

A NEW INGOLFIELLID AMPHIPOD CRUSTACEAN FROM SANDY BEACHES OF THE GURA ICI ISLANDS, WESTERN HALMAHERA (NORTH MOLUCCAS)

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ABSTRACT. — *Ingolfiella moluccensis*, a new species of ingolfiellid amphipod (Ingolfiellidae), is described from coarse coral sands of the Gura Ici islands (northern Moluccas; Indonesia). The species is unique among ingolfiellideans in the display of a rounded outgrowth on the proximo-lateral margin of basis of P5, and of a sexually-dimorphic, modified medial margin of coxa in the same limb. Other features point to close affinities with a group of seven insular species that show a broad but punctuated distribution along the Atlantic and SW Pacific oceans. These species share the combined display of four denticles on the posterior margin of dactylus of G1 & G2; three comb rows of denticles on the medial margin of the protopod of U2; a trifid unguis of P3–P4; and a bifid unguis of P5–P7. The placement of ingolfiellideans among the amphipods is briefly discussed in relation to current analyses. An overview of all species of *Ingolfiella* within a comparison of 12 characters is provided, including the eight new species described since 2003.

KEY WORDS. — Stygofauna, Amphipoda, Ingolfiellidea, marine interstitial, groundwater, Indonesia

INTRODUCTION

Ingolfiellideans are extremely modified amphipod crustaceans strongly adapted to life in aquatic subterranean habitats. Despite their low diversity—so far 45 species are recognised, distributed in two families and six genera—they are present in all continents and major oceanic basins, except in Antarctica and the polar seas (Vonk & Schram, 2003). Within this vast geographical range, the group covers an amazingly broad range of biotopes, spanning from deep-sea ooze at 4,800 m in the North Atlantic (Mills, 1967) to alluvial sediments up to 2,000 m above sea level in the Argentinian High Andes (Noodt, 1965). These extremely diverse environmental tolerances are unique in the entire crustacean world.

Ingolfiellideans display a vermiform aspect, a feature that occurs also in other groups of malacostracans adapted to life in the interstices of non-consolidated sediments, viz. bathynellacean syncarids, gnathostenetroidoid, microcerberid and microparasellid isopods, or bogidiellid amphipods. Other ingolfiellidean features were once considered to be so remarkable as to give the group a separate suborder rank within the amphipods (see Hansen, 1903), a category that

has been customarily maintained by most specialists. These features include the display of presumed eyestalks; the presence of foliaceous, uniramous unsegmented pleopods; the lack of an ischial endite [= outer plate] on the maxilliped; and the carpo-subchelate gnathopods. Advancement in the knowledge of amphipod diversity has nevertheless shown that some of these traits occur also in other amphipod groups (like carpo-subchelate gnathopods and the absence of an ischial endite on the maxilliped), or represent novel structures lacking the presumed phylogenetic relevance they were supposed to bear (the presumed eyestalks, which we regard now as hinged integumentary extensions of the anterolateral margin of the head, are thus non-homologous to the proper eyestalks of other peracarids; Dahl, 1977; Lowry & Poore, 1989). Furthermore, the odd modified pleopods of ingolfiellids do not represent the plesiomorphic condition of the group anymore after the discovery of *Metaingolfiella* Ruffo, 1969, which displays ordinary, biramous pleopods. Lowry & Poore (1989) have gone further in suggesting the placement of ingolfiellideans in a basal position within the gammarideans, together with some primitive families such as the leucothoids. Contrary to this evidence, the combined analysis of 18S rRNA sequences and morphological characters performed

by Wilson (2009) maintains the ingolfiellideans as a sister-group of a polymorphic clade of Gammaridea, Caprellidea, and Hyperidea.

As stated above, the current diversity of ingolfiellideans is probably grossly underrepresented due to their cryptic, mostly inaccessible habitat. Estimations for marine biodiversity in general reveal that one to two-thirds remain to be discovered yet (Appeltans et al., 2012). In the case of ingolfiellideans, most taxa are known only from one sex, a single specimen or a few at most, rendering the phylogenetic relationships among taxa extremely difficult to resolve. Whereas the single member of the subfamily Metaingolfiellidae Ruffo, 1969, and the cluster of six southern African ingolfiellid taxa in the genera *Stygobarnardia* Ruffo, 1985, *Trogloleupia* Ruffo, 1974a, *Rapaleupia* Vonk & Schram, 2007 and *Proleupia* Vonk & Schram, 2003 are easily characterised on the basis of their comparatively large body size (>10 mm) and features pertaining to the pleopods and uropods (see Griffiths, 1989, 1991 and references therein), the bulk of ingolfiellideans—less than 3 mm in length—are customarily placed in *Ingolfiella* Hansen, 1903 despite their heterogeneity (see Tables 1 & 2). Indeed, the diversity found in some sexually-dimorphic features suggests that *Ingolfiella* is most probably paraphyletic, but until more species and males are known it will not be possible to split it convincingly into natural subunits (Stock, 1976; Dojiri & Sieg, 1987; Ruffo & Vigna Taglianti, 1989; Lowry & Poore, 1989; Vonk & Sánchez, 1991).

Here we describe a new species of marine littoral *Ingolfiella* from coarse coral sands sampled at Pulau [=Island] Lelei of the Gura Ici archipelago, a group of eight small islets stretched over 10 km, west off Halmahera, in the northern Moluccas (Indonesia; Fig. 1). The species is unique among ingolfiellideans in the display of a rounded outgrowth on the proximo-lateral margin of basis of P5, and of a sexually-dimorphic, modified medial margin of coxa in the same limb. Other features point to a group of seven insular species that show a broad but punctuated distribution across the Atlantic and SW Pacific oceans as its closer relatives.

MATERIAL AND METHODS

Samples were taken during a Naturalis Zeeteam / LIPI expedition in 2009 (Hoeksema & Van der Meij, 2010) in coarse coral sand beaches using a biophreatical Bou-Rouch groundwater pump and steel pipes (see Bou, 1974) placed near to the waterline. When the marine groundwater flow was not steady and pipe holes or pump cylinder were clogged with sand and silt, the pump was placed directly in the sea. Low tide was the preferable time to sample but since the tidal difference was low (between 1–2 m) and locations logistically restricted, sampling was performed at all tides. The 2% formalin-preserved samples (short time for hardening tissue) were later sorted in the LIPI Ternate field station laboratory under a dissecting microscope and transferred to 70% ethanol. Before study, specimens were treated with lactic acid to soften the cuticle and remove internal tissues to facilitate

observation. Drawings were prepared using a camera lucida on a Leica DM 2500 microscope equipped with Nomarski differential interference contrast. Material preserved on slides was mounted in lactophenol and the coverslips sealed with nail varnish. Body measurements were derived from the sum of the maximum dorsal dimensions (including telescoped portions) of head, pereionites, pleosomites and urosomites, and exclude telson length. Material is deposited in the Crustacea collection of Naturalis Biodiversity Center, Leiden; in the Zoological Reference Collection (ZRC) of the Raffles Museum (RMBR) Singapore; and in the Division of Zoology, Museum Zoologicum Bogoriense, Indonesian Institute of Sciences (LIPI), Cibinong, Indonesia. Other stygobiont amphipods found in the same samples are described in Vonk et al. (2011). Following Watling (1989), the term “spine” in descriptions is restricted for rigid armature elements with a hollow central core that do not articulate basally to the body integument. Gnathopods I and II, and pereopods III to VII appear abbreviated elsewhere as G1–G2 and P3–P7, respectively; pleopods II–III, and uropods I–III, as PL2–PL3 and U1–U3.

