Tropical Natural History, Supplement 8 (2025): 493–511
https://doi.org/10.58837/tnh.25.8.268420

Morphology and Molecular Phylogeny of a New Species, *Macrobrachium debaratae* sp. nov. (Caridea, Palaemonidae) from Songkhram River, Northeast Thailand

WARUT SIRIWUT[1]*, APISARA CHAOWVIENG[1], EKGACHAI JERATTHITIKUL[1], RATMANEE CHANABUN[2], SOMSAK PANHA[3,4] AND CHIRASAK SUTCHARIT[3]

[1]*Animal Systematics and Molecular Ecology Laboratory, Department of Biology, Faculty of Science, Mahidol University, Bangkok 10400, THAILAND*
[2]*Program in Animal Science, Faculty of Agricultural Technology, Sakon Nakhon Rajabhat University, Sakon Nakhon 47000, THAILAND*
[3]*Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, THAILAND*
[4]*Academy of Science, The Royal Society of Thailand, Bangkok 10300, THAILAND*
*Corresponding author. Warut Siriwut (warut.sir@mahidol.ac.th)
Received: 11 July 2025; Accepted: 11 September 2025; Date of Publication: 17 November 2025
https://zoobank.org/urn:lsid:zoobank.org:pub: EE36C248-F390-47C9-BC95-47841A4A4AB0

ABSTRACT.– The recognized diversity of *Macrobrachium* prawns in Thailand has increased recently due to taxonomic investigation using integrative approaches, i.e. from morphology and DNA barcoding. The freshwater habitats in northeast Thailand such as riparian wetland ecosystems provide diverse ecological conditions that promote adaptive diversification among organisms. The varying condition of the freshwater bodies can support the existence of cryptic species among the aquatic animal fauna, including in prawns of the genus *Macrobrachium*. Several *Macrobrachium* species have previously been reported in association with the vast network of tributaries that form the Mekong River basin. Newly described species and unidentified morphospecies have particularly been reported from this area in previous systematic studies, which indicates that the current known diversity of the aquatic fauna is likely to be largely incomplete. In this study, a new species of the genus *Macrobrachium* from the Songkhram River, one of the Mekong tributaries, is described and named as *Macrobrachium debaratae* Siriwut, sp. nov. This new species contains several distinct morphological characters from its congeneric and co-existing species group, such as the rostral teeth formula, the size and the shape of second pereiopods, and the tooth present on the cutting edge of the fingers of the chelae of the second pereiopods. Genetic distance analysis among the known *Macrobrachium* species supported this morphological classification as a new species with an interspecific COI divergence of 13%. The COI phylogenetic tree indicated that *M. debaratae* Siriwut, sp. nov. was monophyletic and was placed close to *M. sirindhorn*, a member within the *M. pilimanus* species group. This study highlights the need for a detailed morphological inspection to examine the variability in the taxonomic characters of *Macrobrachium*, particularly in the *M. pilimanus* species group found in mainland Southeast Asia tributaries. Further taxonomic review based on intensive sampling is required to provide a more adequate understanding of the diversity of *Macrobrachium* in the Mekong basin.

KEYWORDS: *Macrobrachium*, Thailand, Songkhram River, New species, COI barcode

INTRODUCTION

The Mekong River basin, a world-renowned freshwater basin, harbors mega-aquatic fauna and flora (Meynell, 2017). The Khorat plateau in northeastern Thailand constitutes a fluvial network of Mekong freshwater tributaries (Mekong River Commission, 2005). The Chi-Mun and Songkhram River basins occupy the majority of the hydrological networks in this plateau. Aquatic animal diversity and population density are highly abundant in the Mekong basin. The biota has played an important role as food, both as wild caught and more recently from aquaculture as well, for the indigenous peoples over a long historical period (Kang and Huang, 2022).

However, concerns regarding the impacts of development activities and poaching of the native fauna have given rise to critical concerns in this region (Meynell, 2017; Morovati et al., 2024; Sun et al., 2025). The decline of aquatic animal populations over the past few decades is considered as a crisis indicator for conservation ecology and environmental changes in this river basin (Fukushima et al., 2014; Morovati et al., 2024). Ecological surveys and taxonomic studies of several invertebrates and vertebrates (e.g. fish (Zhang et al., 2021), other land vertebrates (Buckton and Safford, 2004; IUCN, 2013), annelid worms (Jirapatrasilp et al., 2019), freshwater molluscs (Ng et al., 2020), and decapods (Hanamura et al., 2011)) have all indicated that the Mekong basin supports a diverse local fauna. Moreover, migration and changes in some aquatic fauna compositions are previously reported along this river basin during seasonal floods (Lukoschek et al.,

2011; Adamson et al., 2012; Imai et al., 2014; Meynell, 2017; Sor et al., 2020).

Freshwater prawns of the genus *Macrobrachium* Spence Bate, 1868 are utilized as palatable food and protein resources for local consumption (Holthuis, 1980) and are being promoted regionally for the aquaculture industry (New and Nair, 2012; Wowor and Ng, 2007). Comprehensive taxonomic records and review of the Thai *Macrobrachium* species have been conducted in which 36 species were recorded (Naiyanetr, 1998; Cai et al., 2004). However, recent approaches such as species delimitation and DNA barcode studies, have suggested that the fauna diversity is underestimated (Siriwut et al., 2021). Additionally, morphological surveys of *Macrobrachium* in some remote areas have revealed previously undescribed species such as *M. spelaeus* Cai and Vidthayanon, 2016, *M. sirindhorn* Naiyanetr, 2001, *M. suphanense* Saengphan, Panijpan, Senapin, Laosinchai, Ruenwongsa, Suksomnit & Phiwsaiya, 2018, and *M. chainatense* Saengphan, Panijpan, Senapin, Laosinchai, Ruenwongsa, Suksomnit & Phiwsaiya, 2019. Several new discoveries have enhanced the knowledge of habitat uniqueness, and endorsed the need for reevaluation of the freshwater fauna richness and endemism level. For this reason, the study of *Macrobrachium* diversity in Thailand requires intensive attention to fill the gaps in knowledge and update the regional checklist.

The Songkhram River basin, one of the minor tributaries, is connected to the middle Mekong River. This basin has complex ecosystems, such as swamp and flooded forest areas due to the seasonal cycle of freshwater levels (Mekong River Commission, 2005; Meynell, 2017). Currently, the Songkhram River supports a unique fauna that includes some aquatic animals, such as sponges (Ruengsawang et al., 2024), molluscs (Jeratthitikul et al., 2024), copepods (Sanoamuang and Dabseepai, 2021) and prawns (Chaowvieng et al., 2024; Macharoenboon et al., 2023). In addition to this richness and high endemism of the fauna, the Songkhram River also shares aquatic animals with neighboring rivers on the Khorat plateau. To date, three endemic species of *Macrobrachium* prawns have been discovered from the Khorat plateau: *M. thai* Cai, Naiyanetr & Ng, 2004, *M. puberimanus* Siriwut, 2020 and *M. rostrolevatus* Chaowvieng & Siriwut, 2024. In this study, a morphologically and genetically distinct species of *Macrobrachium* was found in the middle part of the Songkhram River. This new *Macrobrachium* species is proposed, and the species boundary is discussed based on its morphology and COI barcode sequence.

MATERIALS AND METHODS

Field sampling, specimen preservation, and identification

Macrobrachium specimens were collected from the Songkhram River in the northeastern part of Thailand (Fig. 1). Hand nets and prawn traps were set and deployed during both day and night. Collected prawn specimens were euthanized with a two-step method following the American Veterinary Medical Association (AVMA) protocol (AVMA, 2020). All procedures used during sampling were systematically conducted following the approved Protocol Number MUSC66-026-656 under the Mahidol University-Institute Animal Care and Use Committee (MU-IACUC). Representative specimens were selected and photographed to record their habitat and life colouration. After initial specimen preparation, all samples were preserved in 95% (v/v) ethyl alcohol for further morphological and molecular studies.

Taxonomic identification was performed based on the guidelines and records from previous *Macrobrachium* studies in Thailand and adjacent countries (Cai and Dai, 1999; Yeo, 1999; Cai and Ng, 2002; Cai et al., 2004; Hanamura et al., 2011). Morphologically diagnostic characters were observed under light microscopy (SZX 7 Olympus stereomicroscope). Variations in some taxonomic characters were illustrated by vector line drawings in Adobe Illustrator (under license agreement by Mahidol University). The terminology and abbreviations used in the species description have been standardized with previous taxonomic studies on *Macrobrachium* prawns (Cai et al., 2004; Wowor 2010; Siriwut et al., 2020), whilst mouthpart terminology follows that illustrated by Bauer (2023) and Abdelsalam (2018).

DNA extraction, PCR amplification and molecular phylogenetic analysis

Molecular DNA analysis was performed using COI gene fragment sequences. A partial sequence of the target gene was obtained through PCR amplification using the standard universal forward primer LCO1490 (Folmer et al., 1994), and two modified reversed primers; MacroNancy (Siriwut et al., 2020) and HCOout (Schwendinger and Giribet, 2005). Genomic DNA, used as PCR template, was extracted from abdominal tissue using G-spin™ Total DNA Extraction Mini Kit (iNtRON Biotechnology). The presence and yield of extracted DNA were checked on 1% (w/v) agarose gel electrophoresis prior to PCR amplification process. The PCR mixture was prepared as previously reported for *Macrobrachium* prawns (Siriwut et al., 2021) with 34 thermal cycles of 94 °C for 30 seconds, 44–49 °C for 40 seconds, and 72 °C for 15 seconds. These PCR

