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A new species of *Tmethypocoelis* Koelbel, 1897 (Crustacea: Decapoda: Brachyura: Dotillidae) from Ambon Island, Indonesia

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Abstract. A new species of intertidal dotillid crab in the genus *Tmethypocoelis* Koelbel, 1897, is described from Ambon Island, Maluku Archipelago, Indonesia. This is the fourth species of *Tmethypocoelis* to be described from Indonesian waters. *Tmethypocoelis* is restricted to the central tropical Indo-West Pacific region from the South China Sea to north-western Australia. *Tmethypocoelis malukensis*, new species, differs most obviously from its seven other congeners by a combination of male chela, pleon, and G1 characters.

Key words. dotillid crabs, estuarine, intertidal, Maluku Archipelago

INTRODUCTION

Species of the genus *Tmethypocoelis* Koelbel, 1897, are typically small and inconspicuous intertidal estuarine crabs found on mud or sandy-mud banks, and despite being relatively widespread, they have been largely overlooked and under-collected. *Tmethypocoelis* species are only known from the tropical central Indo-West Pacific region from the South China Sea southwards to north-western Australia.

The type species of the genus, *Dioxippe* (*Tmethypocoelis*) *ceratophora* Koelbel, 1897, was first described from Hong Kong in 1897, and the genus was considered monotypic until 1990. *Tmethypocoelis ceratophora* (Koelbel, 1897) as it is now known, is also found in other parts of China and Taiwan (Huang et al., 1992; Davie & Kosuge, 1995; Shih et al., 2015). Since 1990, six more species have been described: *T. koelbeli* Davie, 1990, from the Northern Territory, Australia; *T. odontodactylus* Davie, 1990, from north-eastern New Guinea (Davie, 1990; Davie & Kosuge, 1995); *T. choreutes* from the Ryukyu Islands, Japan (Davie & Kosuge, 1995); *T. liki* Murniati, Asakura, Nugroho, Hernawan & Dharmawan, 2022, from Papua, Indonesia (Murniati et al., 2022); *T. celebensis* Murniati, Asakura & Davie, 2023, and *T. simplex* Murniati, Asakura & Davie, 2023, both from Sulawesi, Indonesia (Murniati et al., 2023). We here describe a further new species from Ambon in the Maluku (= Moluccas) Archipelago, Indonesia. All species show narrow allopatric vicariant distributions, with *T. ceratophora* living across the widest area, within the southern China and Taiwan region (Shih et al., 2015). The species are all outwardly similar in morphology, but separable using male chela, pleon and gonopod characters. Speciation seems to have been driven by the complex palaeogeography of the Indonesian Archipelago that has affected modern circulation patterns and consequently restricted dispersal capability (Davie & Kosuge, 1995; Murniati et al., 2023).

The present work is the result of larger ongoing studies of intertidal crabs throughout the broader region by both authors. Additional new species of *Tmethypocoelis* will be proposed in a forthcoming paper (in preparation), and genetic data supporting the separation and recognition of the numerous species will also be presented at that time.

MATERIAL AND METHODS

This study was conducted on preserved specimens collected by the Rumphius I expedition in 1973 from the Galala estuary, Ambon (Fig. 1). Other brachyurans collected by this expedition have already been reported by Serène et al. (1974). Attempts to collect fresh material from the Galala estuary in September 2024, to enable genetic analyses, were unsuccessful.

Morphological terms follow those of Davie et al. (2015). Measurements are given in millimetres (mm) of carapace width (cw) measured at the widest point, and carapace length (cl) measured from the mid-front to the mid-posterior margin; G1 = male first gonopod; P2–P5 = pereopods 2–5 (walking legs 1–4); Pl1–Pl6 = pleonites 1–6. Drawings were made by hand using a microscope camera lucida, and several were enhanced using a Wacom drawing pad and Adobe Illustrator CC2015 software.

