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A new species of copepod (Copepoda: Calanoida) from the floodplain of the lower Mekong River Basin in Thailand and Cambodia, with an amended diagnosis of the genus *Dentodiaptomus* Shen & Tai, 1964

Laorsri Sanoamuang^{1,2*} & Santi Watiroyram³

Abstract. The genus *Dentodiaptomus* Shen & Tai, 1964, is widely distributed in aquatic habitats in Asia, but only one species, *D. javanus* (Grochmalicki, 1915), has been described. During our intensive collections of freshwater copepods from several localities in the floodplain of the lower Mekong River Basin in Thailand and Cambodia in 2002 and 2007, a new species of *Dentodiaptomus* was discovered from five and six localities, respectively. To date, *Dentodiaptomus orientalis*, new species, is the second member of the genus found to be endemic to Thailand and Cambodia. The new species is rare and closely allied with *Dentodiaptomus javanus*, which is widely distributed across Southeast Asia and Southern China. *Dentodiaptomus orientalis* is found in both temporary and permanent water habitats throughout the year. It differs from its congeners in many morphological aspects, especially in the composition of the fifth leg. In this paper, the diagnostic characters of the genus *Dentodiaptomus* are revised based on specimens of the new species and *D. javanus* from Thailand and Cambodia.

Key words. *Dentodiaptomus javanus*, Diaptomidae, endemic species, micro-crustaceans, Southeast Asia

INTRODUCTION

The Mekong River originates from the Tibetan Plateau, with a length of approximately 4,350 km before it drains into the South China Sea. It is the longest river in Southeast Asia, and is one of the world's most biodiverse rivers. The upper Mekong flows 1,960 km through the mountains and plateaus of southwestern China, which accounts for approximately one-fourth of its total distance. The lower Mekong is 2,390 km in length, draining from the border between Myanmar and Laos through the Khorat Plateau of northeastern Thailand, the Annamese Mountains in Laos and Vietnam, and most of Cambodia before reaching the sea through the distributary channels of its delta in southern Vietnam (White et al., 2021). The Mekong River Basin drains an area of 795,000 km², transports and discharges 475 km³ of water annually, and is the habitat of at least 430 species of mammals, 1,200 species of birds, 800 species of reptiles, 20,000 species of plants (Sanoamuang & Watiroyram, 2018), and 877 species of fish (Ziv et al., 2012). Over one million tons of freshwater fish are caught annually in the Cambodian and

Vietnamese floodplains alone, which makes the sustainability of floodplain fisheries a major food security issue in both of those countries (Ziv et al., 2012).

Copepods are a group of micro-crustaceans that are commonly found in different kinds of freshwater habitats, including lakes, swamps, permanent and temporary ponds, pools, rivers, and groundwater habitats (Boxshall & Defaye, 2008). Members of the orders Calanoida, Cyclopoida, and Harpacticoida are usually the dominant members of the freshwater communities, and they are major food organisms for small fish and other invertebrates. Calanoid copepods predominate in the plankton samples collected in tropical countries. During the last 25 years, there has been a significant increase in the number of biodiversity studies of planktonic calanoid copepods from the lower Mekong River Basin, particularly in Thailand (Dumont & Ranga Reddy, 1994; Dumont et al., 1996; Ranga Reddy & Dumont, 1998; Ranga Reddy et al., 2000; Sanoamuang, 1999, 2001a–c, 2002, 2004; Sanoamuang & Yindee, 2001; Sanoamuang & Athibai, 2002; Sanoamuang & Teeramaethee, 2006; Proongkiat & Sanoamuang, 2008; Watiroyram & Sanoamuang, 2017; Boonmak et al., 2018; Sanoamuang & Watiroyram, 2018, 2020; Saetang et al., 2020; Sanoamuang & Dabseepai, 2021). However, similar studies in other neighbouring countries, including Laos (Sanoamuang & Sivongxay, 2004; Sanoamuang & Watiroyram, 2018, 2019), Cambodia (Sanoamuang & Watiroyram, 2018, 2020), and Vietnam (Tran et al., 2016; Sanoamuang & Watiroyram, 2018), are comparatively scarce.

During our seasonal sampling of freshwater copepods from several localities in the floodplain of the lower Mekong River

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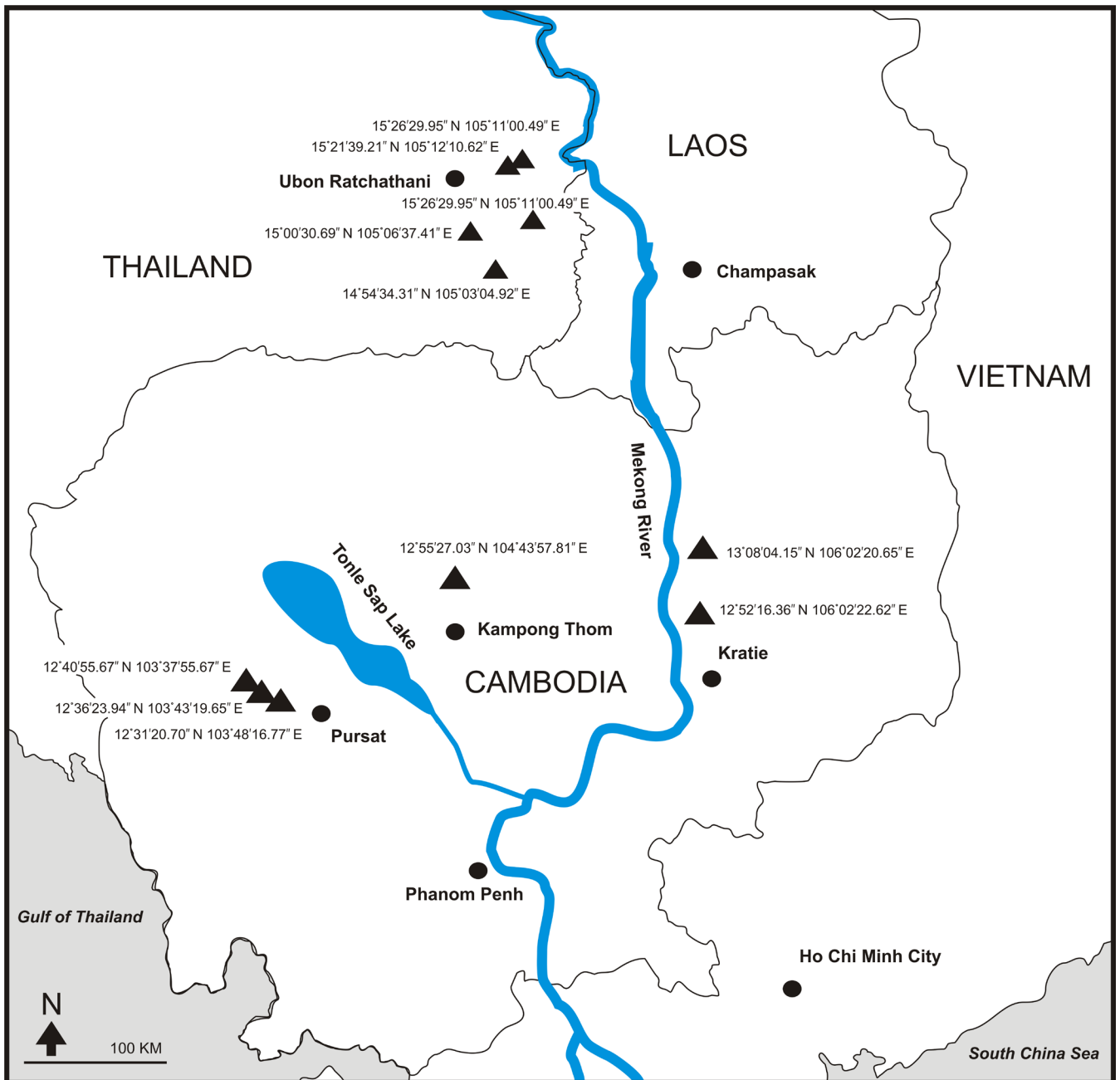


Fig. 1. A map showing the distribution of *Dentodiaptomus orientalis*, new species, from Thailand and Cambodia. Legend: black triangle = sampling location, black circle = city name.

Basin in Thailand and Cambodia, we encountered another hitherto unknown species of *Dentodiaptomus* Shen & Tai, 1964. In the present paper, we describe *Dentodiaptomus orientalis*, new species, from five localities in the Ubon Ratchathani Province of Thailand, and from six localities in three provinces of Cambodia. The diagnostic characteristics of the genus *Dentodiaptomus* have also been revised, and they are presented herein.

MATERIAL AND METHODS

Copepod samples were collected using a plankton net with a mesh size of 60 µm. Plankton samples were taken from several localities in the floodplain of the lower Mekong River Basin (Fig. 1). A total of 198 samples from 163 localities in

Ubon Ratchathani Province, Thailand, were collected from June to October 2002, while 252 samples from 236 localities in seven provinces (Banteay Meanchey, Battambang, Siem Reap, Kampong Thom, Pursat, Kratie, and Stung Treng) in Cambodia were collected from February to October 2007. All samples were preserved in 70% ethanol or 4% formaldehyde immediately after collection. Specimens were cleaned and isolated under an Olympus SZ51 stereomicroscope (Olympus Corporation, Tokyo, Japan) at 40× magnification. Adults were placed in a mixture of glycerol and 70% ethanol prior to transfer, and then dissected in pure glycerol under a stereomicroscope at 40–100× magnification. Permanent slides were prepared in pure glycerine and sealed under glass cover slips with transparent nail varnish. Specimens for scanning electron microscopy (SEM) were prepared according to the method published by Watiroyram & Sanoamuang (2017).

All appendages and body ornamentation were examined at 1000× magnification under an Olympus CX31 compound microscope. The drawings were made using an Olympus U-DA drawing tube mounted on a compound microscope. The final versions of the drawings were made using the CorelDRAW® 12.0 graphics program (Corel Corporation, Ottawa, Ontario, Canada).

The descriptive terminology follows Huys & Boxshall (1991), including analysis of caudal setae (I–VII). The following abbreviations are used throughout the text and figures: a, aesthetasc; Enp, endopod; Exp, exopod; Exp/Enp-n, exopodal segment n/endopodal segment n; P1–P5, legs 1–5; s, spine. Specimens were deposited at the Thailand Natural History Museum, Pathum Thani, Thailand (THNHM), and the Applied Taxonomic Research Center, Khon Kaen University, Khon Kaen, Thailand (KKU).

TAXONOMY

Order Calanoida Sars, 1903

Family Diaptomidae Baird, 1850

Subfamily Diaptominae Kiefer, 1932

Dentodiptomus Shen & Tai, 1964

Type species. *Dentodiptomus javanus* (Grochmalicki, 1915).

Other included species. *Dentodiptomus orientalis*, new species.

Amended diagnosis. Moderate body size, longer than 1 mm excluding caudal setae. Cephalothorax with fused suture dorsally indicating incomplete incorporation. Antennule reaches distal end of caudal setae or shorter.

Male: Right antennule 22-segmented. Pedigers 4 and 5 separated, asymmetrical. Genital somite asymmetrical, with a tiny spine on distal outer corner of right side; urosomites 2–5 and caudal rami without ornamentation. P5 intercoxal sclerite unproduced at distal margin. Right P5: coxa produced at distal outer corner into a large lobe, coxal spine reduced; Exp-2 with a principal spine on distal outer margin, and a longitudinal ridge on posterior surface terminated nearby insertion of principal spine; Enp one-segmented, elongated. Left P5: Exp-2 with inner roundish prominence, apex with one seta; and 1–10 denticles on distal inner margin.

Female: Antennule 25-segmented. Pedigers 4 and 5 fused, with suture laterally; lateral wings asymmetrical, with dorsal and posterior spines. Genital double-somite more asymmetrical than symmetrical. P5 slightly asymmetrical, Exp-3 with two spines on small segment, Enp with row of spinules on distal end.

Dentodiptomus orientalis, new species

(Figs. 2–7)

Type locality. A roadside canal in Okreng, Sambo District, Kratie Province, Cambodia. The geographic coordinates are 13°08'04.15"N, 106°02'20.65"E.

Material examined. Holotype: one adult male (THNHM-Iv-18782), dissected and mounted in glycerol on one slide. **Allotype:** one adult female (THNHM-Iv-18783), dissected and mounted in glycerol on one slide. **Paratypes:** three adult males and three adult females (THNHM-Iv-18784), undissected and preserved in 70% ethanol in one microtube; and, three adult males and three adult females, (KKU-COP-2021-T01), undissected and preserved in 70% ethanol in one microtube. All specimens collected from the type locality on 11 February 2007 by Rachada Chaicharoen.

Other localities. (1) a permanent pond, Kratie District, Kratie Province, Cambodia; two males collected on 11 February 2007; (2) a permanent pond, Kampong Svay District, Kampong Thom Province, Cambodia; two males collected on 9 June 2007; (3) a temporary pond, Bakan District, Pursat Province, Cambodia; two males collected on 10 June 2007; (4) a roadside canal, Boeung Khnar District, Pursat Province, Cambodia; two males collected on 21 October 2007; (5) a permanent pond, Slor Prah District, Pursat Province, Cambodia; two males collected on 21 October 2007; (6) a temporary pond, Ban Dong Pleuy, Tansoom District, Ubon Ratchathani Province, Thailand; three males and one female collected on 9 June 2002; (7) a pond in a rice field, Ban Samrong, Tansoom District, Ubon Ratchathani Province, Thailand; two males and one female collected on 9 June 2002; (8) a temporary pond, Road Number 24 (Km 9), Muang Det Sub-district, Det Udom District, Ubon Ratchathani Province, Thailand; two males collected on 11 June 2002; (9) a temporary pond, Road Number 2213 (Km 2), Nayia District, Ubon Ratchathani Province, Thailand; two males collected on 11 June 2002; and, (10) a temporary pond, Road Number 2172 (Km 18), Pibool Mungsahan District, Ubon Ratchathani Province, Thailand; two males collected on 21 October 2002. Specimens from Cambodia and Thailand were collected by Rachada Chaicharoen and Panna Wansuang, respectively.

Description of adult male. Body length (Figs. 2A, 3A) excluding caudal setae, 1.63–1.70 mm (mean = 1.62 mm, n = 5), smaller and slender than female. Prosoma about twice as long as urosome, without ornamentation. Cephalosome with dorsal suture representing fused ancestral segments (cephalon and the first thoracic somite). Rostral spines with two teeth-like processes on anterior margin. Pedigers 4 and 5 (Fig. 3A) completely separated, slightly asymmetrical, pediger 5 wings with minute hyaline spines (left spine slightly larger than right spine). Urosome (Fig. 3B, C) five-segmented, asymmetrical. Genital somite (Fig. 3B) slightly enlarged at right distal corner, tipped with a minute spine apically. Urosomites 2–5 (Fig. 3C) without ventral ornamentation. Caudal rami (Fig. 3B, C) with row of setules along inner margin, five plumose setae (seta II–VI), and bare dorsal (VII) seta; dorsal seta thinner than others, but longest.



Fig. 2. *Dentodiptomus orientalis*, new species, male: A, habitus, dorsal view; B, P5, posterior view; C, P5, frontal view; D, left P5 Enp and Exp, posterior view.

Left antennule (Fig. 4A) 25-segmented, not extending beyond tip of caudal rami. Setal formula (Arabic numerals = number of setae, Roman numerals = segment numbers): 1(I), 3+a (II), 1+a (III), 1(IV), 1+a (V), 1 (VI), 1+a (VII), 1+s (VIII), 2+a (IX), 1 (X), 1 (XI), 1+a+s (XII), 1 (XIII), 1+a (XIV), 1 (XV), 1+a (XVI), 1 (XVII), 1 (XVIII), 1+a (XIX), 1 (XX), 1 (XXI), 2 (XXII), 2 (XXIII), 2 (XXIV), 5+a (XXV).

Right antennule (Fig. 3D) 22-segmented, geniculated between segment 18 and 19, with setal formula as: 1+a(I), 3+a (II), 1+a (III), 1 (IV), 1+a (V), 1 (VI), 1+a (VII), 1+s (VIII), 2+a (IX), 1+s (X), 1+s (XI), 1+a (XII), 1+a+s (XIII), 2+a+s (XIV), 2+a+s (XV), 2+a (XVI), 1+s (XVII), 1+s (XVIII), 1+a+2s (XIX), 2+s (XX), 2 (XXI), 5+a (XXII); segment 20 (antepenultimate segment) with smooth process reaching distal end of later segment.

Antenna (Fig. 4B) biramous. Coxa small, with inner seta distally. Basis with two inner setae distally. Exp-1-6 with 1, 3, 1, 1, 1, and 1, respectively. Exp-7 with one inner seta and three setae apically. Enp two-segmented: Enp-1 with two inner median setae and small spinules on distal outer margin; Enp-2 with eight inner setae subapically and six

setae apically; both segments with row of spinules along distal outer margin.

Mandible (Fig. 4C) with seven strongly chitinised teeth; two three-cusped, three two-cusped, and one mono-cusped teeth; with one dorsal seta on gnathobase. Basis with one seta proximally and three setae distally along inner margin. Enp two-segmented; Enp-1 with four inner setae distally, Enp-2 with nine setae apically and transverse row of tiny spinules on posterior surface. Exp four-segmented, with setal formula as 1, 1, 1, 3.

Maxillule (Fig. 4D) with eight strong spiniform setae distally; five slender setae subapically on praecoxal arthrite. Coxal endite and coxal epipodite with four and seven setae, respectively. Basal endite with three setae proximally and four setae distally; basal exite with outer seta. Enp with eight setae distally. Exp with six setae.

Maxilla (Fig. 4E) with three setae on both praecoxal endites. Coxal endite with three setae on proximal and distal endites. Allobasis with three setae. Enp two-segmented, with three setae each.

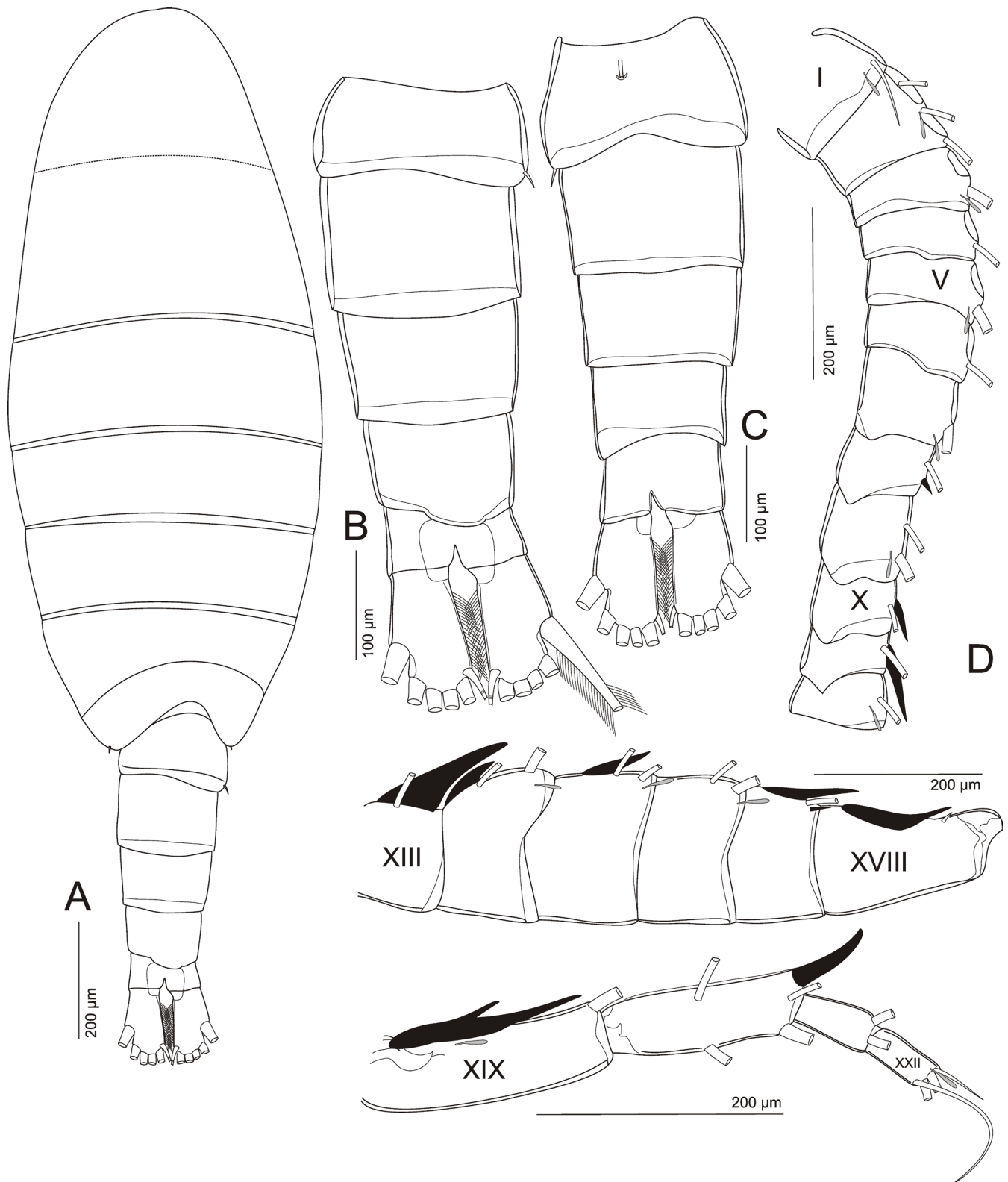


Fig. 3. *Dentodiptomus orientalis*, new species, male: A, habitus, dorsal view; B, urosome, dorsal view; C, urosome, ventral view; D, right antennule (segments I–XXII).

Maxilliped (Fig. 4F) with four endites on syncoxa, with setal formula as 1, 2, 3, 4; distal inner corner protruded into subspherical lobe, ornamented with tiny spinules. Basis with three inner setae distally, ornamented with tiny spinules proximally. Enp six-segmented, setal formula as 2, 3, 2, 2, 2, 4.

P1–P4 (Fig. 5A–D) with biramous, three-segmented rami except P1, and two-segmented Enp. Intercoxal sclerite bare. Coxa with distal inner pinnate seta. P1–P3 basis bare. P4 basis with reduced outer seta distally. Armature formula of P1–P4 as shown in Table 1.

Table 1. Armature formula of swimming legs (P1 to P4) of *Dentodiptomus orientalis*, new species.

	Coxa	Basis	Exp			Enp		
			1	2	3	1	2	3
P1	0-1	0-0	I-1	0-1	I-3-2	0-1	1-2-3	----
P2	0-1	0-0	I-1	I-1	I-3-3	0-1	0-2	2-2-3
P3	0-1	0-0	I-1	I-1	I-3-3	0-1	0-2	2-2-3
P4	0-1	1-0	I-1	I-1	I-3-3	0-1	0-2	2-2-3

(The Arabic and Roman numerals indicate the number of setae and spines, respectively; outer-inner or outer-apical-inner indicate seta/spine)

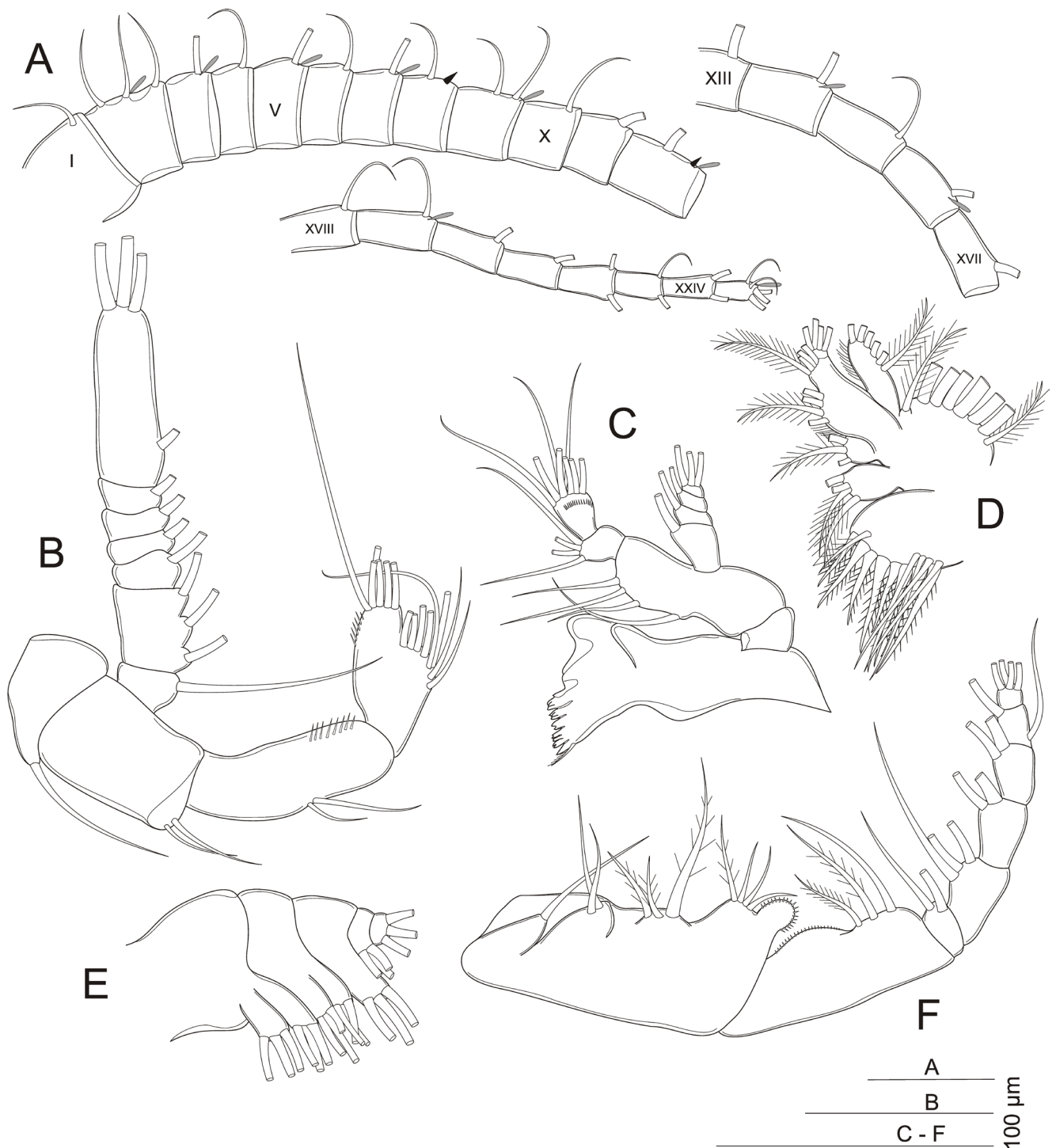


Fig. 4. *Dentodiptomus orientalis*, new species, male: A, left antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped.

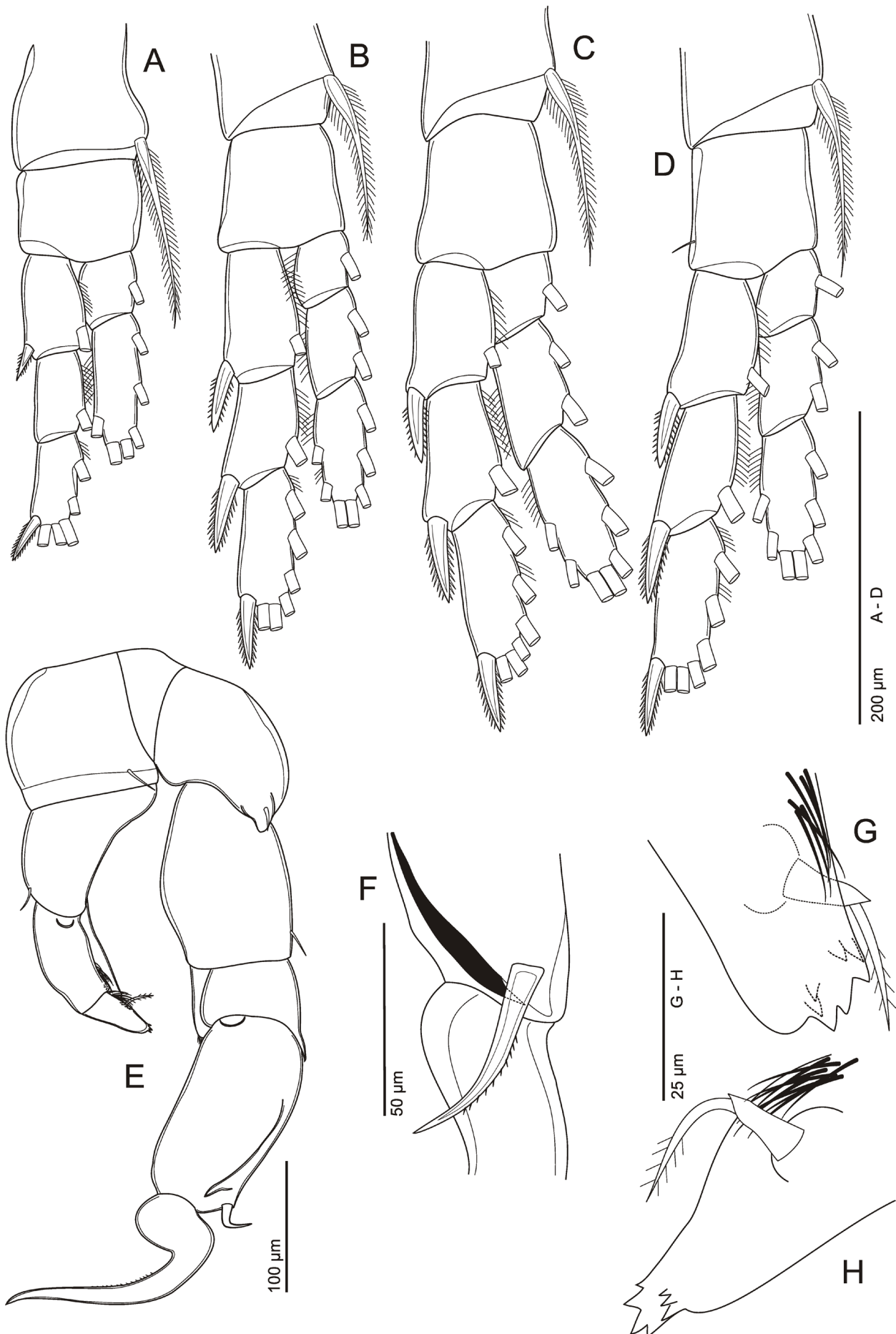


Fig. 5. *Dentodiptomus orientalis*, new species, male: A, P1; B, P2; C, P3; D, P4; E, P5, posterior view; F, a part of the right P5 Exp-2, lateral view; G, left P5 Exp-2, posterior view; H, left P5 Exp-2, frontal view.

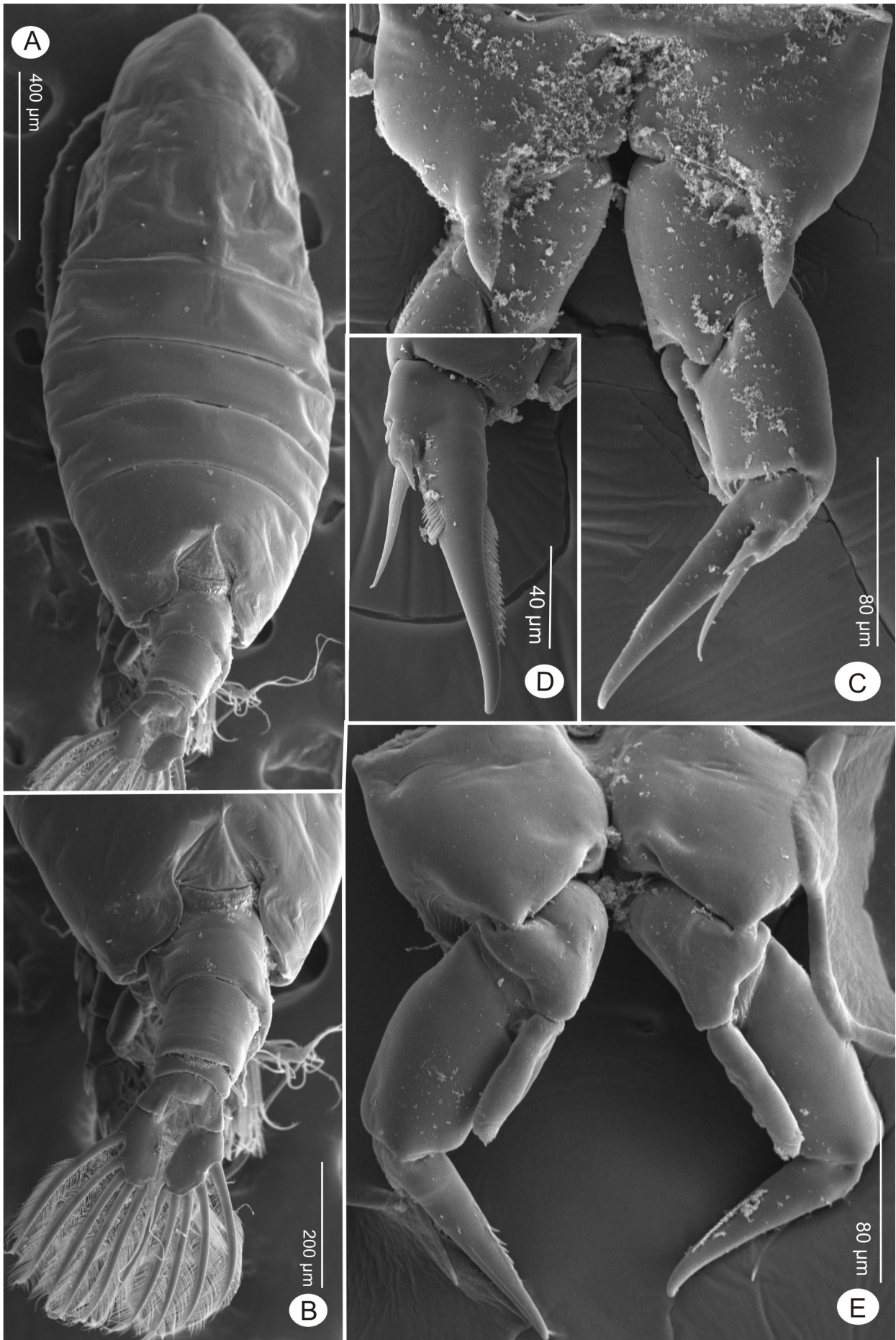


Fig. 6. *Dentodiptomus orientalis*, new species, female: A, habitus, dorsal view; B, pediger 4–5 and urosome, dorsal view; C, P5, posterior view; D, left P5 Exp-2–3, posterior view; E, P5, frontal view.

P5 (Figs. 2B–D, 5E–H) asymmetrical, right leg enlarged. Distal margin of intercoxal sclerite straight. Right P5: coxa with finger-like extension on distal outer corner, accompanied with one small hyaline spine inserted on posterior surface. Basis (Figs. 2B, C, 5E) elongated, about 1.5 as long as wide; without hyaline lamella on inner margin; no projection on posterior surface; sensory seta on distal outer margin short. Exp-1 (Figs. 2B, C, 5E) shorter than wide, with acute process at distal outer corner and semi-circular posterior knobs on distal margin. Exp-2 (Figs. 2B, C, 5E, F) slightly oval, about twice as long as wide, with lateral ridge on posterior surface ending with acute spine. Lateral spine (Figs. 2B, C, 5E, F) articulated, curved backward, acutely pointed, 0.1 times as long as Exp-2, inserted sub-distally, close to end claw. End claw (Figs. 2B, C, 5E) sickle-shaped, robust, with acute tip, about as long as Exp-2. Enp (Fig. 2B, C) rectangular, reaching slightly beyond Exp-1, tipped with spinules.

Left P5 (Figs. 2B–D, 5E, G, H) reaching posterior margin of right P5 Exp-1. Coxa as long as wide, with one small posterior seta inserted near inner corner distally. Basis trapezoidal, without hyaline lamella on inner margin; with one thin seta near outer corner distally and small knob-like outgrowth apically. Two-segmented Exp (Figs. 2B–D, 5E), Exp-1 fusiform, with field of tiny spinules at distal inner corner. Exp-2 (Figs. 2E, 5E, G, H) conical, smaller than Exp-1; with few long setules and short spinules at proximal half of segment inner margin, one pinnate seta at 1/2 length of inner margin; and 6–10 denticles sub-terminally. Enp (Figs. 2D, 5E) unsegmented, longer than Exp-1, tipped with row of spinules distally.

Description of adult female. Body length (Fig. 6A), measured from anterior margin of rostrum to posterior margin of caudal rami, 1.65–1.77 mm (mean = 1.70 mm, $n = 5$). Prosoma as in male except pedigers 4 and 5 fused, with suture laterally. Pediger 5 with asymmetrical postero-lateral wings (Fig. 7A), right wing posteriorly triangular in dorsal view, but rectangular on left side; each wing with one dorsal spine and one larger posterior spine. Urosome (Fig. 6A, B) symmetrical, three-segmented. Genital double-somite (Figs. 6A, C, 7A) symmetrical, separated dorsally, shorter than urosomite 2, anal somite and caudal ramus combined; slightly expanded proximally; with one pair of genital spines laterally, inserted directly on segment, sub-similar in size. Urosomite 2 symmetrical, shortest, usually beneath former segment. Anal somite (Fig. 6C) expanded distally; anal operculum small with posterior margin concave. Caudal rami, antennule, antenna, mouthparts, and P1–P4 similar to those in male.

P5 (Figs. 6C–E, 7B, C) slightly asymmetrical. Coxa with stout spine arising from posterior lobe located on distal outer margin. Basis trapezoidal, with short, bare seta on distal outer margin, reaching about 1/4 length of Exp-1. Exp-1 (Figs. 6C–E, 7B, C) rectangular, slightly curved, about twice as long as wide. Exp-2 slightly asymmetrical, right side more triangular, with acute tip, longitudinal conveyor canal on frontal view. Left side stouter, with blunt tip; with row of strong spinules along margins, more spinules on inner

margin. Exp-3 (Fig. 6C, D) minute, as long as wide, not articulated; with two bare spines, lateral spine short, about 1/4 of apical spine. Enp (Figs. 6E, 7B, C) rectangular, about 4–5 times as long as wide, slightly shorter than Exp-1, with circular row of spinules terminally. Adult females with egg sac were not found in examined samples.

Variations. One of five females photographed by SEM showed a thin spine instead of a strong spine on P5 Exp-3. The left P5 Exp-2 of the males ($n = 5$) with the number of denticles varied from six to ten denticles on the distal inner margin that are clearly presented in frontal view.

Etymology. The specific epithet, *orientalis* (Latin, adj., of the east), alludes to the “Eastern region”, which includes Thailand and Cambodia, the countries where it was first recorded. The name is used as an adjective.

Geographic distribution. In Thailand, *D. orientalis*, new species, was found only in temporary water habitats in five localities in Ubon Ratchathani Province (Fig. 1) during the rainy season (June and October). It was found together with 1–5 other diaptomids, including *Eodiaptomus phuvongi* Sanoamuang & Sivongxay, 2004, *Mongolodiptomus malaindosinensis* (Lai & Fernando, 1978), *Neodiaptomus laii* Kiefer, 1974, *Neodiaptomus songkhramensis* Sanoamuang & Athibai, 2002, and *Vietodiptomus blachei* (Brehm, 1951). In Cambodia, the new species was recorded from six localities in three provinces; Kratie, Kampong Thom, and Pursat (Fig. 1). It was recorded throughout the year and usually lived together with 1–3 other diaptomids, viz., *E. phuvongi*, *E. phuphanensis* Sanoamuang, 2001, *M. malaindosinensis*, *N. laii*, *Tropodiptomus oryzanus* Kiefer, 1937, and *V. blachei*. This new species is very rare, as evidenced by the fact that it was isolated from 3.1% (5 from 163 localities) and 2.5% (6 from 236 localities) of the sampling localities in Thailand and Cambodia, respectively.

DISCUSSION

On the diagnosis of *Dentodiptomus*. Shen & Tai (1964) established a new genus, *Dentodiptomus*, for *Diptomus javanus* Grochmaliki, 1915, based on the male left P5 with a denticle on the inner margin of Exp-2. The original characteristics used to differentiate *Dentodiptomus* from the closest genus, *Tropodiptomus* Kiefer, 1932, include: 1) the cephalosome with a distinct cervical groove (i.e., dorsal suture); 2) the antennule long, reaching beyond the caudal setae; 3) the female P5 Enp ending with spinules; 4) the male left P5 with two-segmented Exp, Exp-1 and Exp-2 with two and one inner roundish elevations, respectively; and 5) the male left P5 Exp-2 with one denticle and one inner spiniform seta. The first and third characters are also found in the new species. However, the cervical groove is also present in some *Tropodiptomus* species, such as *T. cf. hebereri* (Kiefer, 1930) from Thailand (see Sanoamuang, 2002: fig. 6-3). The antennule of the new species is shorter than the tips of the caudal setae in both sexes. The left P5 Exp-1 in the male of the new species has a single knob-

Table 2. Comparison of some characteristics of the male P5 between *Dentodiptomus orientalis*, *D. javanus*, and *Phyllodiptomus (Ctenodiptomus) praedictus*.

Species & Characters	<i>D. orientalis</i>	<i>D. javanus</i>	<i>P. (C.) praedictus</i> *
Intercoxal sclerite	Without outgrowth	Without outgrowth	With well-developed outgrowth
The right Exp-2			
Shape	Normal	Normal	Hollowing out posteriorly
Longitudinal ridge	Present	Present	Absent
Accessory lateral spine	Absent	Absent	Present mostly
The left Exp-2			
Ornamentation	With 6–10 denticles terminally	With one denticle on inner margin	With fan-like outgrowth (serrated free margin) on inner margin

**P. (C.) praedictus* Dumont & Ranga Reddy, 1994, is a representative of the subgenus *Phyllodiptomus (Ctenodiptomus)* sensu Dumont et al. (1996)

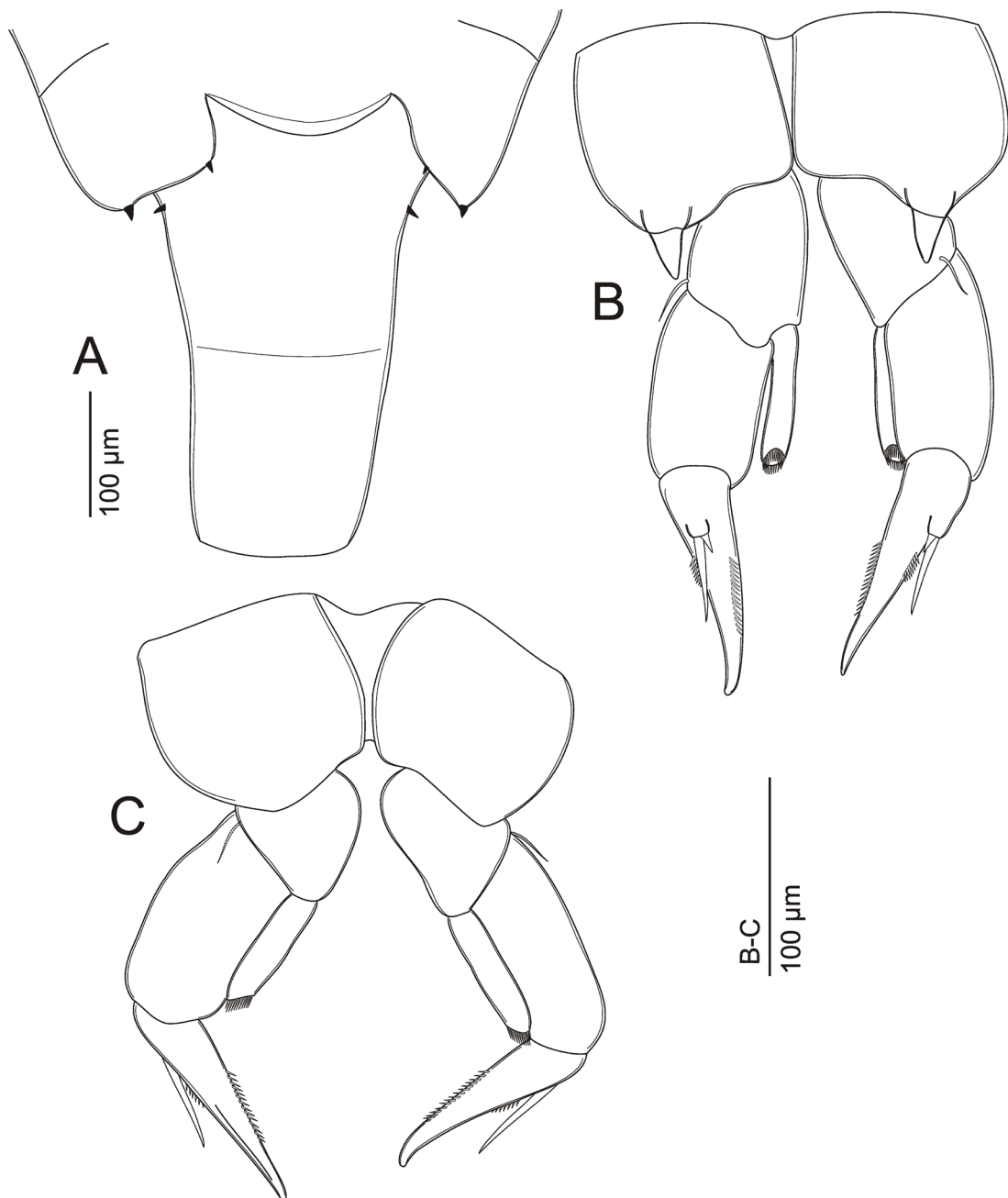


Fig. 7. *Dentodiptomus orientalis*, new species, female: A, pediger 5 and genital double-somite, dorsal view; B, P5, posterior view; C, P5, frontal view.

like structure distally instead of bearing two along the inner margin. Although the figure of *D. javanus* by Grochmalicki (1915: fig. 2) showed two knob-like structures on the P5 Exp-1, the Thai specimens of *D. javanus* share the same appearance as the new species (Figs. 2D, 8F). The left P5 Exp-2 of the new species has 6–10 inner distal denticles instead of one as in *D. javanus*. The presence of at least one ‘denticle’ or ‘tooth-like process’ (Figs. 5G, H, 8F) is a unique character that was used to distinguish the genus *Dentodiaptomus* by Shen & Tai (1964). The new species has an encircling row of 6–10 denticles on the sub-distal margin (Fig. 5G, H), showing a somewhat spinous serration similar to that observed in the subgenus *Phyllodiaptomus* (*Ctenodiaptomus*) Dumont, Ranga Reddy & Sanoamuang, 1996 (see Table 2); however, those serrations are located along the inner margin in *Phyllodiaptomus* (Dumont et al., 1996; Guinto et al., 2018). Ranga Reddy (2013) noted that it should not be surprising when species are found to share characteristics (i.e., synapomorphy) with some members of other genera. The sharing of synapomorphies found in species of different genera probably revealed their evolutionary relationship, including *Dentodiaptomus* and *Phyllodiaptomus* (*Ctenodiaptomus*).

Previous workers who revised diaptomid genera demonstrated special interest in the component of the male right P5 Exp-2, thus resolving a gap in generic diagnoses (Dumont & Ranga Reddy, 1993, 1994; Ranga Reddy et al., 2000; Tran & Brancelj, 2017). *Dentodiaptomus* has only one outer principal spine raised from the distal half of the Exp-2. Between the two species, *D. orientalis*, new species, has a principal lateral spine close to the end claw (similar to species of *Eodiaptomus* Kiefer, 1932), whereas in *D. javanus* it is inserted at the distal third of the length of its segment (similar to those of *Tropodiaptomus*). Two distinct characteristics in the male right P5 of this genus are (1) the coxa is protruded at the outer distal corner into a large lobe, and (2) the Exp-2 has a longitudinal ridge on its posterior surface which is terminated by the adjacent insertion of the principal lateral spine. This ridge is not observed in other genera and is very useful for discriminating *Dentodiaptomus* from all other diaptomids.

On the interspecific distinctions within *Dentodiaptomus*.

Currently, the genus *Dentodiaptomus* contains only two species, viz., *D. javanus* and *D. orientalis*, new species. The new species can be differentiated from its congener by the following characters. The male P5: (a) the right coxa has a small, triangular posterior lobe (Fig. 2B) [versus a large, rectangular lobe in *D. javanus* (Fig. 8B, D)]; (b) the right basis has no hyaline lamella on the inner margin (Fig. 2B) (versus present in *D. javanus*) (Fig. 8B, C)]; (c) the principal lateral spine is inserted near the distal end of the Exp-2 segment, close to the end claw (Fig. 2B) [versus inserted at 1/3 length of the outer margin in *D. javanus* (Fig. 8B, C)]; (d) the end claw is shorter and stouter (Figs. 2B, 5E) than that in *D. javanus* (Fig. 8B, C); and, (e) the left Exp-2 has 6–10 denticles terminally (Fig. 5G, H) [versus only one denticle at inner margin in *D. javanus* (Fig. 8F)]. The female: (a) the genital double-somite is slightly expanded

at the proximal region, and the genital spine is located at the same level as the pediger 5 lateral wings [versus genital double-somite obviously expanded at the sub-proximal region, and genital spines located lower than pediger 5 lateral wings in *D. javanus*]; (b) the P5 coxa has a stout, blunt spine [versus acute coxal spine in *D. javanus*]; and, (c) the P5 Enp is long, almost reaching the distal tip of Exp-1 (Fig. 7B, C) [versus short, about 1/2 the length of Exp-1 in *D. javanus* (Sanoamuang, 2002: fig. 6-2)].

Regarding the Thai and Cambodian specimens of *D. javanus*, the right P5 in the male has a small coxal spine on both sides (Fig. 8B, D), which was missing in the descriptions and figures provided by Grochmalicki (1915), Brehm (1951), or Shen & Tai (1964). The distal end of the longitudinal ridge on the right P5 Exp-2 of the male either has a spinous process (Fig. 8E) or does not (Fig. 8B). The left P5 Enp in the male reaches slightly beyond Exp-1 (Fig. 8F), but it reaches half the length of Exp-2 in Chinese samples (Shen & Tai, 1964: figs. 12, 13), and has a slightly shorter Exp-1 in Indonesian samples (Grochmalicki, 1915: fig. 12d).

Geographic distribution. The genus *Dentodiaptomus* Shen & Tai, 1964, was previously a monospecific genus comprising only one taxon, *D. javanus* (Grochmalicki, 1915). The species was originally described from Java (Indonesia) as *Diaptomus javanus*. Forty-nine years later, it was used as the type species for the erection of the genus *Dentodiaptomus* from Chinese samples (Shen & Tai, 1964). It is currently found in southern China (Yunnan Province), Vietnam (Binh Phuoc and Gia Lai Provinces), Thailand (widely distributed in the northeastern region, but sporadic in the northern, eastern, and western regions) (Sanoamuang & Dabseepai, 2021), Laos (Vientiane), and Cambodia (Tonle Sap Lake and the floodplain of the lower Mekong River Basin) (Brehm, 1951; Shen & Tai, 1964; Sanoamuang, 1999, 2002; Tran et al., 2016; Li et al., 2018; the present study). After the report of Brehm (1951), the presence of *D. javanus* was confirmed by Chaicharoen (2011) in Pursat, Kampong Thom, and Stung Treng Provinces of Cambodia. Although *D. orientalis*, new species, was found in the same region as *D. javanus*, these two species have never been found together in the same locality. To date, *D. orientalis*, new species, is considered to be an endemic species of both Cambodia and Thailand (Fig. 1).

The distributional epicentre of *Dentodiaptomus* appears to be the Mekong River Basin, ranging from Xishuangbanna (the southernmost part of Yunnan Province, China) southward across Thailand, Laos, Cambodia, and southern Vietnam. The presence of *D. javanus* in Java, Indonesia is the only case outside this central area, which may be explained by accidental invasion by natural or human activities. Copepods are easily transported by humans, and many cases were documented by Reid (2001). In fact, *D. javanus* was not found in recent collections from Malaysia, Singapore, the Philippines, or even Java—all of which are outside the Mekong River Basin, which strongly supports our hypothesis that the distributional epicentre of this genus is the Mekong River Basin (Alekseev et al., 2013, 2016; Schmoker et al., 2014; Dela Paz et al., 2018).

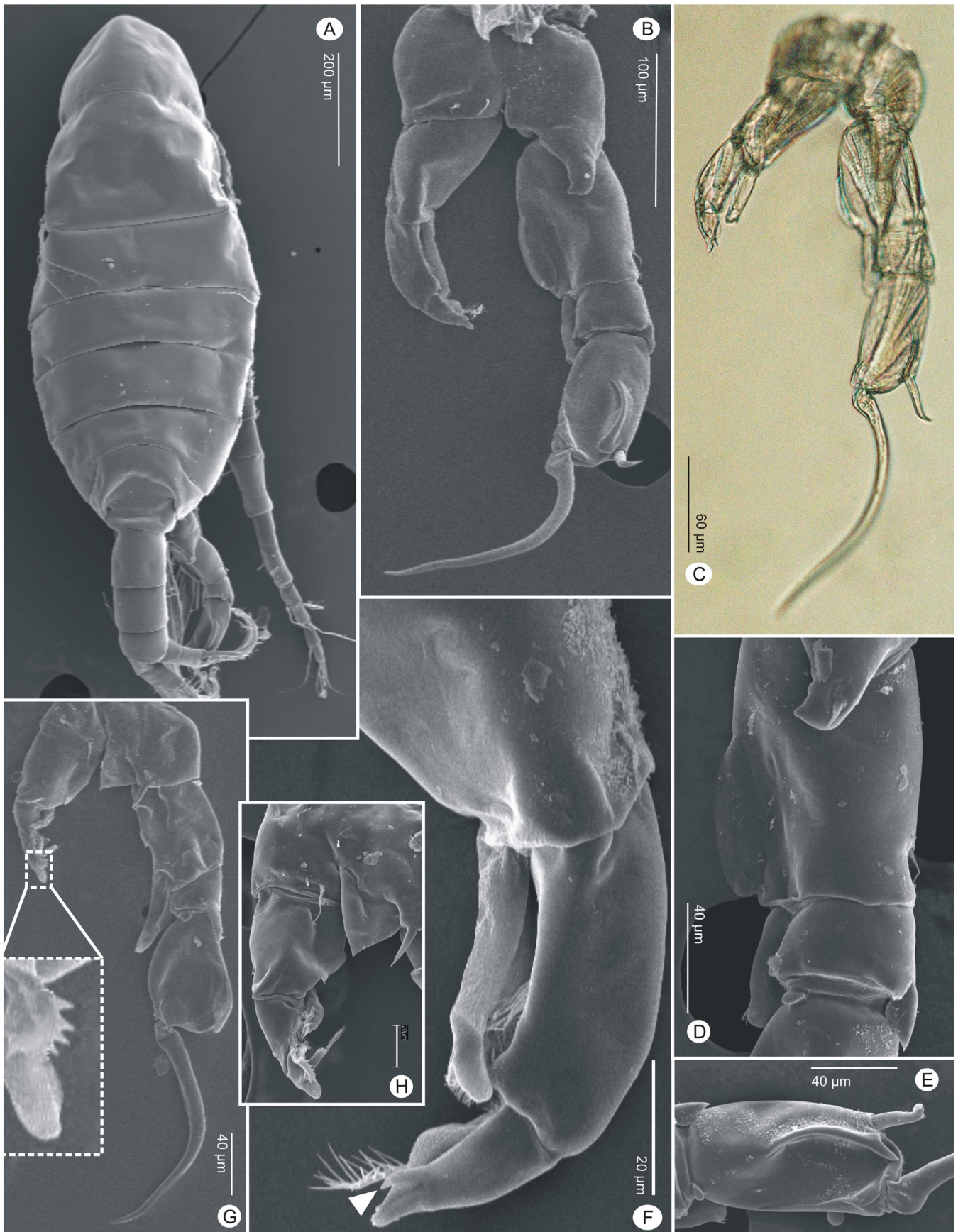


Fig. 8. *Dentodiptomus javanus* (A–F) and *Phyllodiptomus* (*Ctenodiptomus*) *praedictus* (G–H), male: A, habitus, dorsal view; B, C, G, P5, posterior view; D, right P5 basis and Exp-1, posterior view; E, right P5 Exp-2, posterior view; F, left P5 basis, Exp (white arrow points to a denticle on the inner margin of the Exp-2), and Enp, frontal view; H, intercoxal sclerite and left P5, posterior view.

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