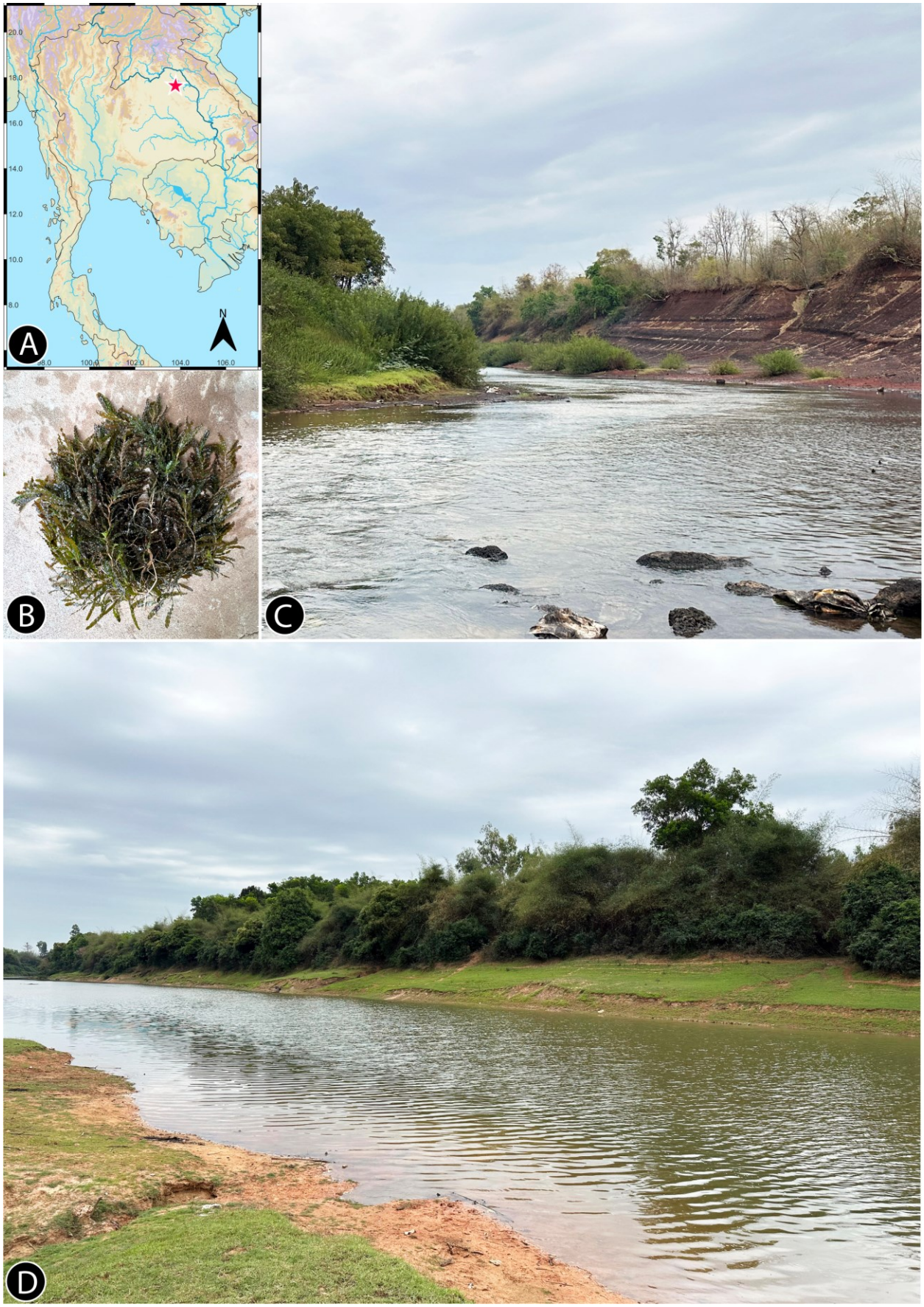

FIGURE 1. Habitat of *M. debaratae* sp. nov. **A.** Location of type locality. **B.** Aquatic plant (*Potamogeton crispus* L.) found dominantly in type locality. **C, D.** Habitat characteristics of middle Songkhram River.

conditions were first optimized using the temperature gradient function in Mastercycler® nexus (Eppendorf). Successful PCR products were later purified using a MEGAquick-spin™ Plus Total Fragment DNA Purification Kit, and then commercially sequenced using Sanger sequencing.

Sequences of the COI fragment gene were edited and annotated in MEGA 12 (Kumar et al., 2024). The organismal identity of the raw sequence was verified using the BLAST search algorithm (Altschul et al., 1990). For phylogenetic reconstruction, the sequence dataset was prepared using a recent study dataset and those *Macrobrachium* sequences in public databases (GenBank and BOLD System). Two sequences from the genera *Palaemon* and *Exopalaemon* were selected for the outgroup rooting in the phylogenetic reconstruction. The list of sampled taxa, accession numbers and sequence references used in this study are shown in Table 1. The DNA dataset was analyzed in MEGA 12 for sequence annotations and pairwise comparison of inter- and intra-specific variation. The DNA substitution model was calculated using jModeltest v.2.1.8 (Darriba et al., 2012) and the best-fit model was later configured in the phylogenetic reconstruction method.

Tree reconstruction was performed using the maximum likelihood (ML) and Bayesian inference (BI) methods. The dataset format was prepared and parameters were adjusted for the selected DNA model using Kakusan 4 (Tanabe, 2007). For ML analysis, the IQ-TREE 2 program (Minh et al., 2020) was used via the online webserver (http://iqtree.cibiv.univie.ac.at/). All parameters were set as default; however, the DNA substitution model and branch support analysis were specified manually. The General Time Reversible (GTR) model (Tavaré, 1986) with a rate of heterogeneity calculation such as invariant site (I) and gammar distribution of nucleotide substitutional rate (G), were implemented. For the BI analysis, the dataset was prepared in the Nexus format with manual parameter adjustment. The Markov Chain Monte Carlo (MCMC) approach with two random seed searches was run for 10,000,000 sampling generations in MrBayes v.3.2.7 (Ronquist et al., 2012). Twenty-five percent of tree topological yield was discarded using the burn-in rejection parameter. A node support value was accepted based on the standard criteria of >95% strong ultrafast bootstrap for ML (Minh et al., 2013) and > 95% posterior probability for BI (Yang and Rannala, 2005). The final tree topology was composed, and BI topology was used as the template for the details of phylogenetic results. The node support value was obtained after reaching the moderate threshold. The final tree topology was configured in Adobe Illustrator software.

RESULTS

Molecular phylogeny and genetic variation of *Macrobrachium* species

In this study, new partial COI sequences (675 bp) were successfully obtained from 22 samples and 6 species of *Macrobrachium* including a new species. After aligning the sequences, the trimmed sequences (266 informative sites) ranges between 440–675 bp, were used for comparison of the pairwise distance of genetic divergence and phylogenetic analyses. The pairwise distance comparison revealed the inter-specific variations among *Macrobrachium* taxa ranged from 6 to 23% (see Appendix).

The COI phylogenetic tree topology obtained from BI analysis indicated a monophyletic group of *Macrobrachium* operational taxonomic units (OTUs), while that from the ML method depicted an unsupported clade topology of *Macrobrachium* taxa (Fig. 2, Clade A). In this study, 19 monophyletic clades of *Macrobrachium* were determined. The sequence of *M. latidactylus* was basally separated from other *Macrobrachium*. Clade B was a monophyletic group of OTUs belonging to the soft freshwater species, *M. yui.* Clades C and D represented two species groups; group 1 was comprised of *M. sintangense* (De Man, 1898), *M. suphanense* and *M. saigonense* Nguyên, 2006; whereas group 2 contained *M. scabriculum* (Heller, 1862), *M. dolichodactylus* (Hilgendorf, 1879), and *M. lanatum* Cai & Ng, 2002. These two monophyletic clades were placed closer to *M. equidens* (Dana, 1852); however, resolution of this topological relationship was unsupported.

In Clade E, two *Macrobrachium* groups formed a monophyletic relationship: *M. hendersoni* (De Man, 1906) (Clade F) and the *M. niphanae* Shokita & Takeda, 1989 –*M. thai–M. chainatense* species complex (Clade G). Inside Clade G, a distinct lineage between *M. chainatense* and the *M. niphanae–M. thai* group was noticed. However, the phylogenetic relationship of *M. thai* and *M. niphanae* was only partially supported in the BI analysis. In Clade H, the topology indicated *M. lanchesteri* (De Man, 1911), *M. panhai* Chaowvieng & Siriwut, 2024 and *M. rosenbergii* (De Man, 1879) formed a monophyletic group in both ML and BI methods.

Clade I contained the majority of OTU samples in this dataset and was comprised of the *M. pilimanus* species complex, a group with high morphological variations. This monophyletic group was based on ten taxa from the studied dataset. Two major clades, such as Clade J and K, formed a strong monophyletic group

TABLE 1. Voucher ID samples and GenBank accession numbers for sequences used in phylogenetic analyses. *indicates unpublished data retrieved via GenBank database. 1 = This study; 2 = Siriwut et al., 2021; 3= Saengphan et al., 2018; 4= Saengphan et al., 2019; 5= Wowor et al., 2009.

Species	GenBank accession	Voucher ID	Molecular ID	Locality	Coordinates	References
M. debaratae sp. nov.	PV651619	MUMNH_MP00375	M482	Songkhram River, Seka, Bueng Kan, Thailand	17°52'56.1"N, 103°51'39.4"E	1
	PV651620	MUMNH_MP00376	M484	Nam Mao, Sri Songkhram, Nakhon Phanom, Thailand	17°44'57.7"N, 104°12'15.6"E	1
	PV651625	MUMNH_MP00381	M574	Pasak, Kham Ta Kla, Sakon Nakhon, Thailand	17°50'30.0"N, 103°47'43.3"E	1
	PV651626	MUMNH_MP00382	M575	Songkhram River, Seka, Bueng Kan, Thailand	17°52'40.7"N, 103°52'07.4"E	1
	PV651627	MUMNH_MP00383	M576	Songkhram River, Seka, Bueng Kan, Thailand	17°52'40.7"N, 103°52'07.4"E	1
	PV651624	MUMNH_MP00380	M573	Pasak, Kham Ta Kla, Sakon Nakhon, Thailand	17°50'30.0"N, 103°47'43.3"E	1
	PV651618	MUMNH_MP00374	M479	Nam Mao, Sri Songkhram, Nakhon Phanom, Thailand	17°44'57.7"N, 104°12'15.6"E	1
M. naiyanetri	PV651630	MUMNH_MP00386	M610	Wat, Hat Yai, Songkhla, Thailand	6°59'36.4"N, 100°21'07.0"E	1
	PV651631	MUMNH_MP00387	M612	Tha Nae, Si Banphot, Phattalung, Thailand	7°42'25.7"N, 99°50'28.2"E	1
	PRSEA117-20	CUMZ_MP00134	M134	Rattaphum, Songkhla, Thailand	7°05'15.8"N, 100°10'54.7"E	2
	PRSEA013-20	CUMZ_MP00030	M014	Mueang, Phetchabun, Thailand	16°24'26.0"N, 101°08'34.1"E	2
	PRSEA161-20	CUMZ_MP00178	MKM016	Banteay Srei, Siem Reap, Cambodia	13°35'43.1"N, 103°57'42.6"E	2
	PRSEA160-20	CUMZ_MP00177	MKM015	Banteay Srei, Siem Reap, Cambodia	13°35'43.1"N, 103°57'42.6"E	2
	PRSEA136-20	CUMZ_MP00153	M155	Chawang, Nakhon Si Thammarat, Thailand	8°23'44.2"N, 99°30'24.9"E	2
M. spelaeus	PRSEA143-20	CUMZ_MP00160	M159	Noen Maprang, Phitsanulok, Thailand	16°40'51.2"N, 100°41'27.4"E	2
	PRSEA142-20	CUMZ_MP00159	M158	Noen Maprang, Phitsanulok, Thailand	16°40'51.2"N, 100°41'27.4"E	2
	PRSEA028-20	CUMZ_MP00045	M029	Pong, Phayao, Thailand	19°07'11.1"N, 100°16'49.8"E	2
M. palmopilosum	PRSEA029-20	CUMZ_MP00046	M030	Song, Phrae, Thailand	18°27'22.9"N, 100°09'42.2"E	2
	PRSEA027-20	CUMZ_MP00044	M028	Rong Kwang, Phrae, Thailand	18°20'23.0"N, 100°19'38.3"E	2
	PRSEA021-20	CUMZ_MP00044	M022	Pong, Phayao, Thailand	19°07'11.1"N, 100°16'49.8"E	2
	PRSEA020-20	CUMZ_MP00037	M021	Pong, Phayao, Thailand	19°07'11.1"N, 100°16'49.8"E	2
	PRSEA030-20	CUMZ_MP00047	M031	Chiang Klang, Nan, Thailand	19°17'32.2"N, 100°51'16.4"E	2
	PRSEA012-20	CUMZ_MP00029	M013	Song Khwae, Nan, Thailand	19°19'04.1"N, 100°42'59.9"E	2
	PRSEA010-20	CUMZ_MP00027	M011	Bo Kluea, Nan, Thailand	19°08'12.6"N, 101°09'03.1"E	2
M. puberimanus	PRSEA137-20	CUMZ_MP00154	M049	Na Yung, Udon Thani, Thailand	17°55'16.6"N, 102°13'11.9"E	2
	PRSEA106-20	CUMZ_MP00123	M121	Phu Ruea, Loei, Thailand	17°24'21.5"N, 101°25'49.6"E	2
	PRSEA087-20	CUMZ_MP00104	M099	Chiang Khan, Loei, Thailand	17°54'11.5"N, 101°40'46.2"E	2
	PRSEA138-20	CUMZ_MP00155	M067	Pak Chom, Loei, Thailand	18°03'39.4"N, 101°47'51.8"E	2
M. dienbienphuense	PRSEA141-20	CUMZ_MP00158	M157	Noen Maprang, Phitsanulok, Thailand	16°41'46.8"N, 100°39'24.5"E	2
M. eriocheirum	PRSEA086-20	CUMZ_MP00103	M098	Xishuangbanna, China	16° 49' 20.63"N, 100°25'56.53"E	2
	PRSEA085-20	CUMZ_MP00102	M097	Xishuangbanna, China	16° 39' 2.88"N, 101°46'22.83"E	2
	PV651629	MUMNH_MP00385	M609	Wat, Hat Yai, Songkhla, Thailand	6°59'36.4"N, 100°21'07.0"E	1
	PV651628	MUMNH_MP00384	M603	Sok, Surat Thani, Thailand	8°54'05.2"N, 98°37'26.4"E	1

TABLE 1. continued.