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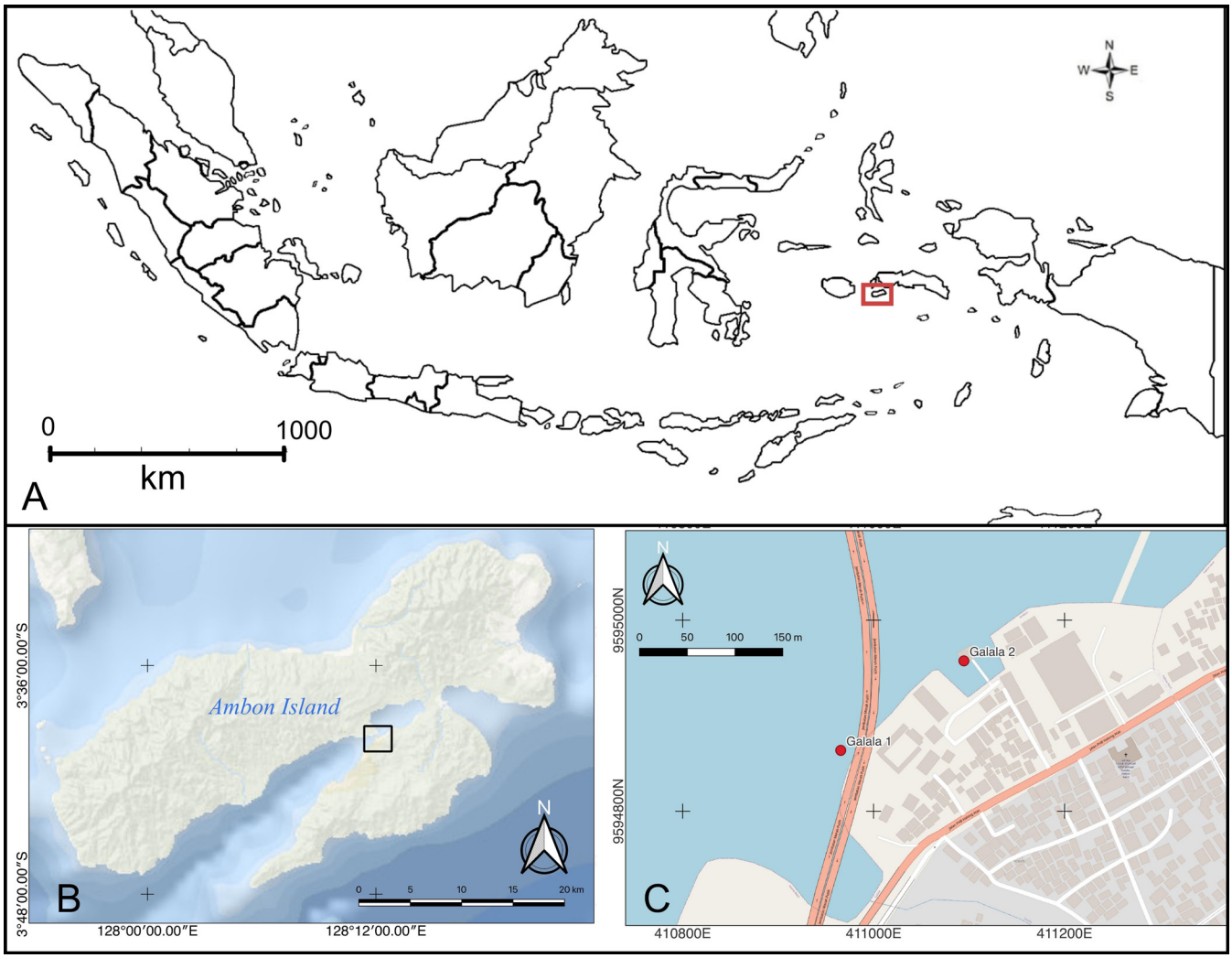

Fig. 1. A, General map of Indonesia, showing location of Ambon Island (red rectangle). B, Map of Ambon Island showing location of Galala Village (black rectangle). C, Map of Galala Village showing the 2 collection sites (red dots). Source: Geospatial Information Agency, Indonesia.

Specimens are deposited in the following repositories: Directorate of Scientific Collection Management, National Research and Innovation Agency, Cibinong, Bogor, Indonesia (under MZB registration numbers), and Queensland Museum, Brisbane (QM).

TAXONOMY

Superfamily Ocypodoidea Rafinesque, 1815

Family Dotillidae Stimpson, 1858

Genus *Tmethypocoelis* Koelbel, 1897

Dioxippe (*Tmethypocoelis*) Koelbel, 1897: 715. — Koelbel, 1898: 574.

Tmethypocoelis – Shen, 1935: 33. — Sakai, 1939: 643; 1976: 625. — Davie, 1990: 463; 2002: 347. — Dai & Yang, 1991: 495. — Huang, Yu & Takeda, 1992: 150 (key), 154. — Wada, 1995: 415 (key). — Davie & Kosuge, 1995: 208. — Ng et al., 2008: 235. — Shih et al., 2015: 61.

Tmethypocoelis malukensis, new species

(Figs. 2; 3A, B; 4A–C)

Material examined. Holotype, male (8.2 × 4.9 mm) (MZB.Cru.7340; = RCO.CRU (unreg.)), Serène Reference Collection BR609, Ambon, Indonesia, Rumphius Expedition I, Stn WR-3, coll. R. Serène, 24 January 1973.

Paratypes, 2 males (6.9 × 4.1 mm, 7.1 × 4.2 mm) (MZB. Cru.6636; = RCO.CRU.1093), Galala, Ambon Island, coll: R. Serène, 14 February 1973. 2 males (7.5 × 4.2 mm, 8.2 × 4.9 mm) (QM-W55126), Serène Reference Collection BR609, Ambon, Indonesia, Rumphius Expedition I, Stn WR-3, coll. R. Serène, 24 January 1973. 7 males (3.7 × 2.4 mm – 6.3 × 3.9 mm) (QM-W55127), Ambon, Rumphius Expedition I, Stn O-2, coll. R. Serène, 24 January 1973.

Comparative material. *Tmethypocoelis celebensis* Murniati, Asakura & Davie, 2023, paratypes, 4 males (7.3 × 3.8 mm – 7.4 × 4.3 mm) (MZB.Cru.5576), 1°05′31.0″S, 120°33′39.6″E, Maleyali, Sausu, Parigi Moutong, Central Sulawesi, coll. DC. Murniati, Muslihun, M. Ikram, 25 June 2021. *Tmethypocoelis liki* Murniati, Asakura, Nugroho, Hernawan & Dharmawan,