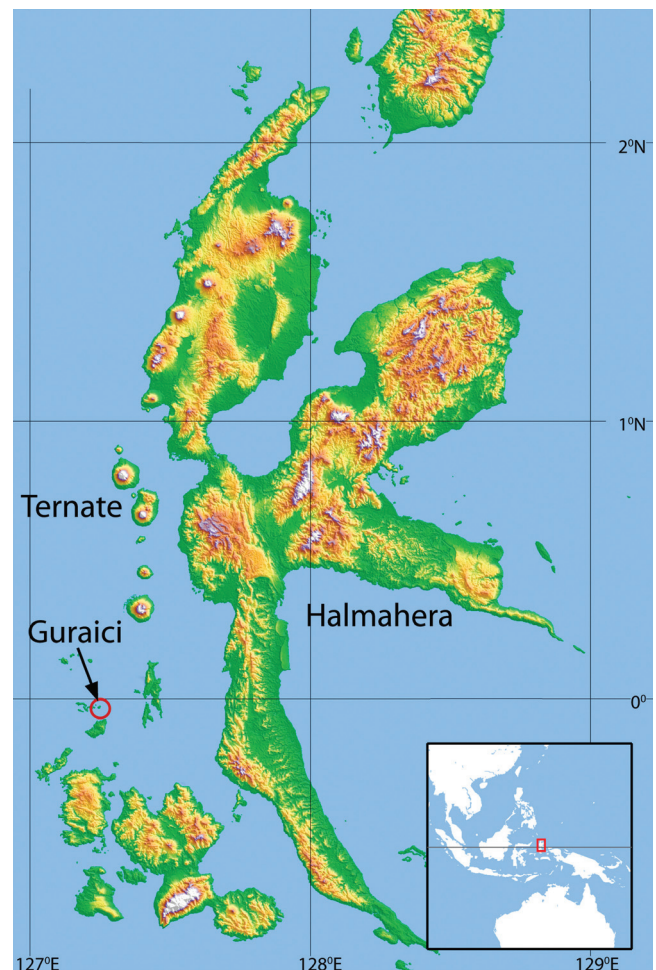


Fig. 1. Map of the northern Moluccas showing the location of the Gura Ici islands, off western Halmahera.

Table 1. Known distribution and diversity of the genus *Ingolfella*.

Species	Distribution & Habitat	Sexes Known		Observations
		M	F	
<i>I. abyssi</i> Hansen, 1903	Davis Strait, NW Atlantic (E Greenland); 3,521 m depth	-	+?	Known from a single specimen, probably juvenile. Supplementary description in Vonk & Schram (2003)
<i>I. acherontis</i> (Karaman, 1933)	Skopje (Macedonia); freshwater well	-	+?	Poorly described; material lost. Supplementary description in Karaman (1959)
<i>I. alba</i> Iannilli, Berera & Cottarelli, 2008	Mindoro and Marinduque islands (Philippines); marine littoral, coral sand	+	+	
<i>I. atlantisi</i> Mills, 1967	NW Atlantic off Bermuda; 4,700 m depth	-	+?	Known from a single specimen, probably female. Supplementary description in Dojiri & Sieg (1987)
<i>I. australiana</i> Lowry & Poore, 1989	Bass Strait (SE Australia); marine, 85 m depth	+	+	
<i>I. azorensis</i> Rubal & Larsen, 2012	Azores; marine, 10–15 m depth	+	-	
<i>I. bassiana</i> Lowry & Poore, 1989	Bass Strait (SE Australia); marine, 121 m depth	+	+	
<i>I. beatricis</i> Ruffo & Vonk, 2001	Slovenia; freshwater cave	-	+	Known from a single female
<i>I. berrisfordi</i> Ruffo, 1974b	Cape Town (S Africa); marine sandy beach	+	-	
<i>I. britannica</i> Spooner, 1960	English Channel; marine, 46 m depth	-	+	Known from both sexes? (probably only females)
<i>I. canariensis</i> Vonk & Sánchez, 1991	Tenerife and El Hierro islands (Canaries); beaches and anchialine cave	+	+	
<i>I. catalanensis</i> Coineau, 1963	France; in alluvial sediments	+	-	Supplementary description in Coineau (1968)
<i>I. cf. catalanensis</i> sensu Vonk & Notenboom (1996)	Spain; freshwater well	+	-	Known from a single male
<i>I. cottarelli</i> Ruffo & Vigna Taglianti, 1989	Tavolara Island (Sardinia); freshwater cave	+	+	
<i>I. fontinalis</i> Stock, 1977	Bonaire (Dutch Antilles); freshwater spring	+	+	Variability in unguis of P3–P4 and P7 (see Table 2) suggest description might be based on more than one taxon
<i>I. fuscina</i> Dojiri & Sieg, 1987	Atlantic coast of North America and Gulf of Mexico; marine, 17–151 m depth	+	+	
<i>I. georgei</i> Andres, 2005	Seine Seamount (NE Atlantic); 210–235 m depth	+	+	
<i>I. grandispina</i> Stock, 1979	Curaçao (Dutch Antilles); anchialine cave	-	+	Known from a single female
<i>I. inermis</i> Shimomura, Ohtsuka & Tomikawa, 2006	Okinawa (Japan); marine sandy beaches	-	+	
<i>I. ischitana</i> Schiecke, 1976	Ischia (Italy); marine, 6–30 m depth	+	+	
<i>I. kapuri</i> Coineau & Rao, 1973	Andaman & Nicobar Islands; marine littoral (coral sand)	-	+?	
<i>I. littoralis</i> Hansen, 1903	Thailand; marine littoral (coral sand)	-	+?	Known from single specimen; probably juvenile. Supplementary description in Vonk & Schram (2003)
<i>I. longipes</i> Stock, Sket & Iliffé, 1987	Bermuda; anchialine cave	-	+	Known from a single female
<i>I. macedonica</i> Karaman, 1959	Macedonia; fresh groundwater	-	+	Known from a single specimen, probably female
<i>I. manni</i> Noodt, 1961	Chile; fresh interstitial groundwater 800 m a.s.l.	+	+	
<i>I. margaritae</i> Stock, 1979	Isla Margarita (Venezuela); freshwater well	+	-	Known from a single male

Table 1. Cont'd.