Species	GenBank accession	Voucher ID	Molecular ID	Locality	Coordinates	References
M. hirsutimanus	PRSEA077-20	CUMZ_MP00094	M083	Noen Maprang, Phitsanulok, Thailand	16˚40’51.2"N, 100˚41’27.4"E	2
	PRSEA031-20	CUMZ_MP00048	M032	Wang Thong, Phitsanulok, Thailand	16°51'13.6"N, 100°36'43.2"E	2
	PRSEA014-20	CUMZ_MP00031	M015	Wang Thong, Phitsanulok, Thailand	16°51'13.6"N, 100°36'43.2"E	2
	PRSEA122-20	CUMZ_MP00139	M139	Wang Thong, Phitsanulok, Thailand	16°51'13.6"N, 100°36'43.2"E	2
M. sirindhorn	PRSEA110-20	CUMZ_MP00127	M126	Chiang Kham, Phayao, Thailand	19°30'04.7"N, 100°16'32.9"E	2
	PRSEA008-20	CUMZ_MP00025	M009	Chiang Kham, Phayao, Thailand	19°30'04.7"N, 100°16'32.9"E	2
	PRSEA007-20	CUMZ_MP00024	M008	Chiang Kham, Phayao, Thailand	19°30'04.7"N, 100°16'32.9"E	2
	PRSEA009-20	CUMZ_MP00026	M010	Chiang Kham, Phayao, Thailand	19°30'04.7"N, 100°16'32.9"E	2
M. lanchesteri	PRSEA123-20	CUMZ_MP00140	M140	Kabin Buri, Prachin Buri, Thailand	13°56'14.8"N, 101°55'19.1"E	
	PRSEA157-20	CUMZ_MP00174	MKM012	Stoung, Kampong Thom, Cambodia	12°56'41.5"N, 104°34'57.9"E	2
	PRSEA156-20	CUMZ_MP00173	MKM011	Puok, Siem Reap, Cambodia	13°27'16.7"N, 103°44'24.0"E	2
	PRSEA066-20	CUMZ_MP00083	M072	Mueang, Nakhon Sawan, Thailand	15°37'16.9"N, 100°05'37.5"E	2
	PRSEA016-20	CUMZ_MP00033	M017	Chiang Klang, Nan, Thailand	19°17'13.8"N, 100°51'24.6"E	2
	PRSEA002-20	CUMZ_MP00019	M002	Wiang Chai, Chiang Rai, Thailand	19°52'10.7"N, 99°56'42.8"E	2
	PRSEA001-20	CUMZ_MP00018	M001	Wang Thong, Phitsanulok, Thailand	16°49'20.3"N, 100°25'51.9"E	2
M. panhai	PRSEA129-20	CUMZ_MP00146	M147	Klaeng, Rayong, Thailand	12°47'05.7"N, 101°40'59.6"E	2
	PRSEA006-20	CUMZ_MP00023	M007	San Sai, Chiang Mai, Thailand	18°53'59.1"N, 99°00'41.1"E	2
M. rosenbergii	PRSEA101-20	CUMZ_MP00118	M115	Mueang, Ranong, Thailand	9°53'13.5"N, 98°38'01.2"E	2
	PRSEA100-20	CUMZ_MP00117	M114	Khlung, Chanthaburi, Thailand	12°28'00.0"N, 102°12'11.6"E	2
M. niphanae	PRSEA146-20	CUMZ_MP00163	M162	Mueang, Chai Nat, Thailand	15°13'20.6"N, 100°06'07.0"E	2
	PRSEA022-20	CUMZ_MP00039	M023	Lom Sak, Phetchabun, Thailand	16°43'46.9"N, 101°14'17.0"E	2
	MF622023	GBCMD28535-19		Suphan Buri, Thailand	-	3
	PRSEA038-20	CUMZ_MP00055	M039	Tha Yang, Phetchaburi, Thailand	12°56'55.8"N, 99°51'16.5"E	2
	PRSEA040-20	CUMZ_MP00057	M041	Thung Song, Nakhon Si Thammarat, Thailand	8°13'59.5"N, 99°40'32.1"E	2
	PRSEA069-20	CUMZ_MP00086	M075	Nam Pat, Uttaradit, Thailand	17°43'46.8"N, 100°41'24.3"E	2
	PRSEA017-20	CUMZ_MP00034	M018	Fak Tha, Uttaradit, Thailand	17°59'48.8"N, 100°52'44.0"E	2
	PRSEA023-20	CUMZ_MP00040	M024	Fak Tha, Uttaradit, Thailand	17°59'48.8"N, 100°52'44.0"E	2
	PRSEA019-20	CUMZ_MP00036	M020	Fak Tha, Uttaradit, Thailand	17°59'48.8"N, 100°52'44.0"E	2
	PV651617	MUMNH_MP00373	M570	Kam, Mueang, Sakon Nakhon, Thailand	17°08'51.1"N, 104°17'22.4"E	1
	PV651623	MUMNH_MP00379	M572	Kam, Mueang, Sakon Nakhon, Thailand	17°08'51.1"N, 104°17'22.4"E	1
	PV651612	MUMNH_MP00368	M565	Tributary of Mekong River, Kaoh Snaeng, Stung Treng, Cambodia	13°43'53.0"N, 105°58'54.9"E	1
	PV651615	MUMNH_MP00371	M568	Mekong River, Stung Treng, Cambodia	13°34'52.6"N, 106°00'10.4"E	1
	PV651621	MUMNH_MP00377	M493	Yam, Akat Amnuai, Sakon Nakhon, Thailand	17°35'40.9"N, 103°58'10.7"E	1
	MH053368	GBCM16418-19		Beung Kan, Thailand	-	3
	PRSEA039-20	CUMZ_MP00056	M040	Bueng Khong Long, Bueng Kan, Thailand	17°58'11.8"N, 104°02'24.3"E	2

TABLE 1. continued.

Species	GenBank accession	Voucher ID	Molecular ID	Locality	Coordinates	References
M. thai	PRSEA061-20	CUMZ_MP00078	M065	Phon Phisai, Nong Khai, Thailand	17°59'41.4"N, 103°03'48.8"E	2
	PRSEA060-20	CUMZ_MP00077	M063	Wang Sam Mo, Udon Thani, Thailand	16°56'49.7"N, 103°28'11.8"E	2
	PV651622	MUMNH_MP00378	M571	Songkhram River, Seka, Bueng Kan, Thailand	17°52'56.1"N, 103°51'39.4"E	1
	PRSEA059-20	CUMZ_MP00076	M062	Mueang, Chaiyaphum, Thailand	15°57'19.4"N, 102°02'01.1"E	2
M. chainatense	PRSEA144-20	CUMZ_MP00161	M160	Mueang, Chai Nat, Thailand	15° 13' 19.81"N, 100° 6' 6.11"E	2
	MT080622-1	THNHM-Iv-18802		Mueang, Chai Nat, Thailand	15°13′20.8″N, 100°6′5.7″ E	4
	MT080621-1	THNHM-Iv-18801		Mueang, Chai Nat, Thailand	15°13′20.8″N, 100°6′5.7″ E	4
	PRSEA059-20	CUMZ_MP00076	M062	Mueang, Chaiyaphum, Thailand	15°57'19.4"N, 102°02'01.1"E	2
	MT080620-1	THNHM-Iv-18800		Mueang, Chai Nat, Thailand	15°13′20.8″ N, 100°6′5.7″ E	4
M. hendersoni	PRSEA130-20	CUMZ_MP00147	M141	Dan Makham Tia, Kanchanaburi, Thailand	13°50'42.9"N, 99°23'59.3"E	2
	PRSEA118-20	CUMZ_MP00135	M135	Si Sawat, Kanchanaburi, Thailand	14°23'04.3"N, 99°08'20.0"E	2
	PRSEA119-20	CUMZ_MP00136	M136	Si Sawat, Kanchanaburi, Thailand	14°23'04.3"N, 99°08'20.0"E	2
M. sintangense	PV651613	MUMNH_MP00369	M566	Mekong River, Stung Treng, Cambodia	13°34'52.6"N, 106°00'10.4"E	1
	PRSEA155-20	CUMZ_MP00172	MKM010	Tonle Sap River, Kandal, Cambodia	11°49'01.8"N, 104°48'35.3"E	2
	PV651632	MUMNH_MP00388	M613	Wat, Hat Yai, Songkhla, Thailand	6°59'36.4"N, 100°21'7.0"E	1
	PRSEA067-20	CUMZ_MP00084	M073	Kui Buri, Prachuap Khiri Khan, Thailand	12°05'29.0"N, 99°48'18.2"E	2
	PRSEA018-20	CUMZ_MP00035	M019	Mueang, Phetchabun, Thailand	16°23'41.8"N, 101°10'15.5"E	2
	PV651614	MUMNH_MP00370	M567	Mekong River, Stung Treng, Cambodia	13°34'52.6"N, 106°00'10.4"E	1
	PV651616	MUMNH_MP00372	M569	Songkhram River, Seka, Bueng Kan, Thailand	17°52'40.7"N, 103°52'07.4"E	1
M. saigonense	FM958080	GBCMD2451-09		Tonle Sap, Cambodia	-	5
*M. scabriculum**	MH468762-1	FBRC/ZSI/INV/1456		India	-	Laskar et al.
*M. scabriculum**	KX866567	CIFEFGB-Ms-4D2		India	-	Ajina et al.
*M. dolichodactylus**	OK184546-1	NMK00002MACRO2		n/a	-	Kochey et al.
M. lanatum	FM958081-1	MACR040		Bengkulu, Sumatra	-	5
	GBCMD2450-09	FM958081		Bengkulu, Sumatra	-	5
M. equidens	GBCMD2468-09	FM958063		Khatib Bongsu, Singapore	-	5
M. yui	PRSEA102-20	CUMZ_MP00119	M116	Mueang, Mae Hong Son, Thailand	19°25'09.9"N, 97°59'53.2"E	2
	PRSEA068-20	CUMZ_MP00085	M074	Mueang, Mae Hong Son, Thailand	19°25'09.9"N, 97°59'53.2"E	2
	PRSEA103-20	CUMZ_MP00120	M117	Mueang, Mae Hong Son, Thailand	19°25'09.9"N, 97°59'53.2"E	2
M. latidactylus	PRSEA088-20	CUMZ_MP00105	M101	Mueang, Krabi, Thailand	8°04'48.9"N, 98°55'08.5"E	2
*Palaemon debilis**	MT666026-1	PH_ref-16			-	Renshaw et al.
Exopalaemon styliferus	FM958057-1			Kp. Juara, Tioman I., Malaysia		5

in both the ML and BI analyses. In Clade J, two endemic species in Thailand were nested together: *M. sirindhorn* and the new proposed species in this study, *M. debaratae* sp. nov. The OTUs of each species were clustered independently and formed a monophyletic group with full support in both the ML and BI methods (Clades M and L). The remaining taxa within the *M. pilimanus* (De Man, 1879) species complex sensu Johnson (1963) were grouped in Clade K, where two distinct lineages were also found. Clade N contained four *Macrobrachium* species: *M. hirsutimanus* (Tiwari, 1952), *M. eriocheirum* Dai, 1984, *M. dienbienphuense* Đăng & Nguyên, 1972, and *M. puberimanus* Siriwut, 2020. In Clade O, *M. palmopilosum* Siriwut, 2020, *M. spelaeus*, and *M. naiyanetri* Siriwut, 2020 were clustered with strong support values for each taxon