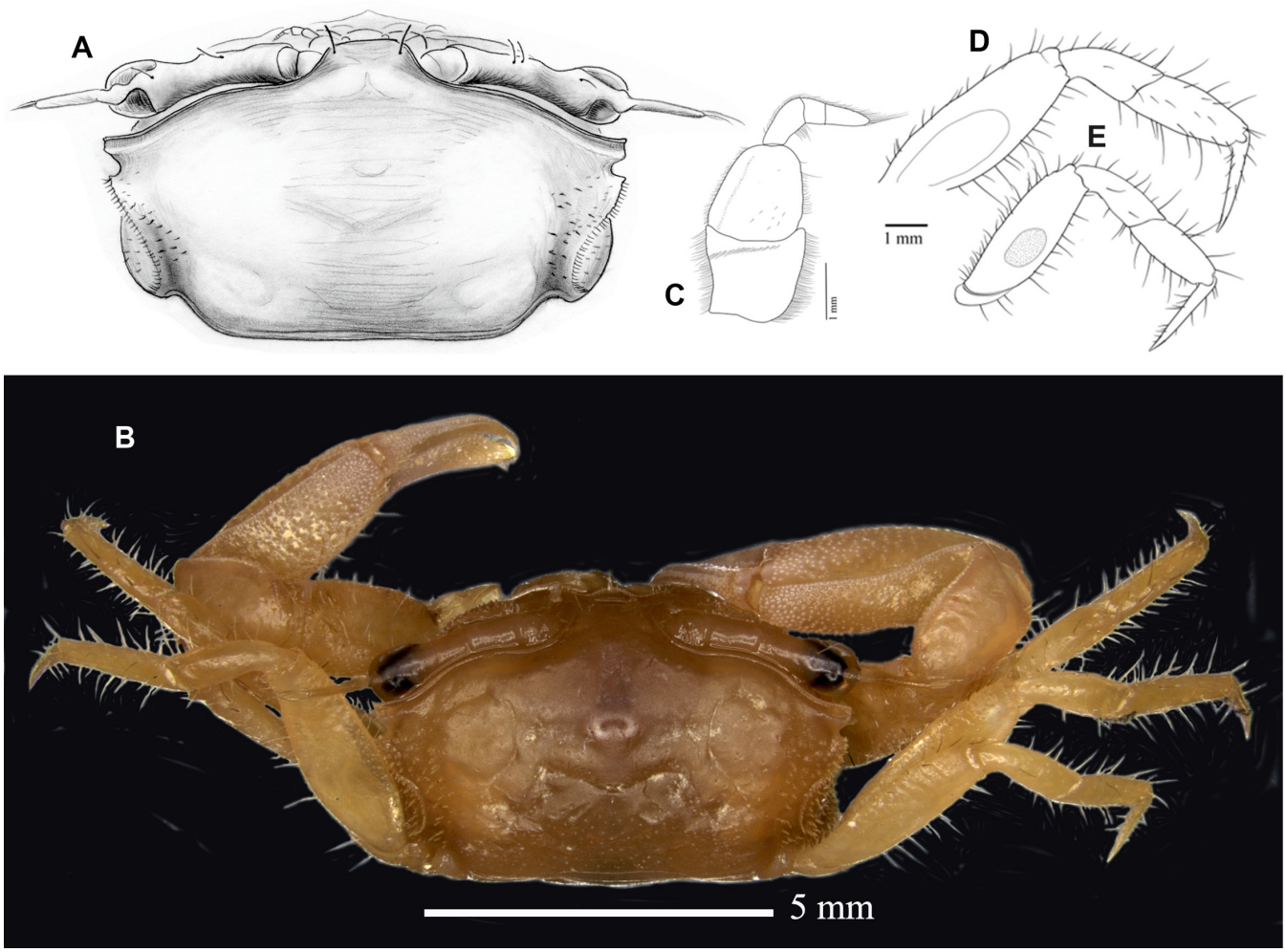

Fig. 2. *Tmethypocoelis malukensis*, new species, A, holotype male (8.2 × 4.9 mm) (MZB.Cru.7340); B, C–E, paratype male (7.1 × 4.2 mm) (MZB.Cru. 6636). A, carapace in dorsal view; B, whole crab in dorsal view; C, left third maxilliped; D, left P4; E, left P5.

2022, paratypes, 5 males (5.3 × 3.1 mm – 5.5 × 3.2 mm) (MZB.Cru.5012), 01°37′25.29″S, 138°44′26.54″E, Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, coll. DC. Murniati, 21 November 2018. *Tmethypocoelis simplex* Murniati, Asakura & Davie, 2023, paratypes, 3 males (4.0 × 2.5 mm – 7.9 × 4.6 mm) (MZB. Cru.5182), 0°43′29.3″S, 119°40′43.9″E, Towale River, Central Banawa District, Donggala, Central Sulawesi, coll. DC. Murniati, D. Permatasari, Hairul, A. Padju, 17 September 2020.

Diagnosis. Carapace subpentagonal, 1.7 times wider than long. Lateral branchial margin converging posteriorly, recurved; protobranchial, mesobranchial and metabranchial regions well defined. Sub-branchial region inflated, bearing regular setae and tubercles. Posterior margin slightly concave, c. 0.57 times distance between exorbital angles. Exorbital angle triangular, acute, directed forward. Epibranchial tooth curved, shorter than exorbital angle. Male pleon twice as long as wide. Male chelipeds long; palm bulky, 1.4 times longer than wide; fingers shorter than palm; pollex short, triangular, cutting margin slightly convex over entire length, without differentiated tooth or lobe; dactylus cutting margin evenly dentate; one enlarged long tooth over proximal half; upper margin with 1 median row of granules in simple row, narrower distally. G1 long, curved, very slender; apical portion forming two poorly defined lobes, with 2 conspicuous curved setae on outer margin becoming slightly longer distally, 2 long setae apically, and 4 short setae on inner margin.