Species	Distribution & Habitat	Sexes	Known	Observations
<i>I. ogasawarensis</i> Shimomura & Kakui, 2011	Ogasawara Islands (Japan); marine, 165 m depth	-	+	
<i>I. petkovskii</i> Karaman, 1957	Macedonia; Bulgaria ?; freshwater wells and alluvial sediments	+	+	Cvetkov (1964) record of the species in Bulgaria to be confirmed
<i>I. cf. petkovskii</i> sensu Bou (1970)	Euboea Island (Greece); freshwater wells	+	+	
<i>I. putealis</i> Stock, 1976	Bonaire (Dutch Antilles); anchialine wells	+	+	Supplementary description in Stock (1977)
<i>I. quadridentata</i> Stock, 1979	Curaçao (Dutch Antilles); shallow sublittoral coarse sand up to 4 m depth	-	+	
<i>I. quokka</i> Gallego Martínez & Poore, 2003	W. Australia; marine sandy beach	+	+	
<i>I. rocaensis</i> Senna & Serejo, 2005	Atol das Rocas (Brazil); marine, 14 m depth (washed sponges)	-	+	Known from a single female
<i>I. ruffoi</i> Stewing, 1958	Peru; brackish water in coarse shingle marine beach	+	+	Supplementary description in Ruffo & Vigna Taglianti (1989)
<i>I. sandroruffoi</i> Andres, 2004	Great Meteor Seamount (N Atlantic); 297–476 m depth	+	+	
<i>I. similis</i> Rondé-Broekhuizen & Stock, 1987	Fuerteventura (Canary Islands); anchialine water in interstittia and well	+	+	Supplementary description in Vonk & Sánchez (1991)
<i>I. tabularis</i> Stock, 1977	Curaçao; Aruba (Dutch Antilles); sandy beaches and anchialine caves	+	+	Supplementary description in Stock (1979); Unguis of P3 & P7 is described as simple instead of bifid in specimens from a site different to the type locality (Table 2)
<i>I. thibaudi</i> Coineau, 1968	France; in alluvial sediments	+	+	
<i>I. unguiculata</i> Stock, 1992	Madeira; anchialine pool	+	+	
<i>I. uspallatae</i> Noodt, 1965	Argentina; in alluvial sediments 2000 m a.s.l.	-	+	Known from a single female
<i>I. vandeli</i> Bou, 1970	mainland Greece; in alluvial sediments	+	+	
<i>I. xarifae</i> Ruffo, 1966	Maldives; marine littoral (washed corals)	-	+?	Only two specimens known, probably females

Table 2. Matrix of some relevant features pertaining to *Ingolfiella* species. Species apparently most closely related to *I. moluccensis* sp. nov. are marked with asterisks.

Species	Cephalic ("ocular") lobes	G1-G2, # denticles on posterior margin of dactylus	U2, # denticle combs on medial surface of protopod	P3-P4 unguis (1: simple; 2: bifid; 3: trifid; 4: multidenticulate)	P5-P7 unguis (1: simple; 2: bifid; 3: trifid)	male G2, bifid robust seta on palm	male G2, modified reverse seta on posterior margin of carpus	male G2 merus, hyaline frill	male U2, basofacial robust seta on protopod	male PL2-PL3	female pleopods	oöstegites
<i>I. moluccensis</i> *	+	4-4	3	3	2	+	-	+	+	+	+	P3-P4
<i>I. abyssi</i>	+	4-4	4	2	1	?	?	?	?	?	+	?
<i>I. acherontis</i>	+	3-3	3	2	2	?	?	?	?	?	?	?
<i>I. alba</i> *	+	4-4	3	3	2	+	-	+	+	+	+	P3-P5
<i>I. atlantisi</i>	+	4-4	3	P3: 2 P4: 1	1	?	?	?	?	?	+	?
<i>I. australiana</i>	+	4-3	5	2	1	-	-	-	-	+	+	?
<i>I. azorensis</i> *	-	4-4	3	3	2	-	-	-	-	+	?	?
<i>I. bassiana</i>	+	3-3	4	2	1	+?	+?	-	+	+	+	?
<i>I. beatricis</i>	+	4-4	3	2	2	?	?	?	?	?	+	?
<i>I. berrisfordi</i>	+	3-3	5	3	1	-	-	-	+	+	?	?
<i>I. britannica</i>	+	4-4	3-4	1	?	?	?	?	?	?	+	P3-P5
<i>I. canariensis</i> *	+	4-4	3	3	2	+	-	+	+	+	+	P3-P5
<i>I. catalanensis</i>	?	3-3	3	2	2	-	+	-	+	-	?	?
<i>I. cf. catalanensis</i>	-	3-3	8	2	2	-	-	-	+	-	?	?
<i>I. cottarelli</i>	-	3-3	6-7	1	1	-	-	-	-	-	-	?
<i>I. fontinalis</i>	+	3-3	3	1/2	P5: 2 P6: 2 P7: 1/2	-	+	-	+	+	+	?
<i>I. fuscina</i>	+	4-4	4	3	2	-	-	-	-	+	+	P3-P5
<i>I. georgei</i>	+	3-3	3-4	4	1	-	-	-	+	+	+	?
<i>I. grandispina</i>	+	3-3	5	4	1	?	?	?	?	?	+	P3-P4
<i>I. inermis</i> *	+	4-4	3	3	2	?	?	?	?	?	+	P3-P4
<i>I. ischitana</i>	+	3-3	4	4	1	-	-	-	-	+	+	P3-P5
<i>I. kapuri</i>	+	4-4	3	3	2	?	?	?	?	?	+	?
<i>I. littoralis</i>	+	0-3	3	2	1	?	?	?	?	?	+	?
<i>I. longipes</i>	+	4-4	3	2	2	?	?	?	?	?	+	?
<i>I. macedonica</i>	-	4-4	4	?	1	-	-	-	-	-	+	?
<i>I. manni</i>	-	3-3	3	1	1	-	-	-	-	+	+	?
<i>I. margaritae</i>	-	3-3	3	2	2	-	+	-	+	+	?	?
<i>I. ogasawarensis</i> *	+	4-4	3	3	2	?	?	?	?	?	+	P3-P5
<i>I. petkovskii</i>	-	3-3	3	2	2	-	+	-	-	+	+	?
<i>I. cf. petkovskii</i>	?	3-3	3	2	2	-	+	-	+	+	+	?
<i>I. putealis</i>	+	3-3	3	2	2	-	+	-	+	+	+	?
<i>I. quadridentata</i>	+	4-4	3	4	2	?	?	?	?	?	+	P3-P4
<i>I. quokka</i> *	+	4-4	3	3	2	+	-	-	+	+	+	?
<i>I. rocaensis</i> *	+	4-4	?	3	2	?	?	?	?	?	+	P3-P4
<i>I. ruffoi</i>	+	4-4	3	2	2	-	-	-	-	+	+	P3-P4
<i>I. sandroruffoi</i>	+	4-4	4	4	3	+?	-	-	-	+	+	P3-P4
<i>I. similis</i>	-	3-3	3	2	2	-	+	-	+	+	+	?
<i>I. tabularis</i>	+	3-3	3	2	2	-	+	-	+	+	+	?
<i>I. thibaudi</i>	?	3-3	5	1	1	?	-	-	?	-	-	?
<i>I. unguiculata</i>	+	3-3	3	2	2	-	+	-	+	+	+	?
<i>I. uspallatae</i>	-	3-3	4	1?	1?	?	?	?	?	?	+	?
<i>I. vandeli</i>	?	3-3	3	2	2	-	+	-	+	+	+	?
<i>I. xarifae</i>	+	3-4	3	3	2	?	?	?	?	?	+	?