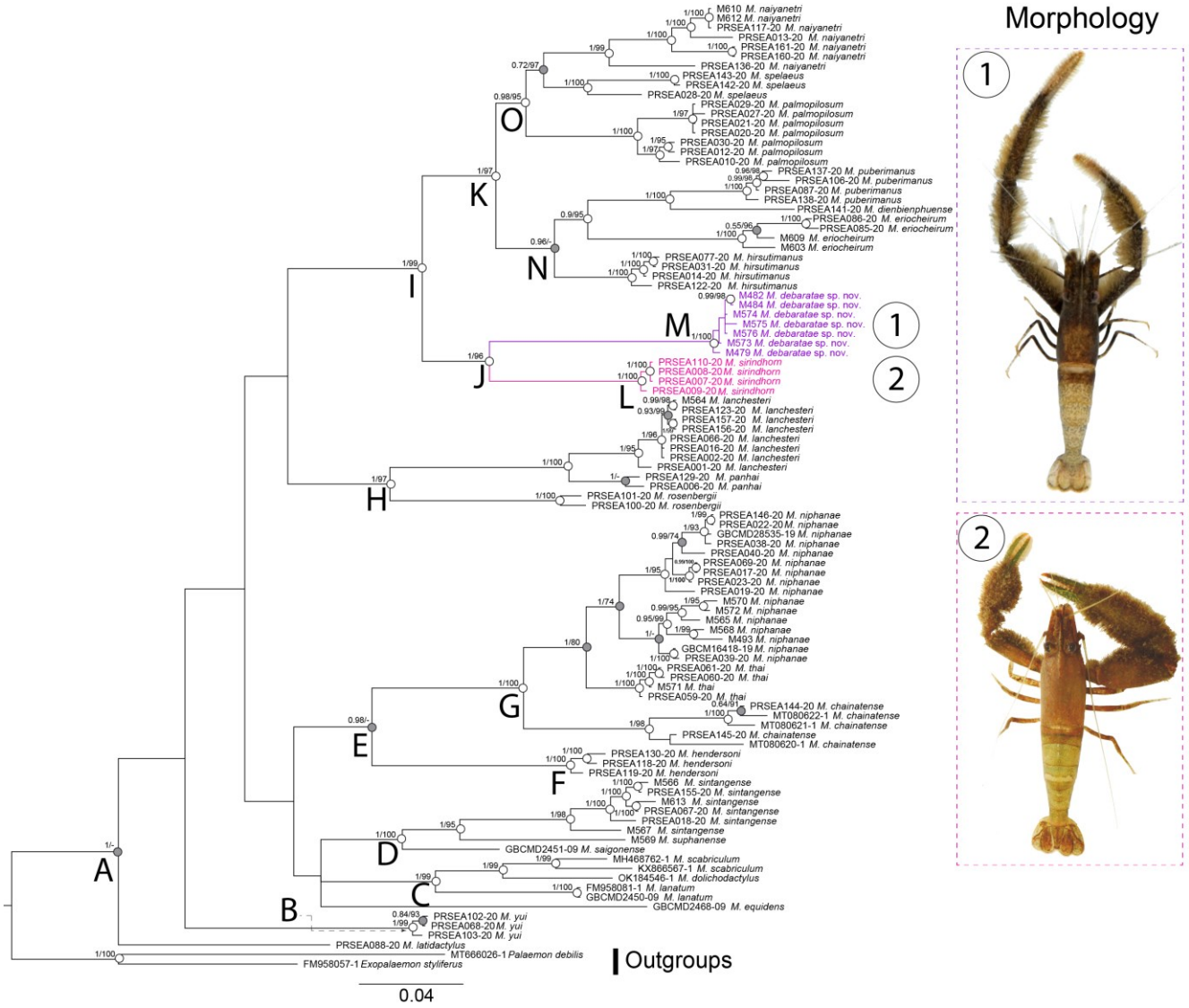

FIGURE 2. Phylogenetic tree, based on BI analysis of COI partial gene sequences (675 bp), indicating the phylogenetic position of *Macrobrachium debaratae* sp. nov. and its congeneric species. Morphological characteristics of new species and sister species, *M. sirindhorn* are provided. Clade designation is indicated by alphabets. Numeric value on tree node indicates the bootstrap and posterior probability support values of ML and BI methods, respectively; a white circle indicates fully supported ML and BI in both analyses, while a grey circle indicates supported in either the ML or the BI analysis only.

lineages. However, the cluster relationship between *M. spelaeus* and *M. naiyanetri* was only resolved in the ML analysis and not in the BI analysis.

Among the *Macrobrachium* species, the comparison of the COI sequences frequently exceeded 10% of the interspecific variation, except for three pairwise comparsons: *M. dienbienphuense* vs. *M. puberimanus* (8%), *M. lanchesteri* vs. *M. panhai* (6%), and *M. scabriculum* vs. *M. dolichodactylus* (9%). In the intraspecific comparisons, the pairwise distance of *Macrobrachium* species ranged from 0 to 5.7% (see Appendix), with the highest and lowest intraspecific variation being found in the *M. sintangense* group and *M. lanatum* respectively. The proportional range comparison of intraspecific variation among species within the three *Macrobrachium* species groups that had broad samples (Clades G, H, and I) indicated different max-min ratios of genetic variation. *Macrobrachium lanchesteri* and *M. rosenbergii* (Clade H) displayed a low intraspecific variation (ranged from 0.3 to 1.9% pairwise distance), whereas the *M. niphanae* and *M. pilimanus* species groups (Clades G and I, respectively) ranged from 0.4 to 4.8% pairwise distance.

According to the high degree of observed morphological and genetic variations, the *M. pilimanus* species group appears to display a vast species richness in Southeast Asia. Several species exhibited a high degree of morphological variation in characters otherwise

viewed as diagnostic. However, the molecular taxonomy, including the COI barcode threshold has been used interactively for species delimitation. In this study, a distinct lineage within the *M. pilimanus* species group was detected and showed a close relationship to one nominal species, namely *M. sirindhorn* (13% of genetic difference). Consequently, *Macrobrachium debaratae* sp. nov. from Thailand is proposed herein as a new species based on the combination of morphological and genetic analyses. The taxonomic description and discussion of further morphological variation related to sister taxa are detailed in the next section.

Taxonomy

Family Palaemonidae Rafinesque, 1815

Genus *Macrobrachium* Spence Bate, 1868

***Macrobrachium debaratae* Siriwut, sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act: D63C2DAC-C779-4348-9764-B86286407A66

(Figs 3–5)

Type materials.– Holotype. • MUMNH_MP00382 one ♂ specimen (CL 14 mm, BL 47 mm), from Ban Dong Tok Paen Temple, Songkhram River, Seka, Buengkan (M575; Fig. 5A)

Paratypes. • MUMNH_MP00375 one ♂ specimen (CL 12.92 mm), Songkhram River, Kham Ta Kla, Sakon Nakhon (M482). • MUMNH_MP00383 one ♂ specimen (CL 11.49 mm), Ban Dong Tok Paen Temple, Songkhram River, Seka, Buengkan (M576). • MUMNH_MP00380 one ♂ specimen (CL 11.88 mm), Pasak viewpoint, Kham Ta Kla, Sakon Nakhon (M573). • MUMNH_MP00381 one ovigerous ♀ specimen (CL), Pasak viewpoint, Kham Ta Kla, Sakon Nakhon (M574). • MUMNH_ MP00374 and MP00376 one ♀ specimen and one ♂ specimens (CL 9.53 and 10.97, respectively), small dam with spill way, Nam Mao, Sam Phong, Si Songkhram District, Nakhon Phanom (M484, M479). • MUMNH_MP00389 two ♂♂ specimens (CL 10.73 mm), Ban Dong Tok Paen Temple, Songkhram River, Seka, Buengkan; one specimen (CL 11.30 mm) was mouth dissected and used for drawing.

Additional materials.– • MUMNH_MP00390 17♂♂ and one ♀ specimens (CL 10.48–14.51 mm), Ban Dong Tok Paen Temple, Songkhram River, Seka, Buengkan. • MUMNH_MP00391 two ♂♂ and one ♀ specimens (CL 6.86–10.94), Songkhram River, Kham Ta Kla, Sakon Nakhon. • MUMNH_MP00392 two ovigerous ♀♀ specimens (CL 9.09 mm), Pasak viewpoint, Kham Ta Kla, Sakon Nakhon. • MUMNH_MP00393 two specimens, Nong Thum, Seka, Buengkan. • MUMNH_MP00394 one ovigerous ♀ specimen (CL 9.62 mm), small dam with spill way, Na Vang, Na Sawan, Mueang Bueng Kan, Bueng Kan. • MUMNH_MP00395 one ♀ specimen (CL 9.62 mm), Hui Pak Klong, Nong Hua Chang, Phon Charoen, Bueng Kan.

Diagnosis.– Rostrum moderately long, anteriorly striate, and upward distally. Rostrum reaching beyond or as long as end of third segment of antennular peduncle. Rostral formula: 14/2–3 teeth. Carapace without spinulation on anterior margin. Epistome trilobed. Second pereiopod strong and robust, similar in shape, different in size. Second pereiopods with long-tufted setae. Fingers of chela of major second pereiopods with 10–15 teeth. Carpus elongated, shorter than palm and merus. Infero-ventral part of merus and ischium of major second pereiopod with spinules. Minor second pereiopod without spinule. T4 unarmed, with moderate posterior submedian plate. T4–T7 with basolateral median plate without median notch. T8 with posteromedial lobes in male, but median process absent. Preanal carina present. Telson moderately long, anterior part with a clump of setae. Telson surface with two pairs of dorsal spines. Posterior projection of telson present. Uropodal diaeresis spine shorter than outer angle.

Composited description (holotype in parenthesis).–

***Rostrum*.** Rostral length 6–8 (8) mm, anteriorly striate with strong lateral carina, reaching beyond third segment of antennular peduncle (Fig. 5C) but shorter than scaphocerite lamina (Fig. 5F). Dorsal part of rostrum with 13–15 (13) teeth, 4–6 (4) teeth on postorbital area. Postorbital teeth extending approximately one-third of carapace length. Ventral part of rostrum with 2–3 (3) teeth on distal half. Fine setae present in ventral margin of rostrum and postorbital region.

***Cephalon*.** Eye well developed. Postantennular carapace margin rounded. Cornea as long as stalk. The basal segment of antennular peduncle longer than wide, lateral carina slightly concave, dorsal carina sinuous. Sharp antennal and hepatic spines present; hepatic spine smaller than antennal spine (roughly equal to antennal spine in holotype). Branchiostegal suture running from hepatic spine to anterior margin of carapace. Ventro-lateral part and branchiostegal regions of carapace without spinulation. Branchiostegal region with short, scattered setae. Epistome trilobed. Scaphocerite with lateral margin and slightly concave with deep depression. Distolateral tooth shorter than lamellar margin.

FIGURE 3. Morphological characteristics and chromatophore pattern variation in *M. debaratae* sp. nov. **A, B, D, E.** Colouration and morphology of male specimens. **C.** Colouration and morphology of female specimen. Scale bar indicates 5 mm.

