

# Syntopy in rare marine interstitial crustaceans (Amphipoda, Ingolfiellidae) from small coral islands in the Molucca Sea, Indonesia

Ronald Vonk · Damià Jaume

Received: 9 August 2013 / Revised: 19 November 2013 / Accepted: 19 November 2013 / Published online: 10 December 2013  
© Senckenberg Gesellschaft für Naturforschung and Springer-Verlag Berlin Heidelberg 2013

**Abstract** *Ingolfiella botoi*, a new species of ingolfiellid amphipod, is described in syntopy with the recently described *I. moluccensis* from the coarse coral sand interstitial medium of the Gura Ici Islands (Molucca Sea, Indonesia). The new taxon is unique among ingolfiellideans in the display of a multidenticulate unguis on P5–P6. The new species shares most character state resemblances with *I. quadridentata* Stock 1979, from coarse sublittoral sands up to 4 m depth in Curaçao (Leeward Antilles). This is the third record of syntopy among members of this elusive group of stygobiont amphipods.

**Keywords** *Ingolfiella botoi* n. sp · Co-occurrence · Marine interstitial medium · Sandy beaches · Subterranean amphipods · Infauna · Halmahera Selatan · Maluku Utara

## Introduction

Ingolfiellid amphipods are a rarely reported group of crustaceans known only from deep-sea sediments and subterranean habitats such as shallow marine interstitial spaces, freshwater caves and wells, and streambeds of high mountain rivers

(Stock 1979; Vonk and Schram 2003). Since their discovery in the frame of the deep-sea Danish ‘Ingolf’ expedition of 1895–1896 (Hansen 1903), only 48 species—most of them known from a single or very few specimens—have been described (Griffiths 1989, 1991; Vonk and Jaume 2013; Iannilli and Vonk 2013). Locations rendering specimens are often placed widely apart and mainly in the tropics and subtropics, mostly in interstitial or cave waters. Species ranges are usually stated as reduced except in some cases where large areas have been methodically surveyed. Examples of species with presumed larger ranges than just pinpoint locations include: (1) *Ingolfiella fuscina* Dojiri and Sieg, 1987, from the shelf sea bottom in the Gulf of Mexico and off the coast of South Carolina, thus on both sides of the Florida peninsula and with a distance of at least 1,000 km between stations; (2) *Trogloleleupia leleupi* (Ruffo, 1951), from wells and caves in Zaire and Zambia, placed up to 350 km apart (Griffiths 1989); (3) *Ingolfiella thibaudi* Coineau, 1968, from the French rivers Gard and Ardèche, covering a stretch of about 150 km along these tributaries of the river Rhone; (4) *I. canariensis* Vonk and Sánchez, 1991, from the Canary islands of Tenerife and El Hierro, with a 200-km distance of deep waters between the islands; (5) *I. alba* Iannilli, Berera and Cottarelli, 2008, from sandy beaches on Mindoro and Marinduque islands in the Philippines (Iannilli et al. 2008), placed ca. 140 km apart; and (6) *Stygobarnardia caprellinoides* Ruffo, 1985, from a well and cave in Namibia placed ca. 80 km apart (Griffiths 1989). Nevertheless, cases of purported broad-range ingolfiellids should be dealt with caution, since the description of the material from the additional localities in some cases does not match completely the original description (see Vonk and Jaume 2013: table 1): namely, *Ingolfiella catalanensis* Coineau, 1963, described from alluvial sediments in France (Narbonne) and allegedly also present in a well in Spain (Castellón), both localities separated by a stretch of about 400 km (Vonc and Notenboom 1996); *I. petkovskii* Karaman, 1957, described from Macedonia

---

R. Vonk (✉)  
Naturalis Biodiversity Center, P. O. Box 9517, 2300 RA Leiden,  
The Netherlands  
e-mail: ronald.vonk@naturalis.nl

R. Vonk  
Institute for Biodiversity and Ecosystem Dynamics,  
University of Amsterdam, Amsterdam 1098 XH,  
The Netherlands

D. Jaume  
Instituto Mediterráneo de Estudios Avanzados, IMEDEA  
(CSIC-UIB), C/ Miquel Marqués 21, 07190 Esporles,  
Balearic Islands, Spain  
e-mail: damiajaume@imedea.uib-csic.es

and later on reported from Bulgaria (Cvetkov 1964) and the Greek island Euboea (Bou 1970) (thus in a triangle of over 500 km); and *I. tabularis* Stock, 1977, from sandy beaches and anchialine caves on Aruba and Curaçao islands (Dutch Antilles), 60 km apart and with depths of 1,000 m in-between (Stock 1979).

Only two cases of syntopic occurrence have been reported in the approximately 50 species of ingolfiellids known today. Both are in the group of the large-bodied freshwater SW African ingolfiellids and occurred in two Namibian wells where *Stygobarnardia caprellinoides* cohabited with *Trogloleupia eggerti* Ruffo, 1964 and with *T. dracospiritis* Griffiths, 1989, respectively (Griffiths 1989). In addition, Stock (1977) described *Ingolfiella fontinalis* from a single freshwater spring on Bonaire (Dutch Antilles); this species shows a remarkable variability in the morphology of unguis of P3–P4 and P7, suggesting the description might correspond to the combination of more than one taxon (Vonk and Jaume 2013: table 1).

Here, we describe a new species of *Ingolfiella* based on a single specimen found mixed in a sample of *Ingolfiella moluccensis* Vonk and Jaume, 2013, after rechecking all specimens for final storage and labeling in the museum collection. These ingolfiellids were collected during a marine expedition in 2009 organized by Naturalis, Leiden, and the Research Centre for Oceanography of the Indonesian Institute of Sciences (RCOLIPI). The ingolfiellids were found on the Gura Ici islands, a group of low calcareous coral rises and mangrove-fringed sand flats in the Molucca Sea (see Vonk and Jaume 2012: fig. 1, for a map showing their precise location).