TAXONOMY

Order Amphipoda Latreille, 1816
Suborder Ingolfiellidea Hansen, 1903
Genus *Ingolfiella* Hansen, 1903
***Ingolfiella moluccensis* sp. nov.**
(Figs. 2–6)

Material examined. — Collected by R. Vonk and Mr. Sumadijo, 9 Nov. 2009. Northern beach of Pulau Lelei, Gura Ici islands, northern Moluccas (0°01'38.64"N, 127°14'38.53"E). Holotype: Preparatory female [= with non-setose oostegites] 1.57 mm, completely dissected and mounted on single slide (MZB, Cibinong). Paratypes: Two males of 1.39 mm (MZB) and 1.43 mm (RMNH, Leiden) and five preparatory females 1.55, 1.55, 1.59, 1.62, and 1.34 mm (ZRC of RMBR, Singapore); all preserved in single 70% ethanol vial.

Diagnosis. — Basis of P5 with proximolateral lobe. Medial margin of coxa V modified, produced ventrally into ridge; ridge sexually-dimorphic, rounded in female, acutely pointed in male. Cephalic ("ocular") lobes present. Dactylus of gnathopods provided with four denticles along posterior margin. Medial surface of protopod of U2 with three denticle combs. Unguis of P3–P4 trifid; that of P5–P7 bifid. Pleopods I–III present in both sexes. Male G2 with bifid robust seta close to palm margin; no modified reverse seta on posterior margin of carpus; merus provided with long hyaline frill extension posterodistally. Male U2 protopod with basofacial robust seta. Oostegites on P3–P4 only.

Etymology. — Species name refers to its currently known distribution, the Moluccas in Indonesia.

Distribution. — Known so far only from the type locality.

Description of female. — Body (Fig. 2A) vermiform, unpigmented, body somites smooth except for sparsely set simple setae distributed as in Figs. 2A, 3A, 6A, C. Head (Figs. 2A, 3A) clearly longer than broad and more than twice as long as pereonite I, with weakly protruding rostrum; lateral lobes and post-antennal sinus each hardly developed; cephalic ("ocular") lobe not overreaching second segment of antennal peduncle. Epimeral plates on pleonites I–III hardly developed as postero-ventral rounded extensions each crowned with simple seta (Fig. 2A).

Antennule (Fig. 3A) peduncle segments 1–3 progressively shorter towards distal, length ratio as 1:0.38:0.34. Flagellum 4-articulate, shorter than peduncle segments 2–3 combined; proximal article unarmed, distal longest; articles 2–4 each provided with aesthetasc, aesthetascs progressively shorter towards distal. Accessory flagellum 3-articulate, shorter than two proximal articles of main flagellum combined.

Antenna (Fig. 3A) slightly shorter than antennule; gland cone short, hardly protruding dorsomedially; protopodal segments 3–5 progressively shorter towards distal, length ratio as 1:0.81:0.76; fourth segment with exceedingly long (as long as fifth protopodal segment), simple robust seta with rounded tip placed subdistally on posterior margin. Flagellum 5-articulate, shorter than protopodal segments 4–5 combined.

Labrum and paragnaths (not figured) ordinary, latter lacking inner lobes.

Mandibles with molar process non-tritulative, spiniform. Left mandible (Fig. 3C) incisor subrectangular, cutting-edge irregularly multi-denticulate; lacinia subrectangular, as broad as incisor, cutting edge 5-denticulate; spine row consisting of three pectinate elements plus ca. four tiny pointed processes; spiniform molar process finely serrated. Right mandible (Fig. 3D) with 7-denticulate incisor and finely multi-denticulate lacinia, latter constricted basally; spine row reduced to three short rounded bulges; spiniform molar process apparently smooth.

Maxillule (Fig. 4D) coxal endite [= inner lobe] with three simple setae; basal endite [= outer lobe] with six robust setae of which one bicuspidate, other 3-cuspidate, other 4-cuspidate, two (longer) 7- and 8-cuspidate, respectively, and one (innermost) comb-like; endopod [= palp] 2-segmented, proximal segment unarmed, distal with two setae 3- and 4-cuspidate, respectively.

Maxilla (Fig. 3E) with short, subequal blunt plates, each bearing five distal setae; three out of setae on outer plate sparsely setulose.

Maxilliped (Fig. 3F) basal endite slender, finger-like, with two simple setae; ischium with three simple setae on inner margin; merus, carpus, and propodus each with single simple seta on medial margin; propodus with row of long setules on outer margin; dactylus (Fig. 3G) short, subtriangular, with simple robust seta proximally on outer margin, pinnate distomedial seta, and long (longer than segment) unguis.

Coxal gills present on P3–P5, ovoid, only that on P5 clearly stalked (Fig. 5A–C). Oostegites (Fig. 5A, B) on P3–P4, short, subrectangular, shorter than corresponding coxal gill, with three short pointed processes (regressed setae suggesting preparatory female condition?) on distal margin; that on P3 with short simple seta subdistally. Oostegites of paratype of 1.34 mm reduced and smooth, suggesting specimen probably juvenile.

Gnathopod I (Fig. 4A) carpo-subchelate, carpus 2.5 times as long as broad, with three short, apparently bifid flagellate robust setae along lateral side of palm margin, stout simple robust seta on palm angle, and two shorter stout simple setae and broad triangular spine on medial surface of segment as figured; palm margin strongly oblique, straight and smooth; posteromedial surface of carpus with excavation apparently to accommodate distal portion of unguis. Dactylus with four slender denticles along posterior margin.