***Mouth appendages*.** Mandible (Fig. 4F) robust, well developed. Teeth on molar process present, separating into four distinct groups. Incisor process strongly developed, with sharp and prominent triangular teeth. Lateral margin of inner basement of incisor process with line of short brush setae. Palp not reaching beyond molar process, as long as incisor process, with long fine, and transverse setae on distal and lateral parts.

Maxillule (Fig. 4E) well developed, separating into three parts but basal parts connecting. Coxal endite slightly crescent, with spine-like setae on distal part. Lateral margin with row of fine setae. Basal endite robust, stout, with long fine setae on lateral part. Dense spine-like setae present on distal part of basal endite. Maxillule palp slapped on distal margin, but straight basally. Palp divided into inner and outer process, short spine-like setae on inner process. Single, long, fine setae present on outer process.

Maxilla (Fig. 4D) transparently thin and flattened. Scaphognathite reaching beyond distal part of endopod palp, with long fine setae on lateral margin. Anterior part of scaphognathite projected narrower than posterior. Two lobes of basal endite present prominently, longer than wide. Spine-like setae on distal margin, fine setae sparsely on lateral margin present in both lobes.

First maxilliped (Fig. 4C) without setae on surface. Epipod, endopod and exopod well developed. Epipod presents two lobes, upper longer than lower lobe. Caridean lobe laterally margin expanding, with dense fine setae on distal part. Exopod long and slender, dense long setae present distally covering one- third of exopod length. Endopod shorter than exopod, located behind exopod. Basal and coxal endites pronounced. Basal endite enlarged and longer than wide, with long brush setae on inner margin. Coxal endite narrow and projected posteriorly, with brush setae on inner margin.

Second maxilliped (Fig. 4B) present regular form. Epipod and podobranch well developed. Endopod robust, covered 50–60% length of exopod. Inner surface of coxa region with sparse setae. Exopod slender, with dense setae on distal margin. Endopod strongly pronounced, basal endite and ischium slightly longer than wide. Carpus shorter than merus. Dactylus smaller than propodus, covering 60–70% of propodus width. Brush setae present on distal margin of dactylus and upper margin of corner between propodus and dactylus.

Third maxilliped (Fig. 4A) reach beyond antennal peduncle and cover 55–65% of scaphocerite length. Endopod of third maxilliped robust, propodus shorter than carpus, both covered by dense setae. Ischiomerus robust, curved with slightly expanded margin. Series of small setae present transversely on marginal of ischiomerus. Exopod of third maxilliped slender, with dense long setae starting from apical to basal regions. Basal and coxa region of third maxilliped with scattered short setae.

First pereiopods (Fig. 5D, E). Long and slender, reaching beyond end of scaphocerite. Fingers shorter than palm. Carpus longer than palm and merus. Long, fine setae present densely on distal part of finger and in lower margin of ischium. Proximal part between palm and carpus with cluster of setae (few setae present in holotype).

***Second pereiopods*.** Robust, 1.2–2 (1.2) times longer than body length, similar in form but unequal in size and length. Merus of major second pereiopods reaching beyond end of scaphocerite.

Major second pereiopod (Fig. 5H, J). Ventro-lateral of mesial surface of merus, ischium, and coxa with spinulation. Finger subcylindrical, 0.8 times shorter or as long as palm. Closed fingers with narrow gaps, cross distally. Dactylus and pollex with 10–13 (11) and 10–15 (10) teeth, respectively; basal teeth more prominently than distal teeth. Fingers with long, fine setae, without oblique carina. Teeth distributed 80–90% of finger length. Razor teeth present on distal part of dactylus about 10–15% of length. Long setae present entirely on surface of fingers, palm, carpus, merus, ischium and coxa. Palm cylindrical, without lateral expansion and spinulation on surface. Carpus elongated, without spinules, 0.8 times shorter than merus. Merus as long as palm. Ischium subconical, 0.4 times shorter than merus.

Minor second pereiopod (Fig. 5I). Short, robust, and smaller than major cheliped. Spinulation present in merus and ischium. Long seta cover surface of palm, carpus, merus, ischium and coxa. Dactylus with 5–11 (7) teeth, pollex with 5–12 (9) teeth. Teeth distributed 50–70% of finger length, concealed by long fined seta. Razor teeth present on distal part of dactylus about 20-30% of length. Carpus subcylindrical elongated, slightly 0.7 times shorter than or as long as merus, 0.8 times shorter than palm. Merus cylindrical, roughly 0.8 times shorter or as long as palm. Ischium subcylindrical, 0.6 times shorter than merus.

Third pereiopods (Fig. 5G). Long and slender, propodus extends to end of scaphocerite. Surface of leg segments without spinule. Fined seta present on all segments, dense in ventral region. Dactylus slightly long, curved, with dorsolateral setae; ventral carina well developed. Propodus 2–2.2 times longer than dactylus, with 4–7 (7) ventral spines. Carpus 0.5 times shorter than propodus, with dorsal-projection on distal part. Merus 2.3 times longer than carpus and propodus. Ischium 0.4 times shorter than merus.

Fourth* and *fifth pereiopods (Fig. 5K, L). Dactylus reaches distal margin of scaphocerite. Spinules absent

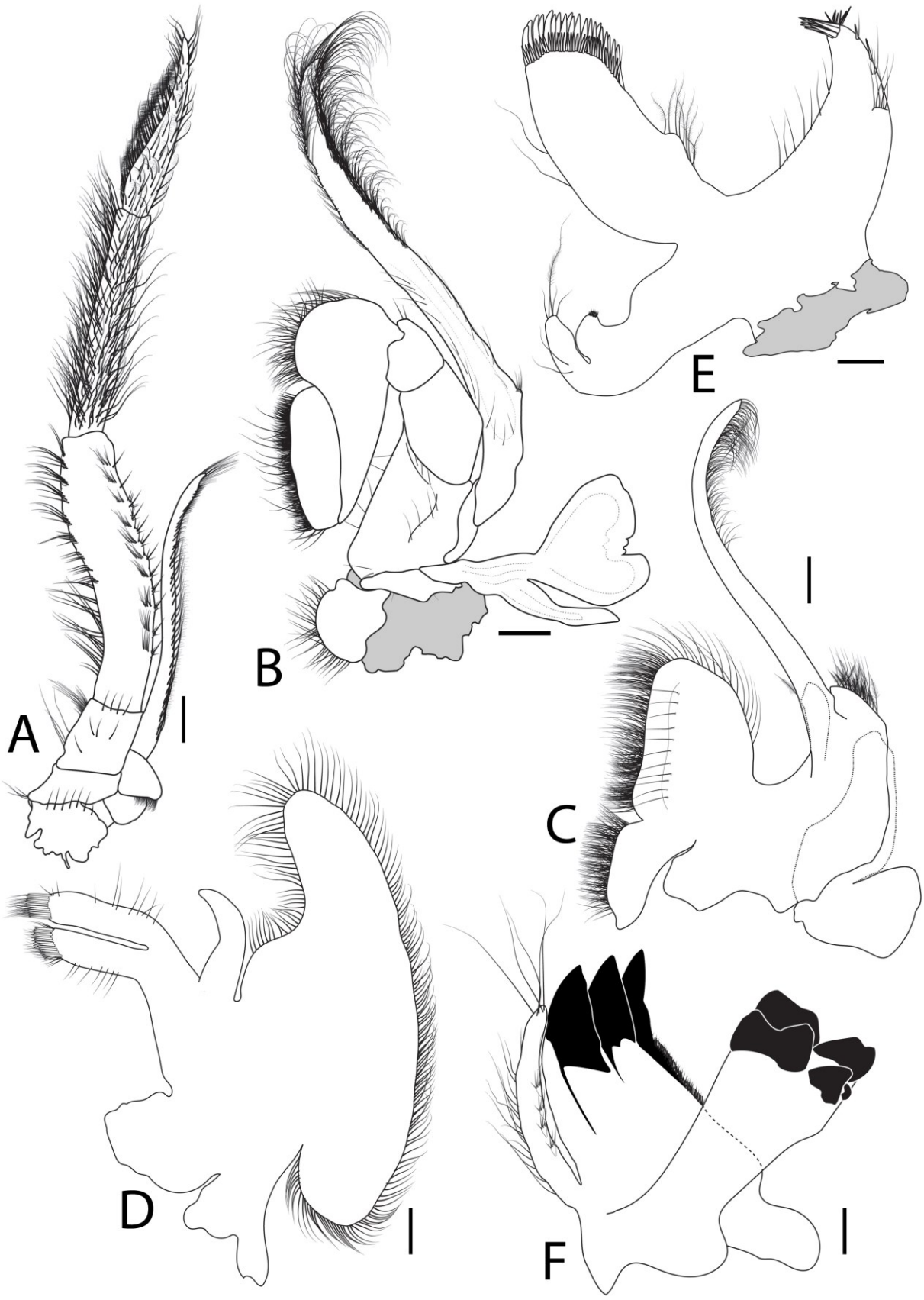

FIGURE 4. Mouth appendages (left) of *M. debaratae* sp. nov. (paratype, male MUMNH_MP00389). **A.** Third maxillipede. **B.** Second maxillipede. **C.** First maxilipede. **D.** Maxilla. **E.** Maxillule. **F.** Mandible. Scale bars on A and F indicate 0.5 mm and on B–E indicate 0.1 mm