## Materials and methods

Sampling was carried out with a so-called Bou-Rouch biophreatical pump and steel pipes (see Bou 1974) placed near to the beach waterline. The 2 % formalin-preserved sample (a short time for hardening of the tissue) was sorted later in the LIPI Ternate field station laboratory under a dissecting microscope and transferred to 70 % ethanol. Before study, the single specimen dealt with was 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. Body measurements were derived from the sum of the maximum dorsal dimensions (including telescoped portions) of head, pereonites, pleosomites, and urosomites, and excluding telson length. 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 1 and 2, and pereopods 3–7 appear abbreviated elsewhere as G1–G2 and P3–P7, respectively, pleopods

1–3, as PL1–PL3, and uropods 1–3, as U1–U3, while exp1 and exp2 denote proximal and distal segments, respectively, of the 2-segmented exopod of uropod 3.

## Taxonomy

Order Amphipoda Latreille 1816

Suborder Ingolfiellidea Hansen 1903

Genus *Ingolfiella* Hansen 1903

*Ingolfiella botoi* sp. nov.

(Figs. 1, 2, 3)

**Material examined** Collected by R. Vonk and Mr. Sumadijo, 9 November 2009. Gura Ici islands, north beach of Pulau Lelei, thick coral rubble bar at waterline fringing shallow reef flat (stn. 09–58; 0°01'38.64"N, 127°14'38.53"E). Holotype: female 1.55 mm with non-setose oöstegites, completely dissected and mounted in lactophenol on single slide; coverslip sealed with nail varnish. Deposited in the Division of Zoology, Museum Zoologicum Bogoriense, Indonesian Institute of Sciences (LIPI), Cibinong, Indonesia. Accompanying fauna: *Ingolfiella moluccensis* Vonk and Jaume, 2013.

**Diagnosis** Cephalic (“ocular”) lobes present. Dactyli of gnathopods provided with four strong denticles along posterior margin. Female G2 palm angle robust seta bifid; posteromedial surface of carpus lacking broad triangular spine. Medial surface of protopod of U2 with three denticle combs. Unguis of P3–P4 multidenticulate with four denticles; that of P5–P6 multidenticulate; that of P7 bifid. Female PL1–PL3 all developed. Oöstegites on P3–P5.

**Etymology** Species named after the late Dr Lazare Botosaneanu (Amsterdam), who in many ways encouraged authors to study the crustacean stygofauna.

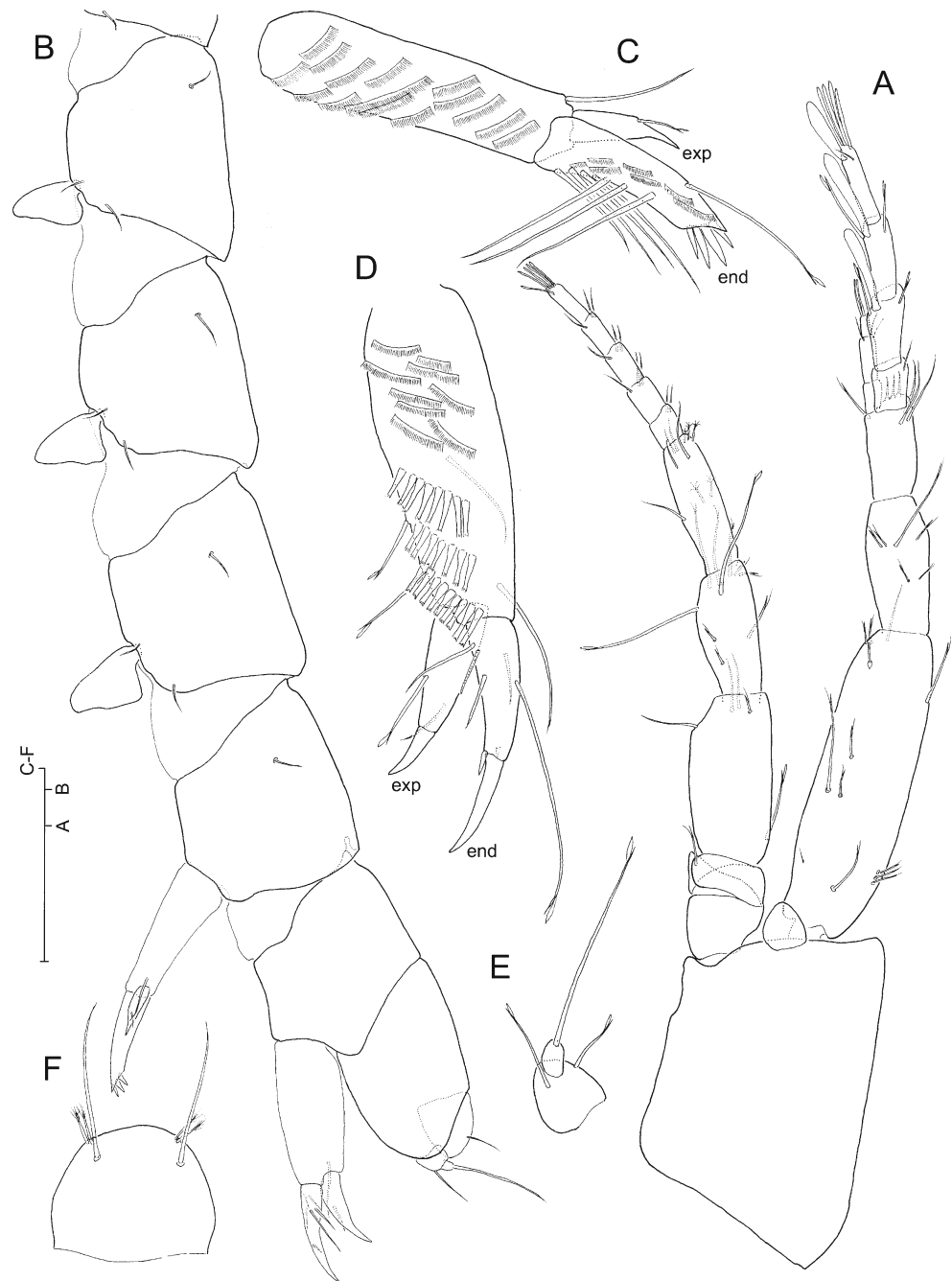
**Distribution** Known thus far only from the type locality.