Description. Carapace (Figs. 2A, B) subpentagonal; slightly convex along mid-dorsal line, slightly convex laterally; 1.7 times wider than long. Dorsal surface smooth, lateral portion with granules, regions semi-defined. Cervical groove well-marked; cardiac region with slight central depression. Branchial margin converging posteriorly, recurved; protobranchial, mesobranchial, and metabranchial regions well defined. Sub-branchial region inflated, bearing regular setae and tubercles. Intestinal and branchial border poorly defined. Lateral margin recurved, with row of tubercles and short stout setae. Posterior margin slightly concave, c. 0.57 distance between exorbital angles; fine ridge parallel to posterior margin forming broad rim. Front with lateral border moderately converging, width at base c. 0.19 times distance between exorbital angles, 0.13 at anterior margin; frontal angle rounded; anterior margin with small central blunt prominence. Carapace widest between exorbital angles. Exorbital angle triangular, acute, directed forward; anterior margin with microscopic tubercles, lateral margin glabrous; one short tubercular ridge parallel to supraorbital margin; posteriorly followed by broad U-shaped sinus. Epibranchial tooth slightly curved, shorter than exorbital

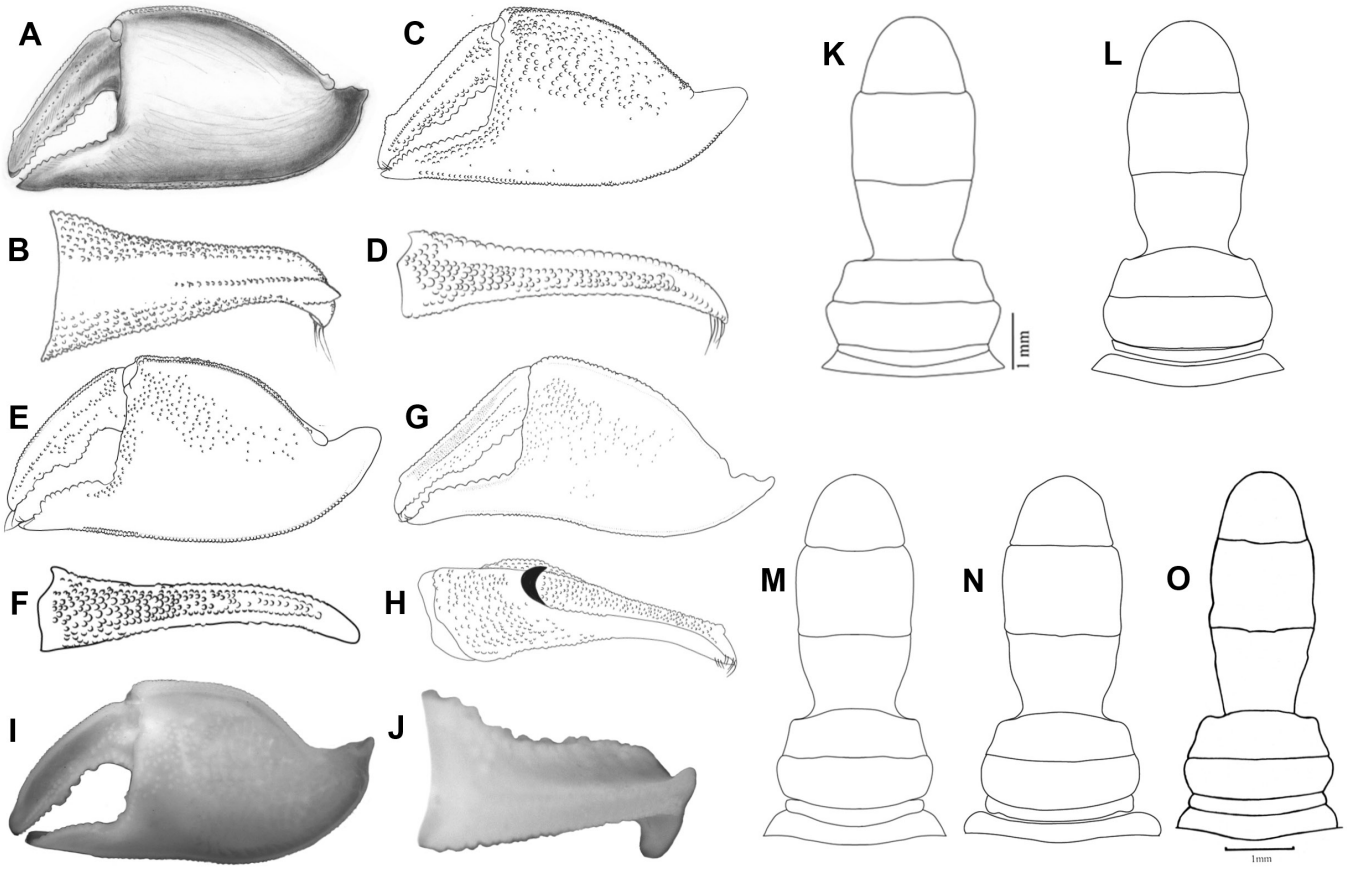

Fig. 3. Male chela (frontal view and dorsal view of dactylus respectively) and male pleon for five species of *Tmethypocoelis*. A, B, *T. malukensis*, new species, holotype, male (8.2 × 4.9 mm) (MZB.Cru.7340); K, paratype, male (7.1 × 4.2 mm) (MZB.Cru. 6636): C, D, L, *T. celebensis*, holotype, male (7.4 × 4.3 mm) (MZB.Cru.5574); E, F, M, *T. simplex*, holotype, male (7.7 × 4.4 mm) (MZB.Cru. 5573): G, H, N, *T. liki*, holotype, male (6.2 × 3.5 mm) (MZB.Cru.5011): I, J, O, *T. koelbeli*, paratype, male (7.3 mm cw) (QM W7982). Figures C–F, L, M after Murniati et al. (2023); G, H, N, after Murniati et al. (2022); I, J, O after Davie (1990).

angle. Posterolateral facet well-defined by crest originating anteriorly from base of exorbital angle. Orbital margins with usual form within the genus.