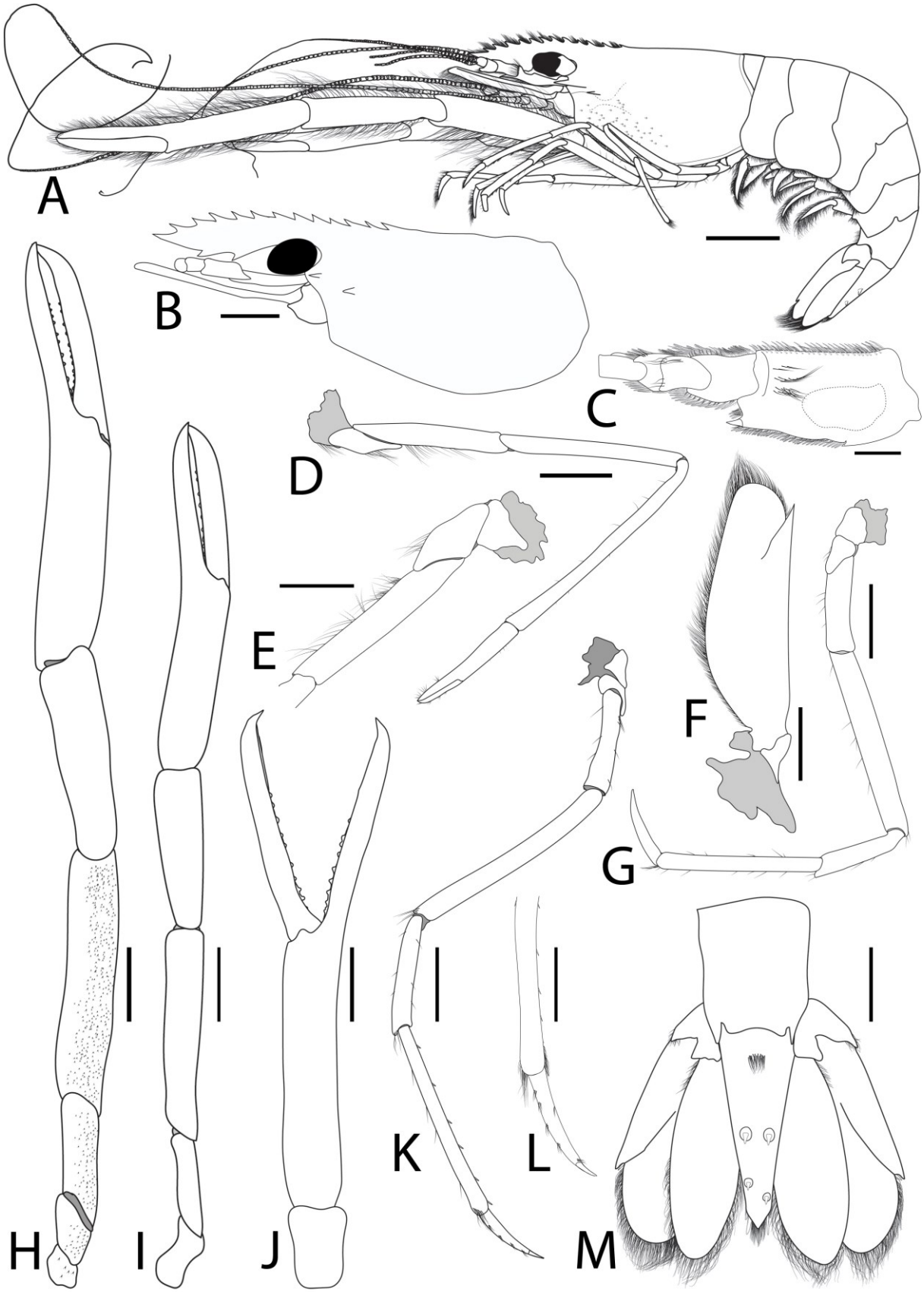

FIGURE 5. Morphology of *Macrobrachium debaratae* sp. nov. (**A** holotype, **B–M** paratypes). **A.** Whole body of holotype. **B.** Rostrum and carapace. **C.** Left antenule appendage. **D.** First pereiopod. **E.** Basal coxa and merus of first pereiopod. **F.** Scaphocerite. **G.** Third pereiopod. **H.** Major second pereiopod with spinulation on ventral surface of coxa, ischium and merus (setae excluded). **I.** Minor second pereiopod. **J.** Opened finger of major second pereiopod. **K.** Fifth pereiopod. **L.** Dactylus and propodus of fifth pereiopod. **M.** Telson. Scale bar on A indicates 10 mm, on B, F, G and H–M indicates 5 mm, and C, D, E indicates 3 mm.

in all segments. Scattered fine setae present in all segments. Propodus with 5–8 ventral spines. Propodus of fifth pereiopods with group setae on distolateral part. Carpus 0.6–0.7 times shorter than propodus and merus, with dorsal-projection on distal part and lateral margin slightly expanded. Merus of fifth pereiopods slightly longer (1.1 times) than or as long as propodus. Ischium 0.5 times shorter than merus.

Thoracic sternum. T4–T7 with transverse plate without median process. T8 with posteromedial lobes in male.

***Abdomen*.** Smooth, with setae on ventro-lateral part of pleural margin of abdominal segments. All abdominal sternite with transverse ridges. First, second, and third abdominal sternites with prominent triangular median process (small median process on third-fourth sternites in some specimens). The fifth sternite obtuse, with median keel. Sharp preanal carina, with small setae in male.

Telson (Fig. 5M). Moderately long, lateral margins straight. Posterior margin bearing two pairs of dorsal spines. Distal projection present. Two posterior spines present each side on distal margin. Inner pair of posterior spines longer than outer spines. Dorsal surface of telson with short transparent spine sparsely. Clump of long fine setae presents on antero-median surface. Short setae present starting after clump of long fine setae to distal projection.

***Uropods*.** Uropodal diaeresis with moveable inner spine, as long as or slightly longer than outer angle (shorter one side in paratype specimen, M479). Exopod about 2.3 times as long as broad, not reaching beyond the end of endopods. Lateral margin of exopod with fine setae (absent in holotype).

Etymology.– The specific name "*debaratae*" derives from "Debaratana", which means the insignia gem of goddess. The name is given in honor of Her Royal Highness Princess Maha Chakri Sirindhorn as a token of recognition. Her Royal Highness has been devoted to supporting and kindly participating in several pioneer projects studying Thai biodiversity and conservation led by government and private sectors.

Size.– A medium-sized *Macrobrachium* species. Adult male with larger body sizes than female; the largest male and female being CL 14.51 and 10.29 mm, respectively and egg size approximately about 1.02 mm in diameter.

Live colouration.– fresh habitus specimen with carapace, abodominal region and appendages having a black to brownish pigmented pattern. Leg with dark colour band on articulation margin. Telson and uropods translucent, with light blue and orange colouration on lateral margin.

Ecology.– This species has a narrow distribution in the main river and some tributaries of the Songkhram River, Northeastern part of Thailand. It was found predominantly living in sheltered fluvial environments, such as under a rock crevice or submerged rotten wood along riverbank. Some ovigerous individuals may live in fast-flowing and highly oxygenated water together with other *Macrobrachium* spp., especially taxa with a lotic preference, such as *M. dienbienphuense* and *M. puberimanus*. Currently, the population of this new species is found mainly in the type locality. The preferred habitat is associated with "Naen" or curly-leaf pondweed (*Potamogeton crispus* L.). This aquatic plant species is usually found submerged and growing predominantly in pond territory and the sinuous area of rivers.

Remarks.– This new species morphologically resembles *M. niphanae* and *M. thai* including in the form of rostrum and elongated second pereiopods. Currently, *M. niphanae* and *M. thai* are commonly distributed in the central and northeastern parts of Thailand. Morphological distinction of *M. debaratae* sp. nov. from the two latter species, based on previous data (Shokita and Takeda 1989; Cai et al., 2004; Hanamura et al., 2011), are as follows: 1) rostral teeth formula, *M. debaratae* sp. nov. differ from *M. niphanae* and *M. thai* by having 13–15/2–3 teeth (vs. 8–10/2–3 and 7–12/2–3 teeth in *M. niphanae* and *M. thai*, respectively), 2) teeth on cutting edge of fingers of major second pereiopods present 10–15 (vs. 18–20 teeth found in *M. thai* and 10–20 teeth in *M. thai*); 3) second pereiopods are unequally in length (vs. being equal on both sides of second pereiopods in *M. niphanae* and *M. thai*).

Furthermore, *M. debaratae* sp. nov. is also morphological close to *M. lanatum*, *M. dolichodactylus* and *M. scabriculum* that were previously reported from Myanmar, Malay Peninsula, and the Indonesian archipelago (Sumatra, Borneo and Java). According to Yeo (1999), the taxonomic identity of *M. dolichodactylus* and *M. scabriculum* were legitimated. Subsequently, Cai and Ng (2002) stated that the Myanmar and Malayan specimens previously identified as *M. dolichodactylus* by Yeo (1999) are distinct species, namely *M. lanatum*. In this study, *M. debaratae* sp. nov. can be distinguished from the three latter species based on the characteristics of the second pereiopods. *Macrobrachium lanatum*, *M. dolichodactylus* and *M. scabriculum* exhibited numerous teeth on the cutting edge of the fingers, and by dense setae being present on the surface of the finger and palm. The shape of epistome,

TABLE 2. Morphological comparisons of *M. debaratae* sp. nov. and some Macrobrachium species in Southeast Asia.

Character	*M. debaratae* sp. nov.	*M. lanatum*	*M. dolichodactylus*	*M. scabriculum*
Rostral formula	4–6+7–9/2–3	4–6(5)+8–11(9)/2–4(2)	3–4(3)+7–10(10)/2–5(3)	4–6(5)+9–11(10)/2–3(2)
Spinulation on anterior carapace surface	absent	absent	absent?	absent?
Epistome	trilobed	bilobed	incompleted bilobed	bilobed
Major second pereiopod				
Ration of leg/body length	>1	>1	>1	≤1
Ratio of finger/palm	≤1	>1	>1	≤1
Ratio of palm/carpus	>1	<1	<1	>1
Ratio of carpus/merus	<1	>1	≥ 1	≥ 1
Teeth on cutting edge of fingers	10–15	26–37	25–37	11–30
Spinulation/tuberculation on ischium and merus surfaces	present	present?	absent?	?
Process on third sternum	prominent	small	small	prominent
Moveable spine on uropodal diaresis	longer than outer angle	slightly shorter than outer angle	distinctively longer than outer angle	shorter than outer angle
References	this study	Cai and Ng, 2002	Yeo et al., 1999; Cai and Ng, 2002	Yeo et al., 1999; Cai and Ng, 2002

rostral formula and proportional ratios between finger-palm, palm-carpus and palm-merus of the second pereiopod are informative and can be used to distinguish this new species from those three species as summarized in Table 2.

The COI phylogenetic analysis revealed that *M. debaratae* sp. nov. is clustered within the *M. pilimanus* group. In this study, the available DNA sequences of *M. lanatum*, *M. dolichodactylus*, and *M. scabriculum* from the GenBank database were included in the tree reconstruction dataset. The result confirmed that the new species is genetically distinct from the aforementioned species and is the closest relative of *M. sirindhorn*, an endemic species in North Thailand. Morphologically, this new species can be distinguished from *M. sirindhorn* by: 1) having 10–15 teeth on the fingers of the major second pereiopods (vs 8–10 teeth); 2) a moderately elongated carpus (vs robust and cupped carpus); and 3) movable spine on the uropodal diaeresis that is longer than or as long as outer angle (vs shorter than outer angle).

Based on some of the morphological characteristics of this new species, the results revealed the further enigmatic problem of morphological variation in second pereiopods of the *M. pilimanus* species group. Previously, members of *M. pilimanus* sensu Johnson (1963) were commonly recognized as true freshwater *Macrobrachium* group, and could be characterized by a blade-like rostrum form and short, stout and setose second pereiopods. Within the *pilimanus* group, the common diagnostic characters include the rostal teeth number, spinulation on carapace surface, the form and length of segments of the second pereiopod, the proportional area of the setose surface, and the number of teeth on the cutting-edge of fingers (Yeo, 1999; Cai et al., 2004; Wowor, 2010; Hanamura et al., 2011; Siriwut et al., 2020).

However, the length and shape of the finger, palm, carpus and merus of the second pereiopod were found to vary in *M. dienbienphuense* among different geographical populations (Holthuis, 1950; Dai, 1984; Cai and Dai, 1999; Hanamura et al., 2011). *Macrobrachium debaratae* sp. nov. prominently exhibits an elongated and conical carpus and merus of the second pereiopod that challenges the traditional characteristics of the *M. pilimanus* species group (cupped carpus shorter than chela and merus). Therefore, the traditional species delimitation of the genus *Macrobrachium* based on morphology alone, and especially in the *pilimanus* species group is increasingly challenged and must be used with caution considering the morphological evidence of the new species. Therefore, integrative taxonomy based on DNA methods, morphological examinations and broad voucher collection from different geographical regions should be strongly considered for further *Macrobrachium* taxonomic reviews.

ACKNOWLEDGEMENTS

The authors thank members of the animal systematics and molecular ecology laboratory, Department of Biology, Faculty of Science, Mahidol University for field and laboratory assistance. Authors are grateful to Nong Thum Subdistrict administration organization and local villagers for assistance and providing habitat information during field collecting. Special thanks are given to Center of Excellence on Biodiversity (BDC), Office of Higher Education Commission for administrative support. This research and innovation activity was funded by the National Research Council of Thailand (NRCT), grant number N34E670115.