Gnathopod II (Fig. 4B) carpo-subchelate, carpus massive, shorter (attaining only 88% of length) and stouter (twice as long as broad vs 2.5 times) than carpus of G1; palm margin strongly convex, sparsely serrated, lined up with three apparently unicuspidate short, flagellate robust setae along lateral side; palm angle marked by stout, slightly curved simple robust seta; medial surface of segment with

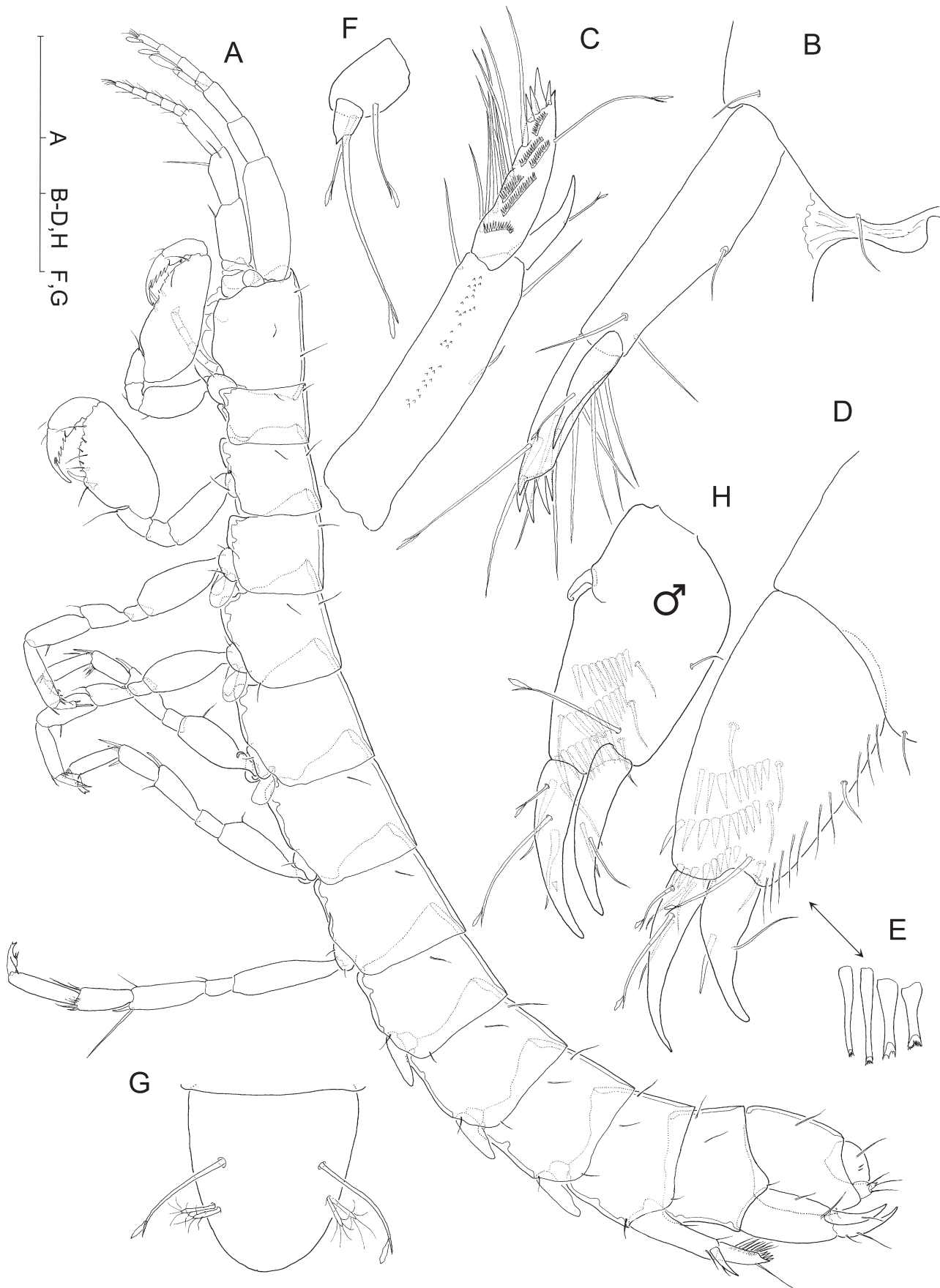


Fig. 2. *Ingolfiella moluccensis* sp. nov. (A: female paratype 1.55 mm; B–G: female holotype; H: male paratype 1.39 mm). A, body, lateral; B, left first uropod, lateral; C, same, medial; D, left second uropod, lateral; E, detail of denticles conforming combs on U2 protopod; F, right third uropod, dorsal [= posterior]; G, telson, dorsal [= posterior]; H, male left second uropod, lateral. Scale bars = 0.1 mm (A), 0.05 mm (B–D, F–H).

