (von Martens, 1868) has very wide distribution throughout the Indo-West Pacific, ranging from India and Sri Lanka to Ryukyu Islands in Japan, Marquesas Islands in French Polynesia and reaching the isolated Pitcairn Island (Holthuis 1950; Chace & Bruce 1993; Irving *et al*. 2017). This species has 11 zoeal stages with a total duration of 57 days, and its salinity tolerance ranges between 17.5‰ and 28.0‰ (Ito *et al*. 2006). In contrary, the land-locked *M. shokitai* Fujino & Baba, 1973, which is endemic to Iriomote Island in the Ryukyu Islands, Japan (Doi *et al*. 2022), has only one larval stage of 20 hours and no salinity tolerance (Shokita 1985).

Among the *M. placidulum* species group members, *M. ngankeeae* **n. sp.** appears to have the most restricted distribution, being presently known only from the southern coast of West Papua Province, Indonesia. However, *M. feunteuni* is also fairly restricted, being found only

on three islands of the Marquesas Islands. The remaning three species are more widespread, with *M. placidum* present from western Sumatra, southern Java and southern Sulawesi in Indonesia to Catanduanes Island in the Philippines; *M. placidulum* ranging from southern Java to the eastern islands of Indonesia, Philippines, Taiwan, Ryukyu Islands, Palau, Vanuatu, New Caledonia, Futuna, Fiji and Samoa; and *M. lepidactyloides* ranging from eastern Indonesia and the Philippines to Taiwan and Ryukyu Islands in the north, and Fiji and French Polynesia in the east.

Key to Species of *Macrobrachium placidulum* species group

1 Rostrum with 3–4 postorbital teeth and epigastric length 0.23–0.26 of carapace length ……..……...……. *M. ngankeeae*, new species

Rostrum with 4–7 postorbital teeth and epigastric length 0.24–0.55 of carapace length ……..…….……2

2 Rostral dorsal margin above eyes flat and straight ……..……. *M. feunteuni*

Rostral dorsal margin above eyes convex ……..……...……..…… 3

3 Ocular beak absent or very poorly developed ...…….…….… *M. placidulum*

Ocular beak well developed ……..…… 4

4 T4 without median process …….…… *M. placidum*

T4 with median process …….…… *M. lepidactyloides*

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641

642 **Legends to figures**

643 **FIGURE 1.** Phylogenetic Bayesian 16S tree of *Macrobrachium placidulum* species-group.
644 Numbers above branches are Bayesian posterior probabilities, numbers under branches are
645 bootstrap values.

646 **FIGURE 2.** *Macrobrachium ngankeeae* n. sp., paratype: male (cl 9.7 mm) (MNHN-IU-2016-
647 11856), Papua Barat Province. a, major second pereiopod; b, major second pereiopod finger;
648 c, minor second pereiopod; d, first pereiopod; e, fifth pereiopod; f, epistome; g, scaphocerite;
649 h, telson; i, cephalothorax.

650 **FIGURE 3.** A, Living male specimen of *Macrobrachium ngankeeae* sp. nov.; B, typical
651 habitat of *M. ngankeeae* sp. nov. (photos by P. Keith).

652 **TABLE 1.** Morphological comparison of the species of the *M. placidulum* species-group.