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A NEW MEMBER OF THE CRUSTACEAN SUBORDER INGOLFIELLIDEA FROM BONAIRE,

with a review of the entire suborder

by

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A single specimen of an ingolfiellid was found in a slightly brackish well (locally called a "pos") on the Bacuna estate in the island of Bonaire (Netherlands Antilles). The specimen differs from all other 21 ingolfiellid taxa, and is described as a new species, *Ingolfiella* (*Gevgeliella*) *putealis*.

The two classification systems in use for the Ingolfiellidea, that of KARAMAN (1959) and that of RUFFO (1970), are compared and both are found not entirely satisfactory in the light of recent discoveries. A new system is devised, in which the suborder is divided into 2 families, together with 3 genera and 5 subgenera. The genera and subgenera do not only represent morphological unities, but also combine species with similar habitat requirements. Within the series, the marine genera are distinctly plesiomorph, the limnic genera show various degrees of apomorphy.

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I am greatly indebted to Mr. J. HERRERA, of Kralendijk (Bonaire) for guiding me on his estate, Bacuna, to the well where the material whereupon this paper is based was collected.

Finally I wish to thank Dr. H. A. TEN HOVE (Zoological Laboratory, Utrecht) for taking a number of well samples from Bonaire, which – though not yielding any Ingolfiellidea – contained several interesting animals. Dr. H. E. COOMANS (Amsterdam) indentified the accompanying snails.

INTRODUCTION

The Ingolfiellidea occupy an isolated position within the Crustacea, as a separate suborder with distinct affinities to the Amphipoda (SIEWING, 1963). Several authors (KARAMAN, 1933, 1959; COINEAU, 1963; LELEUP, 1955) consider the group "primitive" or "archaeic", and as a matter of fact the scattered present-day distribution, the wide habitat range, and the wide bathymetrical range are solid indications for the antiquity of the ingolfiellids. Members of the group have been found in groundwater of river beds and sea beaches, in caves, on coral flats, and in deeper waters reaching from infralittoral sands to the deep-sea. They have been recorded from Europe, Asia, Africa, North and South America.

On the other hand, as SIEWING (1963) pointed out, there is not a single argument in favour of the assumption that the ingolfiellids should be morphologically primitive. NOODT (1965) states, and he is quite justified in my opinion, that the ingolfiellids are developed highest and have reached an extreme degree of adaptation towards the "Lebensformtyp Mesopsammon" (REMANE, 1952), expressed by an elongated, worm-like body, loss of pigmentation and eyes, aberrant reproduction, progressive reduction of the appendages (mostly starting at the posterior end of the body), and a small body size.

Although nothing factual about the reproduction is known, SCHIECKE (1973: 109), commenting upon the poorly developed brood-plates incapable of holding the eggs, wonders whether this "morphologisch extrem apomorphe Form ihre Eier frei ablegt – ein bei Peracariden einmaliger Vorgang".

SYSTEMATICS OF THE INGOLFIELLIDEA

Up to recently, the Ingolfiellidea were considered morphologically very uniform, showing no differences on a level higher than the specific one, notwithstanding the enormous habitat range (from continental cave waters, through mesopsammal habitats, to the deep-sea). In recent years, two attempts have been made to break the group up in generic units. The oldest, and only partial, attempt is that of S. KARAMAN, 1959 (p. 78–79), who distributed the six known species over four monotypic genera, leaving two species "vorderhand nicht eingeteilt". In a later, elegant, attempt, RUFFO, 1970, used a combination of morphological and ecological characters to subdivide the known species (the number of which had risen to 14 at that time) into two families and four genera. The small-sized mesopsammal forms fall, according to RUFFO's system in two genera: *Balcanella* Karaman, 1933, and *Ingolfiella* Hansen, 1903, the former without ocular lobes and distributed in phreatic, continental waters, the latter with ocular lobes and distributed in bathybenthic, mesopsammal or macroporous reef habitats.