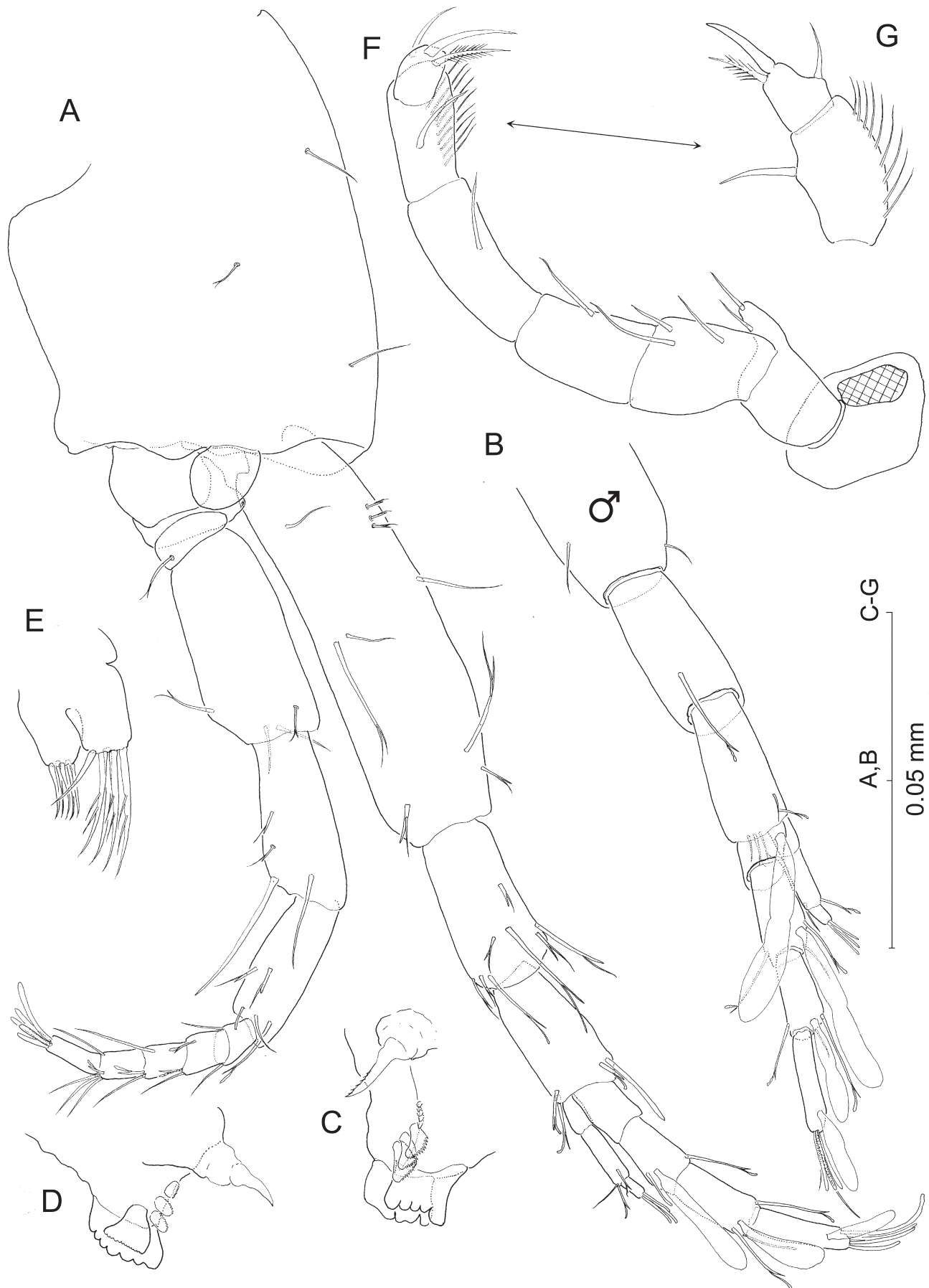


Fig. 3. *Ingolfiella moluccensis* sp. nov. (A, C–E: female holotype; B: male paratype 1.39 mm). A, head with right antennule and antenna, lateral; B, distal portion of male left antennule, lateral; C, left mandible; D, right mandible; E, right maxilla, posterior [= ventral]; F, right maxilliped, posterior; G, inset of distal segments of maxillipedal endopod.

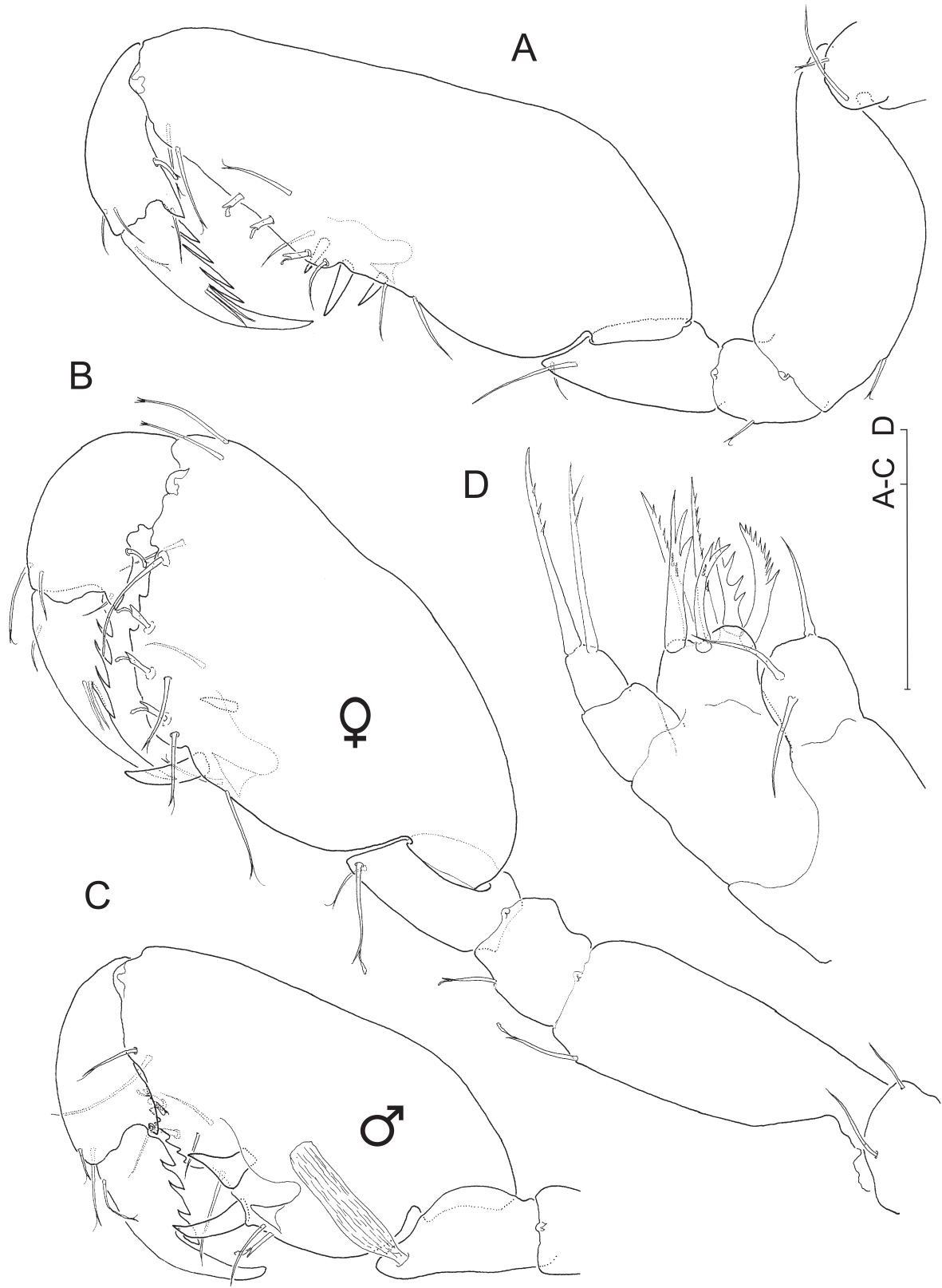


Fig. 4. *Ingolfiella moluccensis* sp. nov. (A, B, D: female holotype; C: male paratype 1.39 mm). A, left gnathopod I, lateral; B, left gnathopod II, lateral; C, male right gnathopod II, medial; D, right maxillule, posterior [= ventral]. Scale bars = 0.05 mm (A–C), 0.025 mm (D).