**Description of female Head** (Fig. 1a) with weakly protruding rostrum; lateral lobes and postantennal sinus hardly developed; cephalic (“ocular”) lobes subtriangular in lateral aspect, reaching halfway of first segment of antennal peduncle. **Epimeral plates** (Fig. 1b) on pleonites hardly developed, each crowned with simple seta.

**Antennule** (Fig. 1a) peduncle segments 1–3 progressively shorter towards distal, length ratio as 1: 0.44: 0.37; flagellum 4-articulate, longer than peduncle segments 2–3 combined; articles 2–4 each with aesthetasc. Accessory flagellum 3-articulate, shorter than two proximal articles of main flagellum combined.

**Antenna** (Fig. 1a) slightly shorter than antennule; gland cone short, hardly visible and pointing anteroventrally; protopodal segments 3–5 length ratio as 1: 0.90: 0.83; fourth segment with cluster of long flagellate setae near distal margin. Flagellum 5-articulate, shorter than protopodal segments 4–5 combined.

**Fig. 1** *Ingolfiella botoi* sp. nov., holotype female: **a** head with left antennule and antenna attached, lateral (ornamentation of flagellum of antennule incompletely resolved); **b** detail of pleonites, urosomites and telson, lateral; **c** left uropod 1, medial; **d** left uropod 2, medial; **e** right uropod 3, dorsal; **f** telson, dorsal. Scale bar (a, c–f) 0.05 mm, (b) 0.1 mm



*Labrum* and *paragnaths* (Fig. 2g) apparently non-setulose, ordinary. *Paragnaths* lacking inner lobes; outer lobes bent into pointed tip, each provided with glandular conduit.

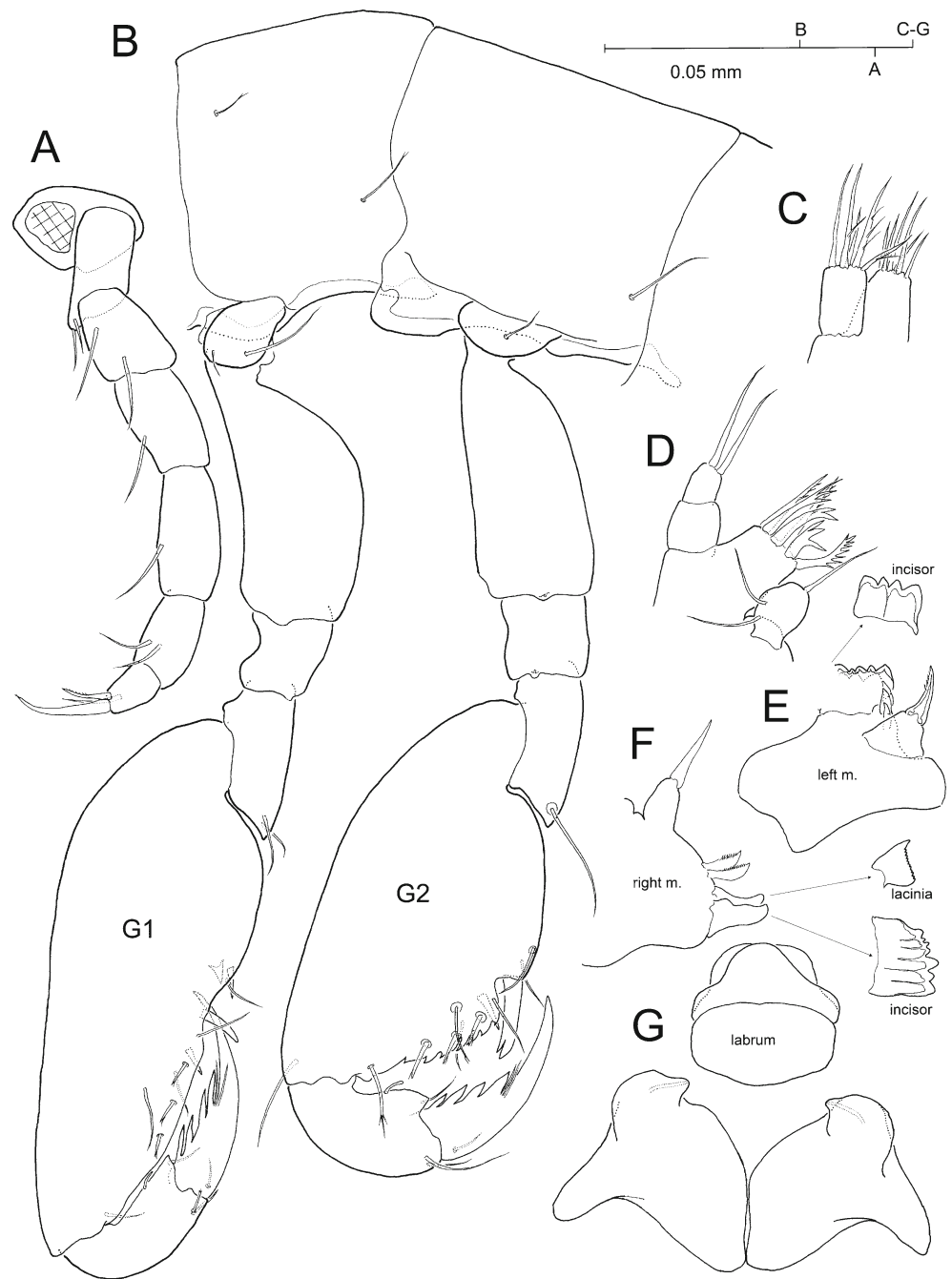
*Mandibles* molar process non-tritulative, spiniform. *Left mandible* (Fig. 2e) incisor subrectangular, cutting-edge 4-denticulate; lacinia subrectangular, as broad as incisor, cutting edge 5-denticulate; spine row consisting of three pectinate elements; spiniform molar process finely serrated. *Right mandible* (Fig. 2f) with 7-denticulate incisor and finely multi-denticulate lacinia, latter constricted basally; spine row reduced to two elements; spiniform molar process apparently smooth.