The discovery of a number of new taxa in the most recent years brings the total number of ingolfiellids known on 21. Some of the newly discovered forms do not support the division between *Ingolfiella* and *Balcanella* on a combined morphological/ecological basis: the limnic genus *Balcanella* contains at least one species, *ruffoi* (Siewing, 1963) from marine beaches, whereas the new species described in the present paper, though having an ocular lobe like *Ingolfiella*, is not marine but is found in inland waters. Several *Ingolfiella* species (e.g., *putealis* n. sp., *kapuri* Coineau & Rao, 1972, *berrisfordi* Ruffo, 1974) have so small an ocular lobe, that one wonders whether this structure has not been overlooked in some of the so-called *Balcanella* species.

We follow RUFFO in subdividing the Ingolfiellidea into two families, the Metaingolfiellidae (with one genus, *Metaingolfiella*), and the

Ingolfiellidae. For the latter family, we will develop in the sequel some new ideas about its possible division into genera and subgenera.

It is quite clear that the family Ingolfiellidae contains two distinct groups of species: a group of large-sized species (up to 23 mm) united in the genus *Trogloleleupia*, and consisting of 3 species, and a larger group of small-sized forms (up to 3 mm). When one analyses the morphological characters of the small-sized group, there appear to be clusters of species, some with more plesiomorph characters, others with clearly apomorph characters. The apomorph characters are not realized simultaneously, but step by step and probably at different evolution speed and along different evolution lines.

We consider the following characters (within the small-sized Ingolfiellidae) as plesiomorph: the carpus ("hand") of the first and second gnathopods are more or less similar in shape; the palm of gnathopod 2 is almost vertical; the finger of gnathopod 2 is very long (3/4 to 9/10 of the posterior margin of the carpus); neither the gnathopods nor the pleopods show secondary sexual differences; the ocular lobe is well-developed.

In more apomorph clusters of species, the ocular lober is in gradual reduction; the differences in shape between gnathopods 1 and 2 get greater; the claw of the 2nd gnathopod gets shorter; certain secondary sexual differences develop in the 2nd gnathopod and in the pleopods. So, the carpus of gnathopod 2 in male bears in the more apomorph species a "differentiated element" (a reversed pectinated spine or a reversed bag-like spine). In plesiomorph species, the pleopods are similar in both sexes: unarmed, triangular plates; in apomorph species, the first male pleopod is setiferous and changes shape, whereas the 2nd and 3rd male pleopods may disappear.

Five clusters of species are found this way (Table 8). Since these clusters unite not only species of similar morphology, but also forms originating from a same type of habitat, in a trend from marine to limnic, each cluster is given nomenclatorial status. Since a number of species is known from one sex only, the location of these species remains presumptive. However, the proposed arrangement leaves at present no "loose ends" in the form of unclassified species.

I have preferred to use subgenera instead of genera for the re-

TABLE 8

SALIENT CHARACTERS ON WHICH THE SUBDIVISION OF THE GENUS *Ingolfiella* S. L. INTO 5 SUBGENERA IS BASED

	1. *Ingolfiella* s. str.	2. *Hanseniella*	3. *Trianguliella*	4. *Gevgeliella*	5. *Balcanella*
Carpus of Gn. 1 and 2	about equal in shape	dissimilar	strongly dissimilar	dissimilar	dissimilar
Palm of Gn. 2	almost vertical	oblique	oblique to transverse	oblique	oblique
Finger of Gn. 2	> ¾ posterior margin of carpus	< ¾	< ¾	≤ ¾	¾
Secondary sexual differences in Gn. 2	absent	absent	absent	present	? **
Pleopods 2 and 3 (♂, ♀)	triangular (asymm.)	triangular (asymm.)	triangular (asymm.) or absent	triangular (asymm.) or absent	elongate spoon-shaped, symmetrical **
Pleopod 1, ♂	as pl. 2, 3	as pl. 2, 3	unlike pl. 2, 3 (setose)	unlike pl. 2, 3 (setose)	? **
Ocular lobe	present	present*)	small or absent	small or absent	absent
Habitat	abyssal	microporous substrates (coral reefs, sand) in medio- and infra-littoral	interstitial waters (both limnic and coastal)	continental groundwater (often near the coast)	continental groundwater (far from the coast)

*) Not mentioned for *H. ruffoi*.

**) ♂ unknown.

arrangement of the species, for a couple of reasons: (1) As compared with the other genera in the suborder Ingolfiellidea (*Metaingolfiella*, *Trogloleleupia*), the differences between the various small-sized ingolfiellids are relatively slight. An equilibrized treatment would be reached by considering the two genera just mentioned plus *Ingolfiella* s.l. as full genera, and by subdividing the latter into 5 subgenera, corresponding with the species clusters found. (2) The five units into which *Ingolfiella* s.l. is subdivided are, at least in part, distinguished by characters of a secondary sexual nature; this means that, if one has only material of one sex available, it might be impossible to classify it with certainty. Since I consider this an undesirable situation – the classification should remain practical after all – I have preferred one large genus *Ingolfiella*, which may stand for pigeon-holing all small-sized ingolfiellids, irrespective of sexual differences on which the subgenera are partly based.

A number of names on the genus-group level was already in use in the alternative systems of KARAMAN and RUFFO, hence only one new subgeneric name had to be proposed for the new system. It must be borne in mind, that the "old" names have got here a new, more strictly defined, meaning, and that the described taxa are rearranged over the subgeneric units.

The supposed evolutionary relations between the Ingolfiellidae are shown in Fig. 17.

KEYS TO THE GENERA AND SUBGENERA AND LIST OF THE SPECIES

The suborder is divided into two families (RUFFO, 1969, 1970):

— Somite bearing gnathopod 1 fused with the head. Second gnathopod chelate. Pleopods biramous. Oostegites of elongate shape. . . . . fam. METAINGOLFIELLIDAE

— Somite bearing gnathopod 1 free. Second gnathopod nonchelate. Pleopods rudimentary, uniramous. Oostegites rudimentary or absent. . . . . fam. INGOLFIELLIDAE

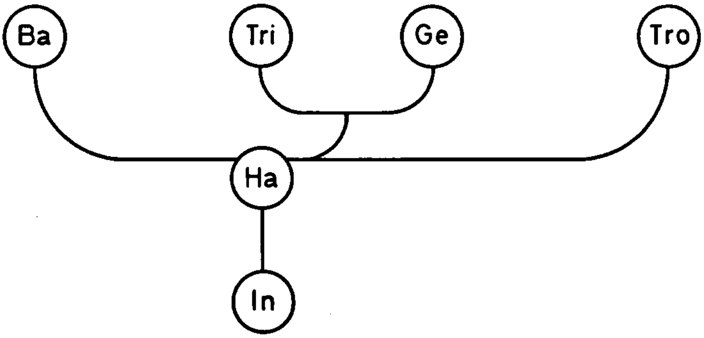

Fig. 17. Supposed EVOLUTIONARY RELATIONSHIPS between various Ingolfiellidae. – From the most plesiomorph units, In (= the abyssal subgenus *Ingolfiella*) and Ha (= the subgenus *Hanseniella* from medio- and infralittoral marine habitats), the more apomorph genera and subgenera are derived. The small-sized Tri (= *Trianguliella* from both limnic and coastal groundwater), Ge (= *Gevgeliella* from limnic, though often near-coast, groundwater) and Ba (= *Balcanella* from purely continental groundwater) form a rather coherent group. The large-sized *Trogloleleupia*, from caves and other larger subterranean water basins is apparently less closely related.

The Metaingolfiellidae are monotypic: they contain only one genus, *Metaingolfiella* Ruffo, 1969, with one species *M. mirabilis* Ruffo, 1969, from a well in southern Italy.

The Ingolfiellidae contains in RUFFO's proposal (1970) three genera. In the present attempt, this number is lowered to two, while one of RUFFO's genera is reduced to subgeneric rank. The two genera can be distinguished as follows:

— Lentiform organs on meso- and metasome very distinct. Body size large (up to 23 mm). Uropod 2 much longer than uropod 1, longer than 3rd urosomite. Peduncle of uropod 2 with more than 15 transverse rows of setae . . . . genus *Trogloleleupia* Ruffo, 1974a

— Lentiform organs poorly developed or absent. Body size small (2–3 mm). Uropod 2 hardly longer than uropod 1, subequal to 3rd urosomite. Peduncle of uropod 2 with lower number of rows of setae . . . . genus *Ingolfiella* Hansen, 1903, s.l.

Trogloleleupia (= *Leleupiella* S. Karaman, 1959, preocc.) contains 3 species: *T. leleupi* (Ruffo, 1951), the type-species by monotypy, *T. eggerti* (Ruffo, 1964), and *T. opisthodorus* (K. H. Barnard, 1966). The latter is considered synonymous with *T. eggerti* by Ruffo, 1970, but if Barnard's description (1966: 195) and drawing (fig. 2d) of the 2nd male gnathopod are correct, the great elongation of the basis prevents synonymization of *opisthodorus* and *eggerti*. Both come from wells in Namibia (S.W. Africa). The generotype, *T. leleupi*, is known from Zaire and Zambia (in caves and wells).

The genus *Ingolfiella* s.l. will contain in my view five subgenera, which can be distinguished as follows (see also Table 8):

1a) Palm of gnathopod 2 vertical. Claw of gnathopod 2 between 3/4 and 9/10 as long as the posterior margin of the carpus . . . . subgenus *Ingolfiella* s. str.
1b) Palm of gnathopod 2 oblique to transverse. Claw shorter . . 2

2a) Pleopods 1 to 3 elongately spoon-shaped, unarmed; each pleopod about symmetrical . subgenus *Balcanella* S. Karaman, 1933
2b) Pleopods 1 to 3 differently shaped (finger-shaped, triangular, setose, or absent). When present, at least pleopods 2 and 3 are asymmetrical. 3

3a) No secondary sexual differences in gnathopod 2 and the pleopods. . . . . subgenus *Hanseniella* S. Karaman, 1959
3b) Either the pleopods, or the pleopods and the gnathopod 2, are sexually dimorph 4

4a) Carpus of 2nd gnathopod strongly triangular (i.e., palm more or less transverse), not sexually dimorph. . . . . subgenus *Trianguliella* nov.
4b) Carpus of 2nd gnathopod roundedly rectangular or ovate, with differentiated reversed process in the male . . . . subgenus *Gevgeliella* S. Karaman, 1959

Ingolfiella contains in the restricted sense proposed above only 2 species, both abyssal (3422–4892 m) in the North Atlantic: *I. abyssi* Hansen, 1903, and *I. atlantisi* Mills, 1967.

Hanseniella contains 6 species, all from medio- or infralittoral (shallow) marine waters, in macroporous habitats like coral assemblages, sand bottoms, or sandy beaches. Except for the type-species *I.* (*H.*) *littoralis* Hansen, 1903 (by original designation, KARAMAN, 1959) from 2 m in the Gulf of Siam, the following taxa can be placed in this subgenus: *britannica* Spooner, 1960, from 45 m in the English Channel; *ruffoi* Siewing, 1963, from sandy beaches in S. Perú; *xarifae* Ruffo, 1966, from shallow reefs in the Maldives; *kapuri* Coineau & Rao, 1972, from intertidal sand beaches in the Andaman Is.; and *ischitana* Schiecke, 1973, from Ischia, 6–30 m.

Trianguliella is a new subgenus for which *Ingolfiella manni* Noodt, 1961, is indicated as type-species. *I.* (*T.*) *manni* lives in coastal and limnic groundwater from Chile. Other species classified with this subgenus are: *macedonica* S. Karaman, 1959, from river sands in Yougoslavia; *thibaudi* Coineau, 1968 from river sands in S. France; and *berrisfordi* Ruffo, 1974, collected at low tide on a South African beach. The subgenus is primarily characterized by its triangular carpus with a more or less transverse palm in gnathopod 2 (♂, ♀) (hence the proposed subgeneric name), the absence of sexual differences in the 2nd gnathopod, combined with the presence of sexually modified first male pleopods.

Gevgeliella is used here in a somewhat modified sense, but remains based of course on the originally indicated type-species, *I.* (*G.*) *petkovskii* S. Karaman, 1957, from limnic groundwater in the S.E. Balkans. Other species of this subgenus are: *catalanensis* Coineau, 1963, from river sands in S.E. France, *vandeli* Bou, 1970, from river sands in Greece, and *putealis* n. sp. from a slightly brackish well in Bonaire.

Under the name of *Balcanella*, used for the first time by S. KARAMAN in 1933, I unite here 2 species with similarly shaped 2nd gnathopods and with peculiar pleopods. Each pleopod is elongately spoon-shaped; a line from the implantation to the *pointed* tip divides the appendage into 2 *symmetrical* halves (in other ingolfiellids the tip is rounded and the two parts on either side of the division line are strongly asymmetrical). The type-species, by monotypy, of this subgenus is *I.* (*B.*) *acherontis* (S. Karaman, 1933), from limnic groundwater in Yougoslavia. A second species is *I.* (*B.*) *uspallatae* Noodt, 1965, from river sands in the Argentinian Andes.

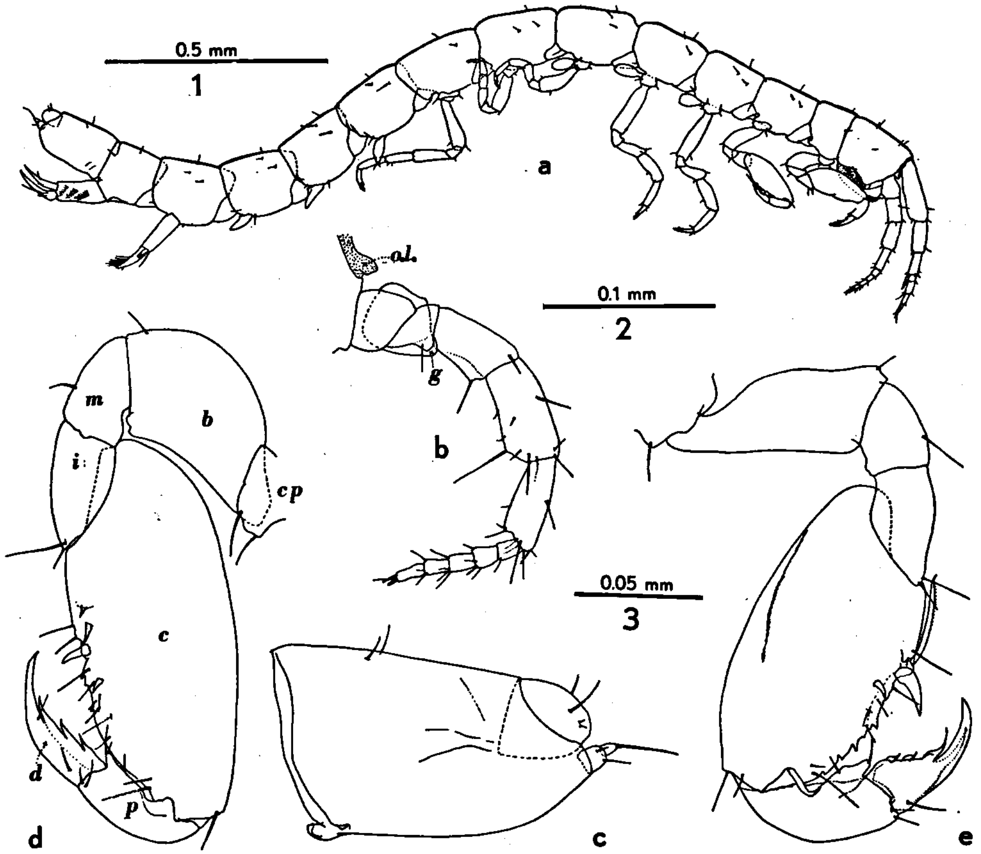

Fig. 18. *Ingolfiella putealis* n. sp., ♂ holotype. – a, entire animal, from the right (scale 1); b, second antenna (2) and ocular lobe (dotted); c, last urosomite, telson, and third uropod, from the left (2); d, first gnathopod (3); e, second gnathopod (3). [*b* = basis; *c* = carpus; *cp* = coxal plate; *d* = dactylus; *g* = gland cone; *i* = ischium; *m* = merus; *o.l.* = ocular lobe; *p* = propodus].

Ingolfiella (Gevgeliella) putealis n. sp. Figs. 10–21

Material examined. – 1♂ (holotype). Bonaire: Estate Bacuna, in a shallow well accessible to cattle (a so-called "pos di pia"), called Pos di Wayaká, situated about 1500 m E.N.E. of the Bacuna plantation house (12°07′57″ N 68°12′27″ W); November 17, 1975; depth of the water about 25 cm; the water is slightly brackish (abt. 800 mg Cl′/l); water temperature 30°.1 C. Accompanying fauna: abundant Ostracoda, some mosquito larvae, numerous *Microcharon* (Isopoda), several *Pyrgophorus parvulus* (Guilding, 1820) (a small snail). The material has been collected with a phreatobiological net (Bou, 1974, fig. 2c). – The holotype (partly dissected and mounted) is preserved in the Zoölogisch Museum, University of Amsterdam, under Amph. No. 105.252a–b.

The type locality is not far from the sea-coast (in straight line, the nearest shoreline is at a distance of 1425 m).

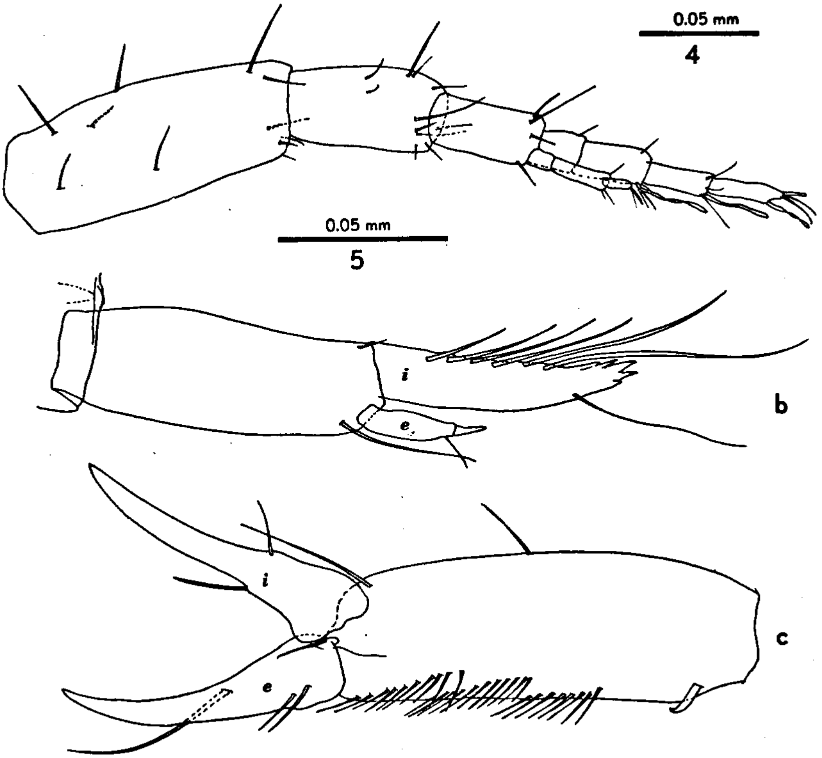

Fig. 19. *Ingolfiella putealis* n. sp., ♂ holotype. – a, first antenna (scale 4); b, first uropod (outer view) (5); c, second uropod (inner view) (5). [*e* = external ramus (= exopodite); *i* = internal ramus (= endopodite)].

Description of the male holotype. – Total body length (without antennae) about 2.0 mm. Body extremely elongated (Fig. 18a), all body somites being longer than high. Small setules occur on each body somite. The head (Fig. 20a) is devoid of eyes, but a small lamina, clearly separated from the lateral head lobes, and ending in a low triangular process, is present. This structure is usually called the "ocular lobe" (*o.l.* in Figs. 18b and 20a). In the present species, the ocular lobe is very small, much shorter than the basal segment of the 2nd antenna.

The first antenna (Fig. 19a) has a 3-segmented peduncle and a 4-segmented flagellum, the latter being shorter than the peduncle. The flagellum bears one sizable aesthete on each of the articles 2, 3, and 4. The accessory flagellum is 3-segmented, and reaches almost to the distal end of flagellum segment 2.

The second antenna (Fig. 18b) has a low gland cone. Peduncle segments 3, 4, and 5 show a low, ventral, triangular "flange" bearing a long seta. The flagellum is 5-segmented; the distal article bears 2 aesthete-like, short, flat setae and 1 normal seta.

The mandible (Fig. 20b) consists of a complex masticatory part, apparently composed of 3 strong teeth, a