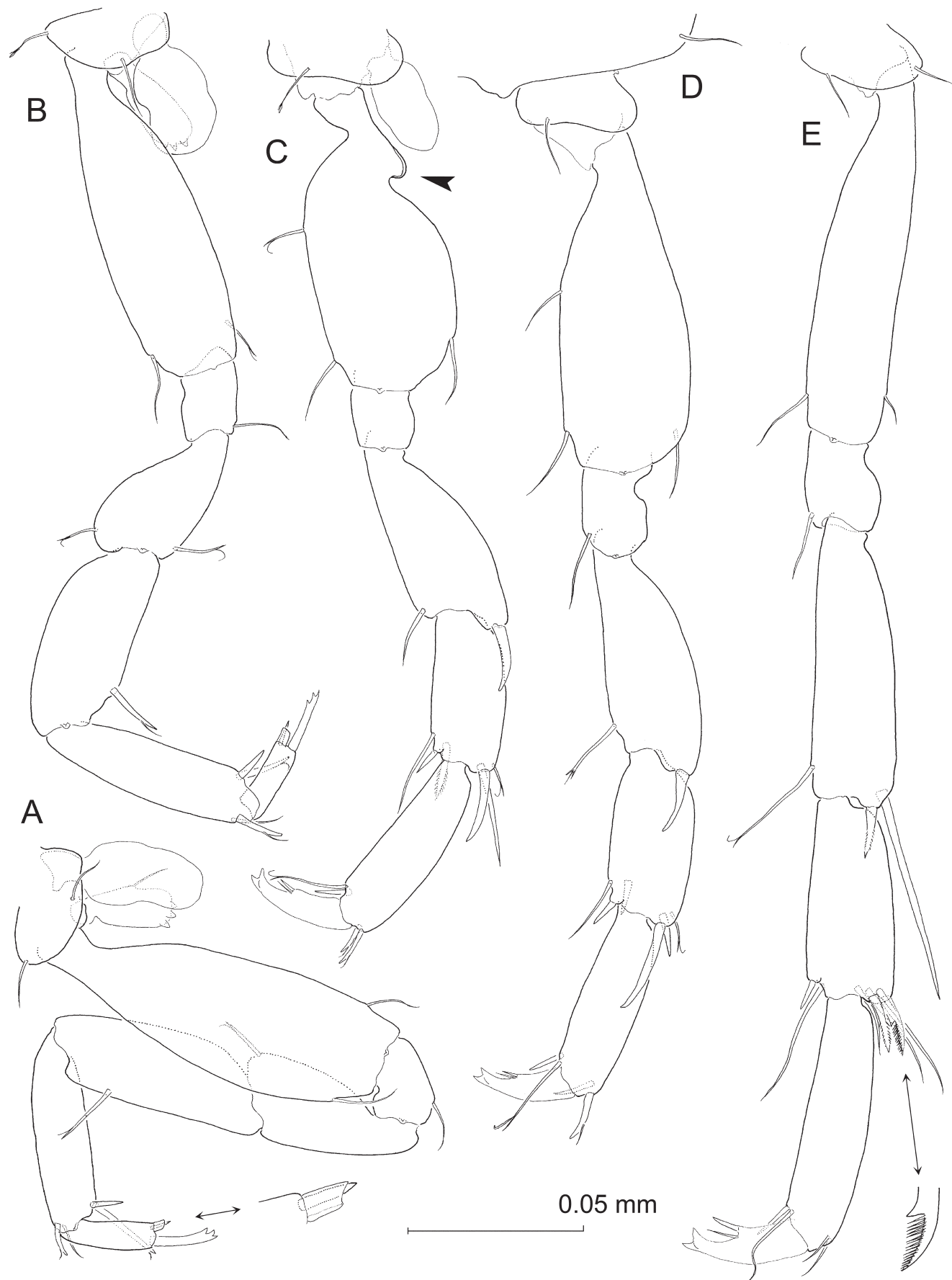


Fig. 5. *Ingolfiella moluccensis* sp. nov., female holotype left pereopods III–VII in lateral view. A, pereopod III; B, pereopod IV; C, pereopod V; D, pereopod VI; E, pereopod VII. Notice oostegites attached on P3–P4. Arrowhead points to proximal bulge on basis of P5.