*Maxillule* (Fig. 2d) coxal endite (=inner lobe) with three simple setae; basal endite (=outer lobe) with six robust setae of which one bifid, two trifid, two (longer) 4- and 5-denticulate, respectively, and one (innermost) comb-like; endopod (=palp) 2-segmented, proximal segment unarmed, distal segment with two apparently simple setae.

*Maxilla* (Fig. 2c) with short, subequal blunt plates, outer plate with five distal setae, inner plate with six; three out of setae on outer plate sparsely setulose.

*Maxilliped* (Fig. 2a) basal endite reduced, almost indistinct, with two simple setae; ischium with two simple setae on

**Fig. 2** *Ingolffiella botoi* sp. nov., holotype female: **a** right maxilliped, posterior; **b** pereonites 1–2 with gnathopods 1–2 attached, lateral; **c** right maxilla, posterior; **d** maxillule; **e** left mandible exposing lacinia and with inset of incisor; **f** right mandible with insets of incisor and lacinia; **g** labrum and paragnaths, ventral



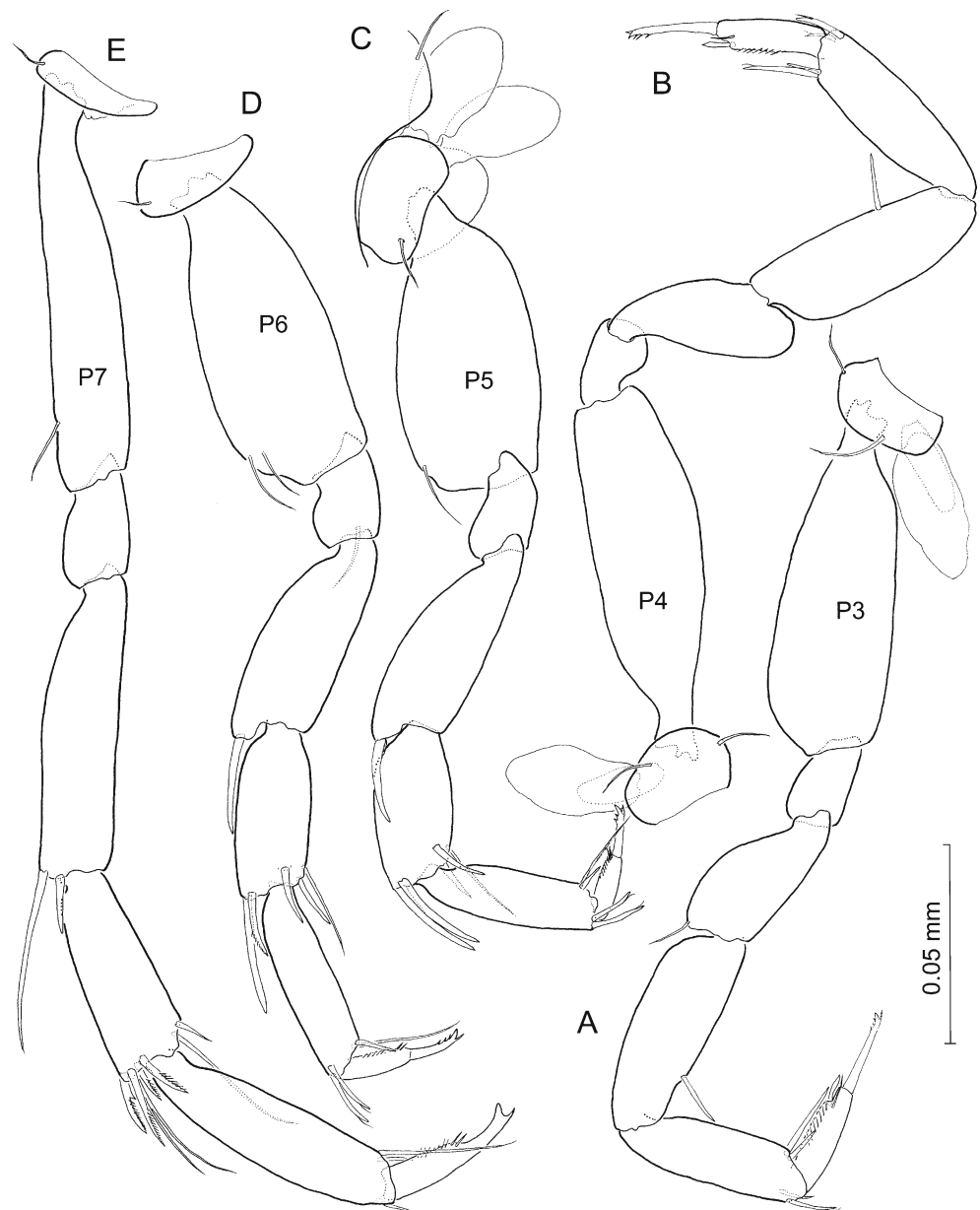
inner margin; merus, carpus, and propodus each with single simple seta on medial margin except propodus of right branch, which wears two; dactylus short, subtriangular, with simple robust seta proximally on outer margin, pinnate distomedial seta, and long (longer than segment) unguis. Neither propodus nor dactylus ornamented with setules.