LITERATURE CITED

Abdelsalam, K.M. 2018. First record of exotic Lysmatid shrimp *Lysmata vittata* (Stimpson, 1860) (Decapoda: Caridea: Lysma-

tidae) from the Egyptian Mediterranean coast. Mediterranean Marine Science, 19(1): 124–131. https://doi.org/10.12681/mms.15591

Adamson, E.A.S., Hurwood, D.A. and Mather, P.B. 2012. Insights into historical drainage evolution based on the phylogeography of the chevron snakehead fish (*Channa striat*a) in the Mekong Basin. Freshwater Biology, 57(11): 2211–2229. https://doi.org/10.1111/j.1365-2427.2012.02864.x

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. and Lipman, D. J. 1990. Basic local alignment search tool. Journal of Molecular Biology, 215(3): 403–410. https://doi.org/10.1016/s0022-2836(05)80360-2

AVMA. 2020. American Veterinary Medical Association Guidelines for the Euthanasia of Animals. https://www.avma.org/sites/default/files/2020-01/2020-Euthanasia-Final-1-17-20.pdf

Bauer, R.T. 2023. *Shrimps, Their Diversity, Intriguing Adaptations and Varied Lifestyles*. Springer Cham. 720 pp. https://doi.org/10.1007/978-3-031-20966-6

Buckton, S.T. and Safford, R.J. 2004. The avifauna of the Vietnamese Mekong Delta. Bird Conservation International, 14(4): 279–322. https://doi.org/10.1017/S0959270904000346

Cai, Y. and Dai, A.Y. 1999. Freshwater shrimps (Crustacea: Decapoda: Caridea) from the Xishuangbanna region of Yunnan Province, southern China. Hydrobiologia, 400: 211–241. https://doi.org/10.1023/a:1003717109973

Cai, Y., Naiyanetr, P. and Ng, P.K.L. 2004. The freshwater prawns of the genus *Macrobrachium* Bate, 1868, of Thailand (Crustacea: Decapoda: Palaemonidae). Journal of Natural History, 38(5): 581–649. https://doi.org/10.1080/00222930210000332 38

Cai, Y.X. and Ng, P.K.L. 2002. The freshwater palaemonid prawns (Crustacea: Decapoda: Caridea) of Myanmar. Hydrobiologia, 487(1): 59–83. https://doi.org/10.1023/a:1022991224381

Cai, Y.X. and Vidthayanon, C. 2016. *Macrobrachium spelaeus*, a new species of stygobitic freshwater prawn from Thailand (Decapoda: Palaemonidae). Raffles Bulletin of Zoology, 64: 117–122.

Chaowvieng, A., Sutcharit, C., Chanabun, R., Srisonchai, R., Jeratthitikul, E. and Siriwut, W. 2024. Molecular phylogeny and taxonomic position of *Macrobrachium lanchesteri* (De Man, 1911), with descriptions of two new species from Thailand (Decapoda, Caridea, Palaemonidae). ZooKeys, 1190: 163–193. https://doi.org/10.3897/zookeys.1190.113898

Dai, A.Y. 1984. A preliminary study on the freshwater prawn genus *Macrobrachium* of China (Decapoda: Caridea). Acta Zootaxonomica Sinica, 9: 244–252.

Dana, J.D. 1852. Conspectus crustaceorum, etc. Conspectus of the Crustacea of the exploring expedition under Capt. C. Wilkes, U.S.N. Macroura including the Paguridea, continued, the Megalopidea, and the Macroura. Paguridea, continued, and subtribe Megalopidea. Proceedings of the Academy of Natural Sciences of Philadelphia, 6: 10–28. https://www.biodiversitylibrary.org/page/1779609

Dang, N.T. and Nguyen, B.Y. 1972. Nouveaux genres, nouvelles espèces de la faune des invertébres des eaux douces et saumâtres du Nord Vietnam. Journal of Biology and Geology, 6: 155–162.

Darriba, D., Taboada, G.L., Doallo, R. and Posada, D. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods, 9(8): 772–772. https://doi.org/10.1038/nmeth.2109

De Man, J.G. 1879. On some species of the genus *Palaemon* Fabr. with description of two new forms. Notes from the Leyden Museum, 1(41): 165–184.

De Man, J.G. 1898. Zoological results of the Dutch scientific expedition to Central Borneo. The crustaceans. Part I. Macroura. Notes from the Leyden Museum 20: 137–161. https://www.marinespecies.org/aphia.php?p=sourcedetailsandid=155736

De Man, J.G. 1906. Diagnoses of five new species of decapod Crustacea and of the hitherto unknown male of *Spirontocaris rectirostris* (Stimps.) from the Inland Sea of Japan, as also of a new species of *Palæmon* from Darjeeling, Bengal. The Annals and Magazine of Natural History, Ser. 7, 17: 400–406. https:// www.marinespecies.org/aphia.php?p=sourcedetailsandid=155740

De Man, J.G. 1911. On the West-African species of the subgenus *Eupalaemon* Ortm. Notes from the Leyden Museum, 33: 261–264. https://www.marinespecies.org/aphia.php?p=sourcedetailsandid=155752

Folmer, O., Black, M., Hoeh, W., Lutz, R. and Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3: 294–299.

Fukushima, M., Jutagate, T., Grudpan, C., Phomikong, P. and Nohara, S. 2014. Potential effects of hydroelectric dam development in the Mekong river basin on the migration of Siamese mud carp (*Henicorhynchus siamensis* and *H. lobatus*) elucidated by otolith microchemistry. PLOS ONE, 9(8): e103722. https://doi.org/10.1371/journal.pone.0103722

Hanamura, Y., Imai, H., Lasasimma, O., Souliyamath, P. and Ito, S. 2011. Freshwater prawns of the genus *Macrobrachium* Bate, 1868 (Crustacea, Decapoda, Palaemonidae) from Laos. Zootaxa (3025): 1–37.

Heller, C. 1862. Neue Crustaceen, gesammelt während der Weltumseglung der k.k. Fregatte Novara. Zweiter vorläufiger Bericht. Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien, 12: 519–528. https://www.marinespecies.org/aphia.php?p=sourcedetailsandid=155339

Hilgendorf, F. 1879. Die von Hrn. W. Peters in Moçambique gesammelten Crustaceen. Monatsbericht der königlich preussischen Akademie der Wissenschaften zu Berlin, Sitzung der Physikalisch-mathematische Klasse. 782–852 pp. https://www.biodiversitylibrary.org/page/36097499

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. I. Subfamily Palaemoninae. Siboga Expeditie Leiden, 39(a9): 1–267.

Holthuis, L.B. 1980. FAO Species Catalogue. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. FAO Fisheries Synopsis 125(1): 1–271.

Imai, H., Yanagihara, K., Lasasimma, O., Kounthongbang, A., Souliyamath, P. and Ito, S. 2014. Genetic isolation among populations of the landlocked freshwater shrimp *Macrobrachium yui* in the Mekong River basin. Biogeography, 16: 1–11. https://ci.nii.ac.jp/naid/120006378219/en/

IUCN. 2013. Ecological Survey of the Mekong River between Louangphabang and Vientiane Cities 2011–2012. Vientiane, Lao PDR: IUCN. 241 pp.

Jeratthitikul, E., Sutcharit, C. and Prasankok, P. 2024. Two new genera and three new species of exceptionally rare and endemic freshwater mussels (Bivalvia, Unionidae) from the Mekong Basin. Zoosystematics and Evolution, 100(4): 1333–1345. https://doi.org/10.3897/zse.100.130929

Jirapatrasilp, P., Backeljau, T., Prasankok, P., Chanabun, R. and Panha, S. 2019. Untangling a mess of worms: species delimitations reveal morphological crypsis and variability in Southeast Asian semi-aquatic earthworms (Almidae, *Glyphidrilus*). Molecular Phylogenetics and Evolution, 139: 106531. https://doi.org/10.1016/j.ympev.2019.106531

Johnson, D.S. 1963. Distributional and other notes on some freshwater prawns (Atyidae and Palaemonidae) mainly from the Indo-West Pacific region. Bulletin Natural History Museum State Singapore, 32: 5–30.

Kang, B. and Huang, X. 2022. Mekong fishes: biogeography, migration, resources, threats, and conservation. Reviews in

Fisheries Science and Aquaculture, 30(2): 170–194. https://doi.org/10.1080/23308249.2021.1906843

Kumar, S., Stecher, G., Suleski, M., Sanderford, M., Sharma, S. and Tamura, K. 2024. MEGA12: Molecular Evolutionary Genetic Analysis version 12 for adaptive and green computing. Molecular Biology and Evolution, 41(12): msae263. https://doi.org/10.1093/molbev/msae263

Lukoschek, V., Osterhage, J.L., Karns, D.R., Murphy, J.C. and Voris, H.K. 2011. Phylogeography of the Mekong mud snake (*Enhydris subtaeniata*): the biogeographic importance of dynamic river drainages and fluctuating sea levels for semi-aquatic taxa in Indochina. Ecology and Evolution, 1(3): 330–342. https://doi.org/10.1002/ece3.29

Macharoenboon, K., Sutcharit, C., Siriwut, W. and Jeratthitikul, E. 2023. A new species of land-locked freshwater shrimp genus *Caridina* (Decapoda: Atyidae) from Middle Mekong Basin, Thailand. Tropical Natural History, Supplement 7: 229–241. https://doi.org/10.58837/tnh.23.7.257589

Mekong River Commission. 2005. Overview of Hydrology of the Mekong Basin. 73.

Meynell, P.J. 2017. Wetlands of the Mekong River Basin, an Overview. In C.M. Finlayson, G.R. Milton, R.C. Prentice, and N.C. Davidson (Eds.), *The Wetland Book: II: Distribution, Description and Conservation* (pp. 1–22). Springer Netherlands. https://doi.org/10.1007/978-94-007-6173-5_244-2

Minh, B.Q., Nguyen, M.A.T. and von Haeseler, A. 2013. Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution, 30(5): 1188–1195. https://doi.org/10.1093/molbev/mst024

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. and Lanfear, R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution, 37(5): 1530–1534. https://doi.org/10.1093/molbev/ msaa015

Morovati, K., Tian, F., Pokhrel, Y., Someth, P., Shi, L., Zhang, K., Nakhaei, P. and Ly, S. 2024. Fishery and agriculture amidst human activities and climate change in the Mekong River: a review of gaps in data and effective approaches towards sustainable development. Journal of Hydrology, 644: 132043. https://doi.org/10.1016/j.jhydrol.2024.132043

Naiyanetr, P. 1998. Checklist of Crustacean fauna in Thailand (Decapoda and Stomatopoda). Office of Natural Resources and Environmental Policy and Planning. 196 pp.

Naiyanetr, P. 2001. *Macrobrachium sirindhorn* n. sp., a new freshwater prawn from northern Thailand (Decapoda, Caridea, Palaemonidae). Crustaceana, 74: 609–616. https://doi.org/10.1163/156854001750377885

New, M.B. and Nair, C.M. 2012. Global scale of freshwater prawn farming. Aquaculture Research, 43(7): 960–969. https://doi.org/10.1111/j.1365-2109.2011.03008.x

Ng, T.H., Jeratthitikul, E., Sutcharit, C., Chhuoy, S., Pin, K., Pholyotha, A., Siriwut, W., Srisonchai, R., Hogan, Z.S. and Ngor, P.B. 2020. Annotated checklist of freshwater molluscs from the largest freshwater lake in Southeast Asia. ZooKeys, 958: 107–141. https://doi.org/10.3897/zookeys.958.53865

Nguyên, V.X. 2006. A new species of freshwater prawn of the genus *Macrobrachium*, similar to *Macrobrachium sintangense* (De Man, 1888) (Decapoda, Caridea, Palaemonidae) from South Vietnam, and description of its first zoea. Crustaceana, 79: 235–254. https://www.marinespecies.org/aphia.php?p=sou r cedetailsandid=155882

Rafinesque, C.S. 1815. Analyse de la nature ou Tableau de l'univers et des corps organisés. Palermo. 224 pp.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M. and Huelsenbeck, J. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematics Biology, 61: 539–542.