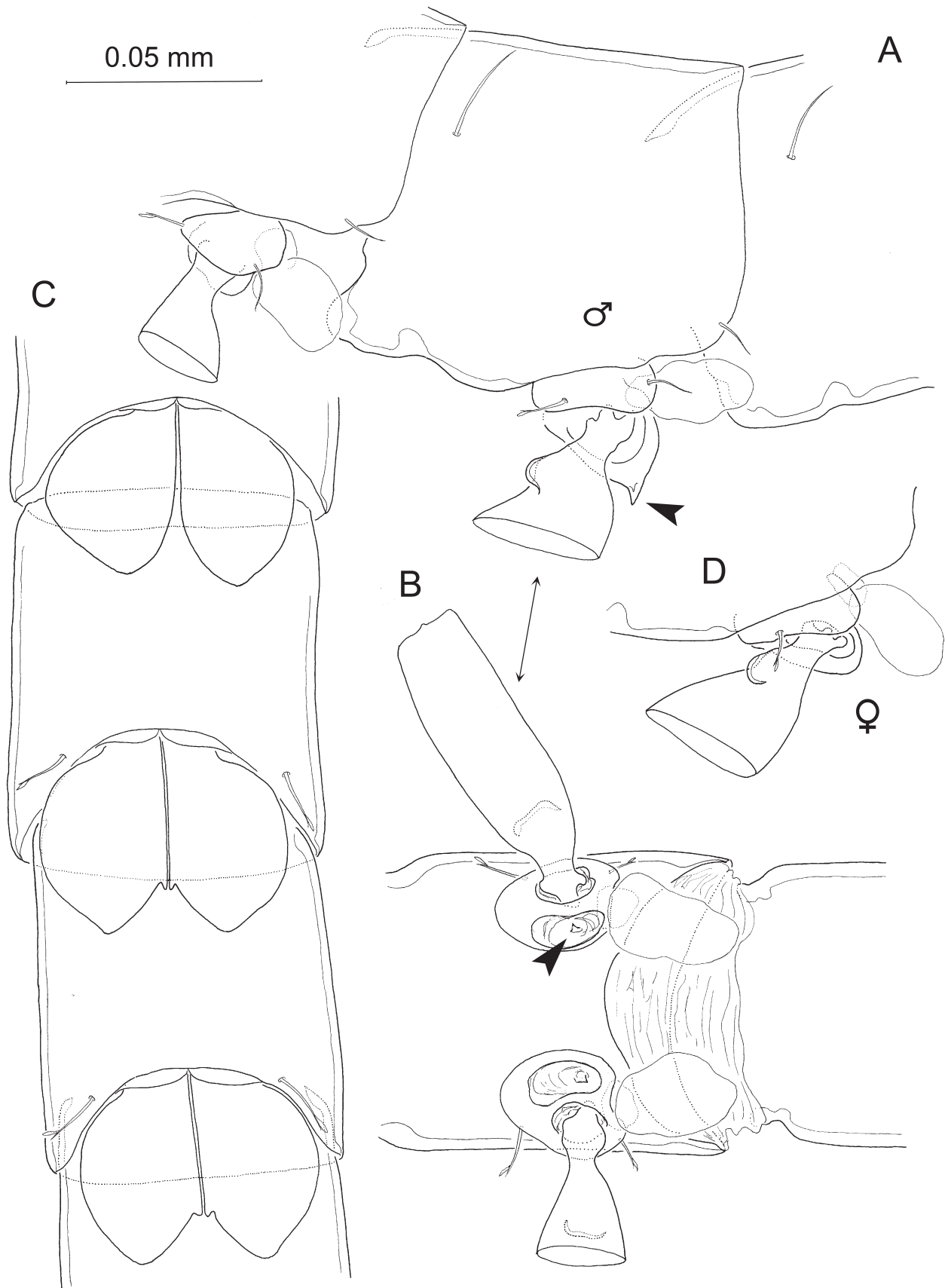


Fig. 6. *Ingolfiella moluccensis* sp. nov. (A–C, male paratype 1.39 mm; D, female holotype). A, detail of proximal portion of left pereiopods VI–V showing pointed process on coxa V, lateral; B, fifth pereonite with fifth pereiopods attached, ventral; C, pleonites I–III with corresponding pleopods, ventral; D, proximal portion of female left fifth pereiopod, lateral. Arrowheads point to pointed process on male coxa V.

short, stout simple robust seta and strong triangular spine as figured; posteromedial surface of carpus with excavation apparently to accommodate distal portion of unguis. Dactylus with four denticles along posterior margin, spines stouter than G1 counterparts.

Pereiopods III–IV subequal except for slightly longer propodus and stouter flagellate robust subdistal seta on posterior margin of carpus in P4 (compare Fig. 5A, B). Dactylus subquadrangular, posterodistal angle spur-like, with short simple robust seta partially embedded into hyaline sheath (see inset of Fig. 5A). Unguis shorter than dactylus, tricuspidate.

Pereiopods V–VII (Fig. 5C–E) progressively longer towards posterior; basis of P5–P6 broad, that of P7 slender; each with dactylus provided with two stiff simple setae on distomedial angle; unguis bifid, with strong triangular tooth subterminally on lateral margin. Basis of P5 (Fig. 5C; arrowed) strongly modified, with rounded outgrowth proximally on outer margin; coxa also peculiar, with medial margin strongly produced ventrally into rounded ridge (see Fig. 6D). Pereiopod VII with one of distal armature elements on distolateral angle of carpus modified into comb-like robust seta provided with proximal spur (see inset of Fig. 5E).

Pleopods as in male (Fig. 6C), foliaceous, unarmed, members of each pair appressed medially, with straight medial margin and evenly rounded lateral margin. Distomedial angle of pleopods II & III produced into short rounded process, that of pleopod I indistinct.

Uropod I (Fig. 2B, C) protopod long and slender, subrectangular, with two simple setae on anterolateral [= ventrolateral] margin and simple seta subdistally on posterolateral [= dorsolateral] margin. Exopod unsegmented, much shorter than endopod, acuminate, with simple seta placed at ca. three-fifths length of outer margin. Endopod with short terminal spine plus row of four stout triangular robust setae subterminally; nine setae disposed on segment as figured. Medial surface of protopod adorned with patch of tiny pointed denticles; that of endopod with series of crescent scales (Fig. 2C).

Uropod II (Fig. 2D) protopod bearing three oblique combs of large denticles on medial surface; denticles apparently triangular but with variably frayed tips (see Fig. 2E); six simple setae distributed on segment as figured, plus row of long setules along posterolateral margin. Rami tapering, exopod stouter and slightly shorter than endopod, more inflated basally, provided with one stout simple seta on medial surface and slender simple seta on dorsolateral margin. Endopod with five simple setae distributed as figured.

Uropod III (Fig. 2F) tiny, uniramous, protopod subquadrate, with simple seta provided with hyaline process on distolateral angle, plus another one midway of distoventral margin of segment. Exopod much shorter than protopod, acuminate, with long simple seta provided with hyaline process placed subterminally on lateral margin of segment.

Telson (Fig. 2G) entire, fleshy, globose (see Fig. 2A), about as long as broad in dorsal aspect, distal margin evenly rounded; armature reduced to two long simple setae provided with hyaline process subdistally and two pairs of short penicillate setae, all disposed dorsally as figured.

Description of male. — None of the male specimens seem to display penile papillae, and contrary to most species, their first pair of pleopods appears undifferentiated with respect to the rest of pleopods and also with those of the female. Both features suggest these two males are juveniles. In any case, relevant differences with respect to the female—aside of body size (see material examined)—pertain to the antennule, gnathopod II, coxal plate V and uropod II. Thus, the male antennule (Fig. 3B) displays the proximal article of the main flagellum expanded basally and provided with a long aesthetasc (vs article unarmed in the female).

The male G2 (Fig. 4C) has a foliaceous hyaline frill implanted close to the posterodistal angle of merus, on medial surface of segment (vs frill absent in female). The carpus wears only two short flagellate robust setae along the palm margin (vs three in the female), whereas the robust seta present on the medial surface of this segment is strongly modified, stout and broadly expanded distally, forked (vs small and simple in the female). In addition, the excavation present on the posteromedial surface of segment (to accommodate unguis) is much more pronounced here than in the female.

The medial margin of the coxa of P5 (Fig. 6A, B) is acutely produced (vs ridge rounded in female).

The U2 (Fig. 2H) protopod has a stout basofacial robust seta with reflexed tip (absent in female). In addition, the setae on the medial surface of endopod are swollen basally (vs ordinary in female).

REMARKS

The new species from Gura Ici differs from any other ingolfiellidean known thus far by the peculiar structure of its pereiopod V, which displays a rounded process proximolaterally on its basis, whereas the coxa has its medial margin produced ventrally into a conspicuous ridge; this ridge is sexually-dimorphic, being rounded in the female and acutely pointed in the male.

Ingolfiella moluccensis sp. nov. is related to a group of seven insular species that show a broad but punctuated distribution along the Atlantic and SW Pacific oceans. Namely, *I. alba*, *I. azorensis*, *I. canariensis*, *I. inermis*, *I. ogasarawensis*, *I. quokka*, and *I. rocaensis* (see Table 1 for their precise distribution). These species share the combined display of four denticles on the posterior margin of dactylus of G1 & G2; three comb rows of denticles on the medial margin of the protopod of U2; a trifid unguis of P3–P4; and a bifid unguis of P5–P7 (see Table 2). They presumably share also the display of three pairs of pleopods in both sexes. The morphology of the male G2 approaches the new species to *I.*

alba from the Philippines and *I. canariensis* from the Canary Islands, although both display oöstegites on P3–P5 whereas *I. moluccensis* sp. nov. displays them only on P3–P4 (see Table 2). Regarding *I. inermis* (Okinawa) and *I. rocaensis* (Brazil), the males of both are unknown, but share with the new species the lack of oöstegites on P5 and might be its closest relatives.

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