*Coxal gills* (Fig. 3a–c) present on P3–P5, ovoid, stalked. *Oöstegites* (Fig. 3a–c) on P3–P5, ovoid, shorter than corresponding coxal gill except oöstegite 5 which is similar in size; oöstegites smooth, none wearing marginal setae nor short pointed processes as those described in other species.

*Gnathopod 1* (Fig. 2b) carpo-subchelate. Coxa with two unequal simple setae. Carpus 2.8 times as long as broad, with three short flagellate robust setae along lateral side of palm margin, and stronger simple robust seta on medial side; palm margin strongly oblique, smooth; palm angle marked by stout, slightly upcurved simple robust seta; simple robust seta plus broad triangular spine placed submarginally on medial surface of segment close to posterior margin. Dactylus with four stout denticles along posterior margin.

*Gnathopod 2* (Fig. 2b) carpo-subchelate, carpus massive, shorter (attaining only 80 % of length) and stouter (2 times as

**Fig. 3** *Ingolfiella botoi* sp. nov., holotype female, pereopods 3–7, lateral: **a** left P3; **b** left P4; **c** left P5; **d** right P6; **e** right P7



long as broad vs. 2.8 times) than carpus of G1; palm margin convex and strongly serrated, lined up with three unicuspidate flagellate robust setae along lateral side, and single, stouter simple robust seta on medial side; palm angle marked by stout, slightly upcurved bifid robust seta; medial surface of segment lacking broad triangular spine placed close to posterior margin. Dactylus with four stout denticles along posterior margin, denticles stouter than G1 counterparts.

*Pereopods 3–4* (Fig. 3a, b) subequal except basis and propodus of P4, which are longer than corresponding P3 counterparts. Dactylus of both limbs with row of setules along medial margin, and with stout simple robust seta and tiny simple seta placed close together near distomedial angle of segment. Unguis of both limbs shorter than corresponding

dactylus, multidenticulate, each with five distal denticles except left P4, which only wears four. Coxae each with two long simple setae as figured.

*Pereopods 5–7* (Fig. 3c–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 and row of setules along medial margin; unguis of P7 completely incorporated into dactylus, bifid, with strong triangular tooth subterminally on lateral margin; unguis of P5 4- or 5-denticulate, that of P6 5-denticulate. Pereiopod 7 (Fig. 3e) with one of distal armature elements on distolateral angle of carpus modified into comb-like robust seta provided with proximal spur. Coxa of P5 with single seta on anteroventral lobe; coxae of P6–P7 each with single seta on posteroventral lobe.

*Pleopods* (Fig. 1b) leaf-like, smooth, and non-setose.

*Uropod 1* (Fig. 1c) protopod long and slender, about 3.6 times as long as broad, with simple seta on anterolateral (=ventrolateral) margin; medial surface of segment adorned with tightly-set, comb-like crescent integumentary scales. Exopod unsegmented, much shorter than endopod, acuminate, with seta placed at ca. three-fifths length of outer margin. Endopod with short terminal spine plus row of four stout triangular robust setae subterminally; row of seven setae disposed on segment as figured; medial surface of segment with crescent scales as in protopod.

*Uropod 2* (Fig. 1d) protopod bearing three oblique combs of large denticles on medial surface; denticles apparently triangular but with variably frayed tips; four simple setae distributed on segment as figured; proximomedial surface of segment ornamented with tightly-set, comb-like crescent integumentary scales. Rami tapering, exopod stouter and shorter than endopod, more inflated basally, provided with two setae. Endopod with seven heterogeneous setae distributed as figured. Pointed distal portion of each ramus separated from proximal portion of segment by suture line; whether this pointed distal portion represents a stout robust seta or corresponds to the distal article of a 2-articulate ramus remains unresolved; nevertheless absence of intrinsic muscles suggests both rami are unsegmented.

*Uropod 3* (Fig. 1e) tiny, uniramous. Protopod subquadrate, with simple seta at each side. Exopod much shorter than protopod, with long simple seta subterminally on tip.

*Telson* (Fig. 1f) about as long as broad with evenly-rounded margins; armature comprising long simple seta and pair of short penicillate setae at each side on dorsal surface.

**Remarks** The new species from Indonesia is unique among ingolfiellideans in the display of a multidenticulate unguis on P5–P6. Aside of this autapomorphy, the new species has most of its character state conditions in common with *I. quadridentata* Stock, 1979, from coarse sublittoral sands up to 4 m depth in Curaçao (Dutch Antilles), based on the combined display of (see Table 1): (1) cephalic (“ocular”) lobes; (2) four denticles on posterior margin of dactylus of G2; (3) bifid (vs. simple) strong robust seta on palm angle of G2; (4) lack of broad triangular spine on posteromedial surface of carpus of G2; (5) three denticle combs on medial surface of protopod of U2; (6) unguis of P3–P4 multidenticulate; (7) unguis of P7 bifid; and (8) retention of the three pairs of female pleopods. However, both taxa differ remarkably in the arrangement of oöstegites (present on P3–P5 in the new species, vs. only on P3–P4 in *I. quadridentata*), among other features. Unfortunately, neither the male of the new taxon nor of *I. quadridentata* are known, impeding any refinement in the establishment of the species complete morphology.

As stated above, the single specimen known of *I. botoi* sp. nov. was found in a sample containing *I. moluccensis*. Both

taxa can be readily distinguished based on the presence in the latter species of only two pairs of oöstegites (vs. three pairs in the new taxon); the trifid condition of unguis of P3–P4 (vs. multidenticulate); G2 palm angle robust seta simple (vs. bifid); broad triangular spine on posteromedial surface of carpus of female G2 present (vs. absent); aside the most remarkable autapomorphic features of both taxa (i.e. multidenticulate unguis of P5–P6 in *I. botoi*; P5 basis with a proximolateral outgrowth in *I. moluccensis*; see Table 1; Vonk and Jaume 2013).