Eyestalks long, not reaching exorbital angle, medial and distal diameters of similar width; ocular style longer than cornea, tipped with setae; medial slope giving twisted appearance; cornea slightly bulging (Figs. 2A,B).

Third maxillipeds (Fig. 2H): ischium subquadrate, outer surface with numerous long setae, one oblique row of long setae near upper margin, upper margin concave, upper-mesial angle with narrow, rounded lobe; lower-mesial angle curved; inner and lower margins with dense setae; lateral margin without setation. Merus slightly larger than ischium, c. 1.3 × longer; outer surface with regularly scattered short setae; lateral margin convex, narrower distally, covered with sparse short setae; mesial margin straight with long setae. Carpus trihedral, subequal in length to propodus and dactylus together; mesial margin and distal portion with long dense setae. Propodus shorter than dactylus; margins entire, with long dense setae. Dactylus slender, with long dense setae laterally.

Male pleon (Fig. 3I): Pl1 trapezoidal, narrow, c. 8.5 × wider than long; anterior margin c. 0.7 × as long as posterior margin; c. 1.3 × wider than Pl2. Pl2 c. 8.6 × wider than long. Pl3 c. 3.4 × wider than long, anterior margin nearly straight, posterior margin convex. Pl4 c. 2.9 × wider than long, widest proximally, narrowing distally, distolateral angle pointed. Pl5 c. 1.5 × wider than long (widest distally), markedly constricted at base. Pl6 ca. 1.35 × wider than long; widest sub-distally; similar length to Pl5; lateral margins subparallel, slightly concave. Male telson rounded, c. 1.3 × wider than long.

Male chelipeds (Figs. 2C–E; 3A, E) stout, long, equal. Carpus shorter than merus, elongate, 1.5 times longer than wide. Palm bulky, 1.4 times wider than long; upper margin with one row of granules, distinct groove extending below granular rows forming clear granular string; lower margin with granules branched into two rows across medial to distal portion; inner surface irregularly granular, upper granulation extending over median portion, curved to sharply defined upper margin of outer surface and base of fingers, lower granulation not extending to base of pollex; outer surface distinctly granular over upper half to base of pollex, lower half scarcely granular. Fingers shorter than palm, broadly gaping at base; curved inwards, expanded distally to form spooned tip; inner margin at tip of both fingers with short row of stout setae. Pollex short, triangular, cutting margin evenly dentate; 0.4 times as wide as palm; inner surface smooth; outer surface with granular row parallel to cutting margin; lower margin defined, granular nearly whole