Ruengsawang, N., Sangpradub, N., Cubeddu, T., Pronzato, R. and Manconi, R. 2024. Biodiversity assessment of the Lower Mekong Basin: evolutionary novelties in gemmular morphotraits of Genus *Corvospongilla* (Porifera: Spongillida) with description of a new species from Khorat Plateau, and biogeographic notes. Zootaxa, 5529(1): 144–158. https://doi.org/10.11646/zootaxa.5529.1.7

Saengphan, N., Panijpan, B., Senapin, S., Laosinchai, P., Ruenwongsa, P., Suksomnit, A. and Phiwsaiya, K. 2018. Morphology and molecular phylogeny of *Macrobrachium suphanense* sp. nov. (Decapoda: Palaemonidae) from Thailand. Zootaxa, 4482(1): 151–163. https://doi.org/10.11646/zootaxa.4482.1.7

Saengphan, N., Panijpan, B., Senapin, S., Laosinchai, P., Ruenwongsa, P., Suksomnit, A. and Phiwsaiya, K. 2019. *Macrobrachium chainatense* sp. nov. (Decapoda: Palaemonidae): a freshwater prawn from Thailand based on morphology and molecular phylogeny. Zootaxa, 4664(2): 274–284. https://doi.org/10.11646/zootaxa.4664.2.9

Sanoamuang, L. and Dabseepai, P. 2021. Diversity, distribution, and habitat occurrence of the diaptomid copepods (Crustacea: Copepoda: Diaptomidae) in Freshwater Ecosystems of Thailand. Water, 13(17): 2381. https://doi.org/10.3390/w13172381

Schwendinger, P. and Giribet, G. 2005. The systematics of Southeast Asian genus *Fangensis* Rambla (Opiliones: Cyphophthalmi: Stylocellidae). Invertebrate Systematics, 19: 297–323. https://doi.org/10.1071/IS05023

Shokita, S. and Takeda, M. 1989. A new freshwater prawn of the genus *Macrobrachium* (Decapoda, Caridea, Palaemonidae) from Thailand. Bulletin of the National Science Museum, Tokyo, 15: 147–154. http://www.marinespecies.org/aphia.php?p=sourcedetailsandid=156100

Siriwut, W., Jeratthitikul, E., Panha, S., Chanabun, R., Ngor, P.B. and Sutcharit, C. 2021. Evidence of cryptic diversity in freshwater Macrobrachium prawns from Indochinese riverine systems revealed by DNA barcode, species delimitation and phylogenetic approaches. PLoS ONE, 16: e0252546. https://doi.org/10.1371/journal.pone.0252546

Siriwut, W., Jeratthitikul, E., Panha, S., Chanabun, R. and Sutcharit, C. 2020. Molecular phylogeny and species delimitation of the freshwater prawn *Macrobrachium pilimanus* species group, with descriptions of three new species from Thailand. PeerJ, 8: e10137. https://doi.org/10.7717/peerj.10137

Sor, R., Ngor, P.B., Boets, P., Goethals, P.L.M., Lek, S., Hogan, Z. S. and Park, Y.-S. 2020. Patterns of Mekong mollusc biodiversity: identification of emerging threats and importance to management and livelihoods in a region of globally significant biodiversity and endemism. Water, 12(9): 2619. https://doi.org/10.3390/w12092619

Spence Bate, C. 1868. On a new genus, with four new species, of freshwater prawns. Proceedings of the Zoological Society of London 1868(2): 363–368.

Sun, J., Baldan, D., Lucas, M.C., Wang, J., Rodeles, A.A., Galib, S. M., Tao, J., Li, M., He, D. and Ding, C. 2025. Widespread and strong impacts of river fragmentation by anthropogenic barriers on fishes in the Mekong River Basin. Communications Earth and Environment, 6(1): 534. https://doi.org/10.1038/s43247-025-02467-y

Tanabe, A.S. 2007. Kakusan: a computer program to automate the selection of a nucleotide substitution model and the configuration of a mixed model on multilocus data. Molecular Ecology Resources, 77: 962–964. http://dx.doi.org/10.1111/j.1471-8286.2007.01807.x

Tavaré, S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. Lectures on Mathematics in the Life Sciences, 17: 57–86.

Tiwari, K.K. 1952. Diagnosis of new species and subspecies of the genus *Palaemon* Fabricius (Crustacea: Decapoda). Annals and magazine of natural history, 5(12): 27–32.

Wowor, D. 2010. *Macrobrachium empulipke*, a new freshwater prawn species (Decapoda, Palaemonidae) from Indonesia. In Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume (pp. 715–726). Brill. https://doi.org/10.1163/9789047427759_053

Wowor, D., Muthu, V., Meier, R., Balke, M., Cai, Y. and Ng, P.K.L. 2009. Evolution of life history traits in Asian freshwater prawns of the genus *Macrobrachium* (Crustacea: Decapoda: Palaemonidae) based on multilocus molecular phylogenetic analysis. Molecular Phylogenetics and Evolution, 52(2), 340–350. https://doi.org/10.1016/j.ympev.2009.01.002

Wowor, D. and Ng, P.K.L. 2007. The giant freshwater prawns of the *Macrobrachium rosenbergii* species group (Crustacea: Decapoda: Caridea: Palaemonidae). The Raffles Bulletin of Zoology, 55: 321–336.

Yang, Z. and Rannala, B. 2005. Branch-length prior influences Bayesian posterior probability of phylogeny. Systematic Biology, 54(3): 455–470. https://doi.org/10.1080/10635150590945313

Yeo, D.C.J., Cai, Y., Ng, P.K.L. 1999. The freshwater and terrestrial decapod Crustacea of Pulau Tioman, Peninsular Malaysia. Raffles Bulletin of Zoology, Supplement No. 6: 197–244.

Zhang, C., Zhu, R., Sui, X., Li, X. and Chen, Y. 2021. Understanding patterns of taxonomic diversity, functional diversity, and ecological drivers of fish fauna in the Mekong River. Global Ecology and Conservation, 28: e01711. https://doi.org/10.1016/j.gecco.2021.e01711

APPENDIX

TABLE A1. Interspecific variation of *Macrobrachium* species based on pairwise comparisons of COI sequences.

Taxon	Inter specific pairwise distance / standard deviation																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 *M. naiyanetri*		0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
2 *M. spelaeus*	0.10		0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
3 *M. palmopilosum*	0.10	0.10		0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
4 *M. puberimanus*	0.12	0.14	0.14		0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
5 *M. dienbienphuense*	0.11	0.14	0.13	0.08		0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
6 *M. eriocheirum*	0.12	0.13	0.13	0.11	0.12		0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
7 *M. hirsutimanus*	0.10	0.11	0.11	0.10	0.11	0.10		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
8 *M. debaratae* sp. nov.	0.16	0.15	0.15	0.14	0.15	0.17	0.15		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
9 *M. sirindhorn*	0.15	0.14	0.14	0.14	0.15	0.17	0.14	0.13		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
10 *M. lanchesteri*	0.20	0.19	0.22	0.20	0.22	0.22	0.19	0.19	0.20		0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
11 *M. panhai*	0.19	0.19	0.21	0.20	0.22	0.22	0.19	0.19	0.20	0.06		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
12 *M. rosenbergii*	0.18	0.18	0.18	0.16	0.18	0.18	0.17	0.17	0.17	0.15	0.14		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
13 *M. niphanae*	0.18	0.16	0.17	0.19	0.20	0.19	0.18	0.19	0.18	0.17	0.18	0.17		0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
14 *M. thai*	0.18	0.16	0.16	0.17	0.19	0.18	0.17	0.19	0.16	0.16	0.17	0.17	0.06		0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
15 *M. chainatense*	0.19	0.18	0.20	0.20	0.21	0.19	0.19	0.20	0.19	0.18	0.18	0.17	0.11	0.12		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
16 *M. hendersoni*	0.19	0.18	0.19	0.20	0.20	0.20	0.19	0.17	0.17	0.17	0.19	0.17	0.16	0.16	0.18		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
17 *M. sintangense*	0.17	0.17	0.17	0.19	0.18	0.17	0.17	0.19	0.17	0.17	0.17	0.17	0.17	0.16	0.17	0.17		0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
18 *M. saigonense*	0.16	0.16	0.17	0.17	0.18	0.17	0.17	0.17	0.16	0.16	0.16	0.16	0.15	0.13	0.17	0.16	0.11		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
19 *M. scabriculum*	0.16	0.17	0.18	0.17	0.18	0.17	0.17	0.17	0.18	0.19	0.18	0.19	0.18	0.18	0.21	0.18	0.17	0.15		0.01	0.01	0.02	0.02	0.02	0.02	0.02
20 *M. dolichodactylus*	0.16	0.16	0.18	0.17	0.18	0.17	0.17	0.17	0.18	0.18	0.17	0.17	0.18	0.17	0.19	0.17	0.17	0.13	0.09		0.01	0.02	0.02	0.02	0.02	0.02
21 *M. lanatum*	0.17	0.16	0.15	0.17	0.18	0.18	0.16	0.15	0.17	0.20	0.20	0.18	0.16	0.16	0.19	0.16	0.17	0.14	0.11	0.11		0.02	0.02	0.02	0.02	0.02
22 *M. equidens*	0.19	0.20	0.19	0.20	0.21	0.21	0.19	0.20	0.19	0.20	0.19	0.20	0.20	0.19	0.22	0.23	0.18	0.18	0.20	0.20	0.20		0.02	0.02	0.02	0.02
23 *M. yui*	0.17	0.17	0.17	0.17	0.19	0.18	0.15	0.19	0.17	0.18	0.20	0.18	0.17	0.16	0.18	0.16	0.17	0.15	0.18	0.17	0.19	0.20		0.02	0.02	0.02
24 *M. latidactylus*	0.17	0.19	0.18	0.17	0.18	0.18	0.16	0.18	0.17	0.18	0.19	0.16	0.18	0.16	0.19	0.19	0.18	0.14	0.18	0.19	0.16	0.19	0.16		0.02	0.02
25 *Palaemon*	0.24	0.24	0.27	0.24	0.24	0.23	0.24	0.25	0.25	0.24	0.23	0.23	0.23	0.23	0.23	0.24	0.24	0.24	0.24	0.23	0.24	0.24	0.25	0.24		0.02
26 *Exopalaemon*	0.22	0.22	0.23	0.22	0.24	0.23	0.22	0.24	0.21	0.23	0.23	0.21	0.22	0.21	0.22	0.23	0.21	0.22	0.21	0.21	0.22	0.24	0.20	0.20	0.19	

TABLE A2. Intraspecific variation within *Macrobrachium* species based on pairwise comparisons of COI sequences.

Taxon	Intra specific variation	Standard deviation
M. scabriculum	0.056	0.01
M. lanatum	0.000	0.00
M. lanchesteri	0.003	0.00
M. niphanae	0.037	0.01
M. sintangense	0.057	0.01
M. debaratae sp. nov.	0.004	0.00
M. thai	0.004	0.00
M. eriocheirum	0.022	0.01
M. naiyanetri	0.038	0.01
M. chainatense	0.048	0.01
M. spelaeus	0.042	0.01
M. puberimanus	0.010	0.00
M. hendersoni	0.014	0.00
M. panhai	0.014	0.01
M. hirsutimanus	0.010	0.00
M. sirindhorn	0.003	0.00
M. yui	0.005	0.00
M. rosenbergii	0.019	0.01
M. palmopilosum	0.015	0.00
M. equidens	n/c	n/c
M. saigonense	n/c	n/c
M. latidactylus	n/c	n/c
M. dienbienphuense	n/c	n/c
M. dolichodactylus	n/c	n/c
Palaemon	n/c	n/c
Exopalaemon	n/c	n/c