## Discussion

The Moluccas are placed in the centre of the Coral Triangle, the area of highest marine species diversity (Hoeksema 2007) with overlapping ranges of many benthic species. Most of these species have a larval phase, and dispersal by ocean currents is common. The low sea level stand during the last glacial maximum and the direction of inter-oceanic currents from the Pacific to the Indian Ocean are considered important determinants of the ranges of coral species (Hoeksema 2007). Because subterranean amphipods are perceived in general as poor dispersers (Lefébure et al. 2006; Notenboom 1991; Vonk 1988), their distribution patterns are expected to respond more to vicariance than to drifting along with oceanic currents (Holsinger 1991; Stock 1993; Myers and Lowry 2009; Bauzà-Ribot et al. 2012). However, subterranean beach environments are very dynamic, even at secluded spots, and their fauna moves with the sediment, suggesting at least some dispersal within coastal areas (Vonk and Sánchez 1991; Vonk and Nijman 2006).

Syntopy, a term coined for related species which occupy the same macrohabitat and occur in the same locality (Rivas 1964), pertains to the two ingolfiellid species in the coral rubble of Lelei island beach in the Gura Ici archipelago, and is only the third instance in which this has been reported for the ingolfiellid group. In general, syntopy is much less recorded than sympatry in benthic crustaceans, although the literature is fraught with incidences when this co-occurrence is relevant to explain behavior in micro-niches (Hoeksema and Fransen 2011; Vázquez-Luis et al. 2009). The opposite is also important to study in its minute aspects. An intensive and detailed study of the large stygobiont freshwater amphipod genus *Niphargus* Schiödte in Slovenia (Fišer et al. 2010) showed that two species occupying the so-called superficial subterranean environment, and found in totally overlapping sympatry, did not co-occur in the same sampling sites. Seemingly, the repetitive probing of the underground by casting the nets in a small area over a long period of time can result in the discovery of several species in slightly different microhabitats at close range to each other (Vonk and Sánchez 1991; Otegui et al. 2012). Thus, on the Caribbean islands of Aruba,

**Table 1** Some relevant features of *Ingolfiella* species. See Yonk and Jaume (2013: table 1) and Iannilli and Yonk (2013) for taxonomic and distributional information on species

	Cephalic lobes ("ocular")	G1–G2, # of denticles on posterior margin of dactylus	G2, palm angle robust seta (1: simple; 2: bifid)	G2, broad triangular spine on posteromedial surface of carpus	U2, # of 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; 4: multidenticulate)	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 PL1–PL3	Oöstegites
<i>I. botoi</i> sp. nov.	+	4–4	2	–	3	4	P5–P6: 4 P7: 2	?	?	?	?	?	+	P3–P5
<i>I. abyssii</i>	+	4–4	1	–	4	2	1	?	?	?	?	?	+	?
<i>I. acherontis</i>	+	3–3	1	?	3	2	2	?	?	?	?	?	?	?
<i>I. alba</i>	+	4–4	1	+	3	3	2	+	–	+	+	+	+	P3–P5
<i>I. arganoi</i>	+	4–4	1	+	2 (m) 3 (f)	3	2	–	–	–	–	+	+	P3–P4
<i>I. atlantisi</i>	+	4–4	1	–	3	P3: 2 P4: 1	1	?	?	?	?	?	+	?
<i>I. australiana</i>	+	4–3	1	–	5	2	1	–	–	–	–	+	+	?
<i>I. azorensis</i>	–	4–4	1	–	3	3	2	–	–	–	–	+	?	?
<i>I. bassiana</i>	+	3–3	2 (m) 1 (f)	?	4	2	1	+	+	–	+	+	+	?
<i>I. beatricis</i>	+	4–4	1	–	3	2	2	?	?	?	?	?	+	?
<i>I. berrisfordi</i>	+	3–3	1	–	5	3	1	–	–	–	+	+	?	?
<i>I. britannica</i>	+	4–4	2	+	3–4	1	?	?	?	?	?	?	+	P3–P5
<i>I. canariensis</i>	+	4–4	1	+	3	3	2	+	–	+	+	+	+	P3–P5
<i>I. catalanensis</i>	?	3–3	1	+	3	2	2	–	+	–	+	–	?	?
<i>I. cf. catalanensis</i>	–	3–3	1	–	8	2	2	–	–	–	+	–	?	?
<i>I. cottarelli</i>	–	3–3	1	?	6–7	1	1	–	–	–	–	–	–	?
<i>I. fontinalis</i>	+	3–3	1	–	3	1–2	–	–	+	–	+	+	+	?
<i>I. fuscina</i>	+	4–4	1	+	4	3	2	–	–	–	–	+	+	P3–P5
<i>I. georgei</i>	+	3–3	2 (m) 1 (f)	–	3–4	4	1	–	–	–	+	+	+	?
<i>I. grandispina</i>	+	3–3	1	–	5	4	1	?	?	?	?	?	+	P3–P4
<i>I. inermis</i>	+	4–4	1	–	3	3	2	?	?	?	?	?	+	P3–P4
<i>I. ischitana</i>	+	3–3	1	?	4	4	1	–	–	–	–	+	+	P3–P5
<i>I. kapuri</i>	+	4–4	1	+	3	3	2	?	?	?	?	?	+	?
<i>I. littoralis</i>	+	0–3	1	+	3	2	1	?	?	?	?	?	+	?
<i>I. longipes</i>	+	4–4	1	+	3	2	2	?	?	?	?	?	+	?
<i>I. macedonica</i>	–	4–4	1	?	4	?	1	–	–	–	–	–	+	?
<i>I. manni</i>	–	3–3	1	?	3	1	1	–	–	–	–	+	+	?
<i>I. margaritae</i>	–	3–3	1	–	3	2	2	–	+	–	+	+	?	?