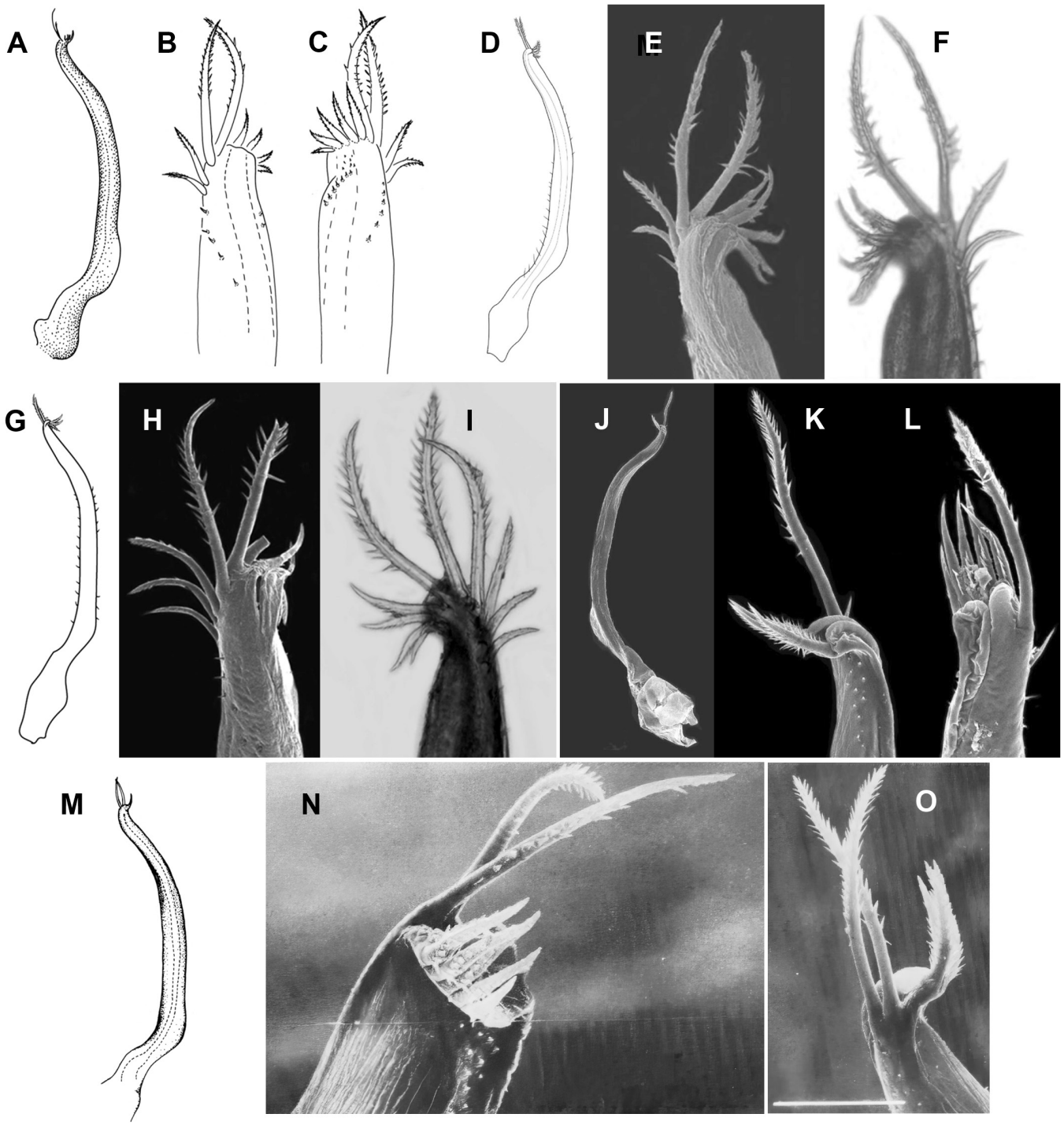

Fig. 4. G1 of five species of *Tmethypocoelis* including enlarged pleonal and sternal views of tip. A–C, *T. malukensis* new species, holotype, male (8.2 × 4.9 mm) (MZB.Cru.7340): D–F, *T. celebensis*, paratype, male (7.3 × 4.4 mm) (MZB.Cru.5180); G–I, *T. simplex*, paratypes, male (4.1 × 2.6 mm) (G, H), (6.9 × 4.0 mm) (I) (MZB.Cru. 5183): J–L, *T. liki*, paratypes, males (5.1 × 3.2 mm) (J–K), (5.0 × 3.0 mm) (L) (MZB.Cru.5012): M–O, *T. koelbeli*, paratype, male (7.3 mm cw) (QM W7982). Figures D–I after Murniati et al. (2023); J–L after Murniati et al. (2022); M–O after Davie (1990).

length. Dactylus 0.8 times as wide as palm; cutting margin unevenly dentate over distal half; one enlarged wide low triangular tooth over proximal half, becoming only weakly discernible in largest specimens (compare Figs. 2C, D); inner surface granular from proximal to median portion near cutting margin, one clutch of granules proximally near upper margin; outer surface with one row of granules near upper margin, densest on proximal portion of surface, granulation extending nearly whole length, irregular granulation near cutting margin; upper margin straight with median row of granules, narrower distally matching shape of upper margin, granulation extending ⅘ length of upper margin ending in small triangular subdistal prominence only evident in largest specimens (Fig. 3E).

Pereiopods slender, elongate (Figs. 2B, F, G); P2–P5 similar; smooth ovate tympanum on anterior and posterior surfaces of meri. Tympani on posterior surfaces becoming

Table 1. Comparison of G1 apical setation of all described *Tmethypocoelis* species.

Group 1 (G1 with apical coronet of similar setae; none unusually elongated)	
*T. ceratophor*a (Koelbel, 1897)	forming two lobes, with fan of 8 serrated and stout setae; inner sternal lobe with 3 setae of similar length; outer pleonal lobe with 5 slightly shorter setae also of similar length (Davie & Kosuge, 1995, fig. 2A, B)
T. choreutes Davie & Kosuge, 1995	forming two lobes, with fan of 11–12 serrated and stout setae. Inner sternal lobe with 6 setae becoming shorter and strongly recurved laterally, and flared away from the terminal aperture; outer pleonal lobe with 6 setae of more even length (Davie & Kosuge, 1995, fig. 2C, D)
T. odontodactylus Davie, 1990	fan of 8–9 serrated, stout setae, setae longest medially, progressively shorter and more recurved either side (Davie, 1990: fig. 3E–G)
Group 2 (G1 with very elongated apical setae)	
T. koelbeli Davie, 1990	2 long apical setae, but lacking row of outer subapical setae; inner margin with row of 5 short distally pointed setae (Fig. 4M–O, after Davie, 1990: fig. 2)
T. simplex Murniati, Asakura, & Davie, 2023	3 very long apical setae; subapically 3 shorter stout setae on outer margin increasing in length distally; 4 short, downwardly reflexed setae on inner margin (Fig. 4D, E, F, after Murniati et al., 2023)
T. celebensis Murniati, Asakura, & Davie, 2023	2 very long recurved apical setae; subapically 3 stout setae on outer margin (proximal seta much smaller than in *T. simple*x); 4–5 short, downwardly reflexed setae on inner margin (Fig. 4G, H, I, after Murniati et al., 2023)
*T. malukensi*s, new species	apically with 2 long setae medially; 2 short setae on outer margin, longer distally, both setae distinctly shorter than median setae; 4 short setae on inner margin, slightly curved, distinctly shorter than median setae (Fig. 4A–C)
T. liki Murniati, Asakura, Nugroho, Hernawan & Dharmawan, 2022	one long and five short apical setae (Fig. 4J,K,L, after Murniati et al., 2022, fig. 20)

progressively smaller from P2–P5. Dactyli nearly straight, pointed, shorter than propodi.

G1 (Figs. 3M, N, O), long, curved, slender; with sub-proximal bulge; apically with 2 long setae medially; 2 short setae on outer margin, longer distally, both setae distinctly shorter than median setae; 4 short setae on inner margin, slightly curved, distinctly shorter than median setae.