Table 1 (continued)

	Cephalic (“ocular”) lobes	G1–G2, # of denticles on posterior margin of dactylus	G2, palm angle	G2, broad triangular spine on posteromedial surface of carpus	U2, # of 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; 4: multidenticulate)	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 PL1–PL3	Oöstegites
<i>I. moluccensis</i>	+	4–4	1	+	3	3	2	+	–	+	+	+	+	P3–P4
<i>I. ogasawensis</i>	+	4–4	1	–	3	3	2	?	?	?	?	?	+	P3–P5
<i>I. petkovskii</i>	–	3–3	1	–	3	2	2	–	+	–	–	+	+	?
<i>I. cf. petkovskii</i>	?	3–3	1	– (m)? (f)	3	2	2	–	+	–	+	+	+	?
<i>I. putealis</i>	+	3–3	1	–	3	2	2	–	+	–	+	+	+	?
<i>I. quadridentata</i>	+	4–4	2	–	3	4	2	?	?	?	?	?	+	P3–P4
<i>I. quokka</i>	+	4–4	2	+	3	3	2	+	–	–	+	+	+	?
<i>I. rocaensis</i>	+	4–4	1	+	?	3	2	?	?	?	?	?	+	P3–P4
<i>I. ruffoi</i>	+	4–4	?	?	3	2	2	–	–	–	–	+	+	P3–P4
<i>I. sandroruffoi</i>	+	4–4	1	+	4	4	3	+?	–	–	–	+	+	P3–P4
<i>I. similis</i>	–	3–3	1	–	3	2	2	–	+	–	+	+	+	?
<i>I. tabularis</i>	+	3–3	1	–	3	2	2	–	+	–	+	+	+	?
<i>I. thibaudi</i>	?	3–3	1	? (m) + (f)	5	1	1	?	–	–	?	–	–	?
<i>I. unguiculata</i>	+	3–3	1	+	3	2	2	–	+	–	+	+	+	?
<i>I. uspallatae</i>	–	3–3	1	–	4	1?	1?	?	?	?	?	?	+	?
<i>I. vandeli</i>	?	3–3	1	– (m)? (f)	3	2	2	–	+	–	+	+	+	?
<i>I. xarifae</i>	+	3–4	1	+	3	3	2	?	?	?	?	?	+	?



Curaçao and Bonaire, five ingolfiellid species have been described after years of intensive sampling and, although none of those co-occurred at exactly one locality, at least some of these species shared a comparable micro-habitat: brackish to oligohaline wells and springs on the land side, marine sands and anchialine pools on the sea side (Stock 1976, 1977, 1979). None of these reports, although close in distance, corresponded to the same well or beach interstitial area after years of repetitive sampling.

**Acknowledgments** We are grateful to Prof. Dr. Suharsono, Director of RCO-LIPI, for sponsoring the research. Ir. Yosephine Tuti assisted in the preparations and logistics of the expedition. We thank Mr. Fasmí Ahmad, head of the LIPI research station in Ternate, for his assistance. Mr. Sumadijo (RCO-LIPI, Jakarta) and students Samar Ishak and Dodi Kahar assisted in the fieldwork and were guides and translators; their help and creativity were indispensable. Bert Hoeksema (Naturalis, Leiden) and Oliver Coleman (Museum für Naturkunde, Berlin) are thanked for helpful comments and suggestions concerning this paper, as is an anonymous reviewer who clarified important matters. The research permit was issued by the Indonesian State Ministry of Research and Technology (RISTEK). Contribution to Spanish MCINN project CGL2012-33597, partially financed with FEDER funds.

## References

- Bauzá-Ribot MM, Juan C, Nardi F, Oromí P, Pons J, Jaume D (2012) Mitogenomic phylogenetic analysis supports continental-scale vicariance in subterranean thalassoid crustaceans. *Curr Biol* 22: 2069–2074
- Bou C (1970) Observations sur les ingolfiellides (Crustacés Amphipodes) de Grèce. *Biol Gallo-Hellenica* 3:57–70
- Bou C (1974) Les méthodes de récolte dans les eaux souterraines interstitielles. *Ann Spéol* 29:611–619
- Coineau N (1963) Présence du sous-ordre des Ingolfiellidea Reibisch (Crustacea, Amphipoda) dans les eaux souterraines continentales de France. *CR Acad Sci* 256:4729–4731
- Coineau N (1968) Contribution à l'étude de la faune interstitielle. Isopodes et amphipodes. *Mém Mus Nat Hist Nat Paris (a)* 55:147–214
- Cvetkov L (1964) Sur l'identification en Bulgare de l'*Ingolfiella petkovskii* Karaman (Crustacea Amphipoda). *Bull Inst Zool Mus (Sofia)* 15:185–190 (in Bulgarian)
- Dojiri M, Sieg J (1987) *Ingolfiella fuscina*, new species (Crustacea: Amphipoda) from the Gulf of Mexico and the Atlantic coast of North America, and partial redescription of *I. atlantisi* Mills, 1967. *Proc Biol Soc Wash* 100:494–505
- Fišer C, Konec M, Kobe Z, Osanič M, Gruden P, Potočnik H (2010) Conservation problems with hypothelminorheic *Niphargus* species (Amphipoda: Niphargidae). *Aquat Conserv: Mar Freshw Ecosyst* 20:602–604
- Griffiths CL (1989) The Ingolfiellidae (Crustacea: Amphipoda) of southern Africa, with descriptions of two new species. *Cimbebasia* 11: 59–70
- Griffiths CL (1991) A new ingolfiellid (Crustacea: Amphipoda) from subterranean waters in western Namibia. *Cimbebasia* 13:75–79
- Hansen HJ (1903) The Ingolfiellidae, fam. n., a new type of Amphipoda. *J Linn Soc (Zool)* 29:117–133
- Hoeksema BW (2007) Delineation of the Indo-Malayan Centre of maximum marine biodiversity: the coral triangle. In: Renema W (ed) *Biogeography, time and place: distributions, barriers and islands*. Springer, Dordrecht, pp 117–178
- Hoeksema BW, Fransen CHJM (2011) Space partitioning by symbiotic shrimp species cohabitating in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. *Coral Reefs* 30:519
- Holsinger JR (1991) What can vicariance biogeographic models tell us about the distributional history of subterranean amphipods? *Hydrobiologia* 223:43–45
- Iannilli V, Vonk R (2013) A new Ingolfiellid (Crustacea, Amphipoda, Ingolfiellidae) from an anchialine pool on Abd al Kuri Island, Socotra Archipelago, Yemen. *Zookeys* 302:1–12
- Iannilli V, Berera R, Cottarelli V (2008) Description of the first marine interstitial ingolfiellid from Philippines, *Ingolfiella alba* sp. nov., with some remarks on the systematic of the genus (Amphipoda: Ingolfiellidae). *Zootaxa* 1675:49–58
- Karaman SL (1957) Eine neue *Ingolfiella* aus Jugoslawien, *Ingolfiella petkovskii* n. sp. *Folia Balc* 1(7):35–38
- Latreille PA (1816) Amphipoda. In: *Nouveau Dictionnaire d'histoire naturelle, appliquée aux Arts, à l'Agriculture, à l'Économie rurale et domestique, à la Médecine, etc. Par une société de Naturalistes et d'Agriculteurs*. 2nd edition. Volume 1. Deterville, Paris, pp 467–469
- Lefébure T, Douady CJ, Gouy M, Trontelj P, Briolays J, Gibert J (2006) Phylogeography of a subterranean amphipod reveals cryptic diversity and dynamic evolution in extreme environments. *Mol Ecol* 15: 1797–1806
- Myers AA, Lowry JK (2009) The biogeography of Indo-West Pacific tropical amphipods with particular reference to Australia. *Zootaxa* 2260:109–127
- Notenboom J (1991) Marine regressions and the evolution of groundwater dwelling amphipods (Crustacea). *J Biogeogr* 18:437–454
- Otegui MBP, Blankenstejn A, Pagliosa PR (2012) Population structure, growth and production of *Thoracophelia furcifera* (Polychaeta: Opheliidae) on a sandy beach in Southern Brazil. *Helgol Mar Res* 66:479–488
- Rivas LR (1964) A reinterpretation of the concepts “Sympatric” and “Allopatric” with proposal of the additional terms “Syntopic” and “Allotopic”. *Syst Zool* 13:42–43
- Ruffo S (1951) *Ingolfiella leleupi* n. sp. nuovo anfipodo troglobio del Congo Belga. *Rev Zool Bot Afr* 44:189–209
- Ruffo S (1964) Studi sui crostacei anfipodi LVII: Un nuovo ingolfiellide delle acque sotteranee dell'Africa di Sud Ovest. *Boll Zool* 31: 1019–1034
- Ruffo S (1985) Un nuovo ingolfiellideo delle acque sotteranee della Namibia: *Stygobarnardia caprellinoides* n. gen. n. sp. *Atti Soc Ital Sci Nat Mus Civ Stor Nat Milano* 126:43–53
- Stock JH (1976) A new member of the crustacean suborder Ingolfiellidea from Bonaire, with a review of the entire suborder. *Stud Fauna Curaçao Caribb Islands* 50:56–75
- Stock JH (1977) The zoogeography of the crustacean suborder Ingolfiellidea, with descriptions of new West Indian taxa. *Stud Fauna Curaçao Caribb Islands* 55:131–146
- Stock JH (1979) New data on taxonomy and zoogeography of ingolfiellid Crustacea. *Bijdr Dierk* 49:81–97
- Stock JH (1993) Some remarkable distribution patterns in stygobiont Amphipoda. *J Nat Hist* 27:807–819
- Vázquez-Luis M, Guerra-García JM, Sanchez-Jerez P, Bayle-Sempere JT (2009) Caprellid assemblages (Crustacea: Amphipoda) in shallow waters invaded by *Caulerpa racemosa* var. *cylindracea* from south-eastern Spain. *Helgol Mar Res* 63:107–117
- Vonk R (1988) The *Niphargus kochianus*-group (Crustacea, Amphipoda) in the Aquitanian Basin, south-western France, and a supposed case of introgressive hybridization. *Stygologia* 4:177–191
- Vonk R, Jaume D (2013) A new ingolfiellid amphipod crustacean from sandy beaches of the Gura Ici Islands, Western Halmahera (North Moluccas). *Raffles Bull Zool* 61:547–560
- Vonk R, Nijman V (2006) Sex ratio and sexual selection in wormshrimps (Crustacea, Amphipoda, Ingolfiellidea). *Contrib Zool* 75:189–194

- Vonk R, Notenboom J (1996) The phreatic aquifer of the 'Plana de Castellón' (Spain): first Iberian record of ingolfiellid Amphipoda. *Boll Mus Civ Stor Nat Verona* 20:337–343
- Vonk R, Sánchez E (1991) A new marine interstitial ingolfiellid (Crustacea, Amphipoda, Ingolfiellidea) from Tenerife and Hierro. *Hydrobiologia* 223:293–299
- Vonk R, Schram FR (2003) Ingolfiellidea (Crustacea, Malacostraca, Amphipoda): a phylogenetic and biogeographic analysis. *Contrib Zool* 72:39–72
- Watling L (1989) A classification system for crustacean setae based on the homology concept. In: Felgenhauer B, Watling L, Thistle AB (eds) *Functional morphology of feeding and grooming in Crustacea*. Balkema, Rotterdam, pp 15–26