Habitat. The intertidal estuarine habitat around Galala Village comprises sandy to muddy substrates and thus is similar to the environments that *Tmethypocoelis* species normally inhabit. The fiddler crab, *Austruca perplexa* (H. Milne Edwards, 1852), was the dominant species in the area, but unfortunately there no longer appears to be an extant population of *Tmethypocoelis*. Over the 52 years since the type material for the new species was collected, the area has undergone massive development. A large bridge was built in 2011 across the inner bay to connect Rumah Tiga Village to the north and Hative Kecil Village to the south, requiring large foundations to be built in the Galala estuarine. All this activity has resulted in massive domestic pollution, high sedimentation, repeated flooding and shore erosion and abrasion (e.g., Smeets et al., 2023; pers. com. with the local people). Therefore, we cannot be certain of the exact sediment characteristics that *T. malukensis* requires. In 1990, the Rumphius Biohistorical Expedition to Ambon successfully collected marine and estuarine invertebrates, including brachyuran crabs (Strack, 1993), however there were no new collections of *Tmethypocoelis*. Broader regional surveys are needed to find populations in less disturbed environments elsewhere on Ambon and surrounding islands.

Distribution. *Tmethypocoelis malukensis*, new species, is so far only known from Ambon Island, though it will presumably be found on other islands in the Maluku Archipelago (= Moluccas), an island group in the eastern part of Indonesia. The palaeogeography of this area is complex with several tectonic plates meeting at the Molucca Sea Collision Zone (Hall & Spakman, 2003). Ambon is located on the Halmahera Plate but the importance and impact of this to the vicariant speciation of intertidal crabs needs further study. This will be discussed in more detail as part of a revision of the entire genus (Murniati & Davie, in prep.).

Etymology. The new species is named after the Maluku Islands (= Moluccas) where the species appears to be endemic; used as an adjective.

Remarks. The species of *Tmethypocoelis* are all generally similar in overall appearance, however there are a number of small but consistent morphological differences that support species differentiation, and this has been discussed previously (Davie & Kosuge, 1995; Murniati et al., 2023). Tables 1–3 present a comparison of the most useful morphological characters separating *T. malukensis*, new species, from

Table 2. Comparison of adult male cheliped characters of all described *Tmethypocoelis* species.

Species	Dactylus dorsal armature	Dactylus cutting margin	Polex cutting margin	Chela palm length to width	Gape at base of fingers	Carpus length to breadth
T. ceratophora	finely tuberculate ridge on upper margin of dactylus terminating in outwardly directed flat triangular tooth (see Davie & Kosuge, 1995 Fig. 1 A, C)	one small low tooth proximally	prominent enlarged convex tooth medially	1.7	wide	1.8
T. choreutes	finely evenly tubercular ridge not terminating in outwardly directed tooth; outer surface with subdorsal ridge ending in prominent triangular subdistal lateral protrusion (see Davie & Kosuge, 1995 Fig. 1 B, D)	low broad triangular convexity, but lacking clearly differentiated tooth	lacking a defined tooth; slightly convex	1.3	not strongly developed	1.3
T. odontodactylus	full length medial granulate ridge; superior granulate crest terminating subdistally in strong upturned tooth (Davie, 1990, fig. 3C)	evenly dentate; slightly deeper medially, but without obvious differentiated tooth	weakly convex; evenly dentate	1.5	not strongly developed	1.5
T. koelbeli	dorsal band of fine granules; superior border straight, terminating in overhanging triangular tooth at about ¾ length; outer surface with two subregular lines of granules, superior one may extend ¾ length to tip, lower one a little less (Fig. 3I, J)	evenly dentate; smaller males with raised platform of teeth differentiated in proximal half, but less evident in mature chela.	evenly dentate	1.3	moderate	subquadrate
T. simplex	finely tuberculate; lacking differentiated subdistal tooth; outer surface with semi-defined granular row medially; irregular granulation near cutting margin (Fig. 3E, F)	evenly dentate; one wide enlarged convex tooth over proximal half	evenly dentate; long flat enlarged dentate tooth over most of length.	1.4	wide	1.5
T. celebensis	finely tuberculate; culminating in subdistal upward upwardly projecting triangular tooth of variable size from high and distinct to low—size not correlated with crab size; outer surface with medial granular row over full length; (Fig. 3C, D)	evenly dentate, larger over proximal half, then finger narrower over distal half	evenly dentate; straight, without differentiated tooth or lobe	1.3	poorly developed	1.4
T. malukensis, new species	upper margin straight with median row of granules, narrower distally; granulation extending 4/5 length of upper margin ending in small triangular subdistal prominence only evident in largest specimens (Fig. 3A, B)	unevenly dentate over distal half; one enlarged wide low triangular tooth over proximal half, becoming only weakly discernible in largest specimens	slightly convex over entire length, evenly dentate, without differentiated tooth or lobe	1.4	moderate	1.5

Species	Dactylus dorsal armature	Dactylus cutting margin	Polex cutting margin	Chela palm length to width	Gape at base of fingers	Carpus length to breadth
T. liki	outer surface bearing one median ridge of granules; upper margin with median row of granules culminating in one relatively small tooth (Fig. 3G, H)	evenly dentate; low raised dentate lobe medially	evenly dentate; smaller males with raised platform of teeth differentiated in proximal half	1.6	not strongly developed	2.2

all other known congeners. Individually, some character differences may not seem great, but in combination they clearly point to the necessary recognition of the new species here described.

The morphology of the male G1 is widely used in species separation. In *Tmethypocoelis* there appears to be two clearly discrete morphological groups based on apical setation patterns. The first group, *T. ceratophora*, *T. choreutes*, and *T. odontodactylus,* all have a coronet of shorter, more evenly sized, stout setae on the tip of the G1 (Davie, 1990, fig. 3E–G; Davie & Kosuge, 1995: fig. 2), whereas *T. malukensis*, new species, falls into the second group that all have one to three markedly elongated apical setae (*Tmethypocoelis simplex*, *T. celebensis*, *T. liki* and *T. koelbeli*) (Fig. 4; also Davie, 1990: fig. 2; Murniati et al., 2022: fig. 20; Murniati et al., 2023: figs 8C–E, 16C, D). Therefore, further morphological comparisons will relate only to this second group of four species.

Of this second species-group, *T. malukensis*, new species, is immediately separable from *T. liki* because that species has only one long and five short apical setae (Fig. 4, J, K, L; Table 1). It is further separable from *T. koelbeli* because that species lacks a row of outer subapical setae and the inner margin has a row of 5 short, distally pointed setae (Fig. 4M–O; also Davie, 1990: fig. 2) versus 4 in *T. malukensis*, new species. The G1 of *T. malukensis*, new species, most closely resembles those of *T. celebensis* and *T. simplex* in terms of setation. All have three separate rows of different sized setae, situated on the outer, inner and apical margins, but the number and length of these setae are consistent and diagnostic of each species (Fig. 4A–I) These differences are detailed in Table 2. In particular: *T. simplex* has 3 very long apical setae (one broken near base in Fig. 4H) versus 2 in both *T. celebensis* and *T. malukensis*, new species; the 2 apical setae are longer in *T. celebensis* than in *T. malukensis*, new species; both *T. simplex* and *T. celebensis* have 3 stout subapical setae on the outer margin versus only 2 in *T. malukensis*, new species; and finally, the 4 short setae on the inner margin of *T. malukensis*, new species are directed anterolaterally (Fig. 4A–C) rather than reflexed downwards as in the other two species.

The chela of adult male *T. malukensis*, new species (Fig. 3A) differs from those of *T. celebensis* (Fig. 3C) and *T. koelbeli* (Fig. 3I) in having only a weakly developed gape between the base of the fingers (versus well developed gape in those two species), but in this regard is similar to *T. simplex* (Fig. 3E) and *T. liki* (Fig. 3G). It can be easily differentiated from *T. liki* because that species has proportionately longer fingers, a concave lower palm margin, and a raised subdistal tooth platform on the cutting margin of the pollex (Fig. 3H). The dactyli of larger *T. malukensis* have a small but definite triangular subdistal tooth (Fig. 3B) which is more prominent than in either *T. simplex* (Fig. 3E) or *T. celebensis* (Fig. 3D), but also much smaller than that of *T. koelbeli* (Fig. 3J).

The male pleon also differs slightly in proportions between the five species (Table 3; Figs. 3K–O), but this is more

Table 3. Comparison of male pleonal somite proportions of *Tmethypocoelis* species.

Species	Pleonite 5 width/ length	Pleonite 5 narrowest proximal width to distal width	Ratio length of Pl 6 to Pl 5	Pleonite 6 width/ length	Telson width/ length
T. ceratophora	1.0	0.74	1.1	1.4	1.5
T. choreutes	1.6	0.65	1.25	1.3	1.4
T. odontodactylus	1.5	0.75	1.1	1.2	1.2
T. koelbeli	1.3	0.7	1.1	1.2	1.2
T. simplex	1.5	0.7	1.1	1.4	1.4
T. celebensis	1.5	0.72	1.1	1.5	1.4
T. malukensis, new species	1.5	0.68	1.2	1.35	1.3
T. liki	1.5	0.71	1.2	1.3	1.5

difficult to apply diagnostically except for *T. koelbeli* which has an obviously narrower pleon, exemplified by a pleonite 5 width/length ratio of 1.3 versus 1.5 in the other four species. Compared to the other three species: *T. malukensis* has a slightly narrower telson (c. 1.3 times length versus 1.4 times); and Pl6 is 1.35 times wider than long versus 1.4 in *T. simplex*, 1.5 in *T. celebensis* and 1.3 in *T. liki*.

DISCUSSION

While the differences between species may seem relatively small, and in the past may have been considered simply intra-specific variation, our work on the genus has shown that the degree and consistency of these differences agrees with described species whose separation has been fully supported by other lines of evidence (e.g., behaviour, feeding morphology, etc. given by Davie & Kosuge, 1995, and Murniati et al., 2023, respectively). Further to this, a preliminary genetic study (Murniati et al., in prep.) has found significant COI intraspecies divergence values (K2P distance) that support and validate the morphological data, and show that there has been allopatric speciation throughout the region with no overlap in ranges. Our unpublished data show K2P distances of 10% between the morphologically similar, and adjacently occurring, *T. celebensis* and *T. simplex*, and as much as 17% between *T. celebensis* and the type of the genus, *T. ceratophora*. An upcoming paper (Murniati & Davie, in prep.) will present the genetic data for the majority of *Tmethypocoelis* species and propose a vicariant biogeographic model of speciation for the Indonesian archipelago and the broader region wherein this genus occurs. It is unfortunate that no sequences have been obtained from the present *T. malukensis* material, and that efforts to get fresh material has so far been unsuccessful, but we are confident that future sequence data, when it is obtained, will support the validity of the morphological decision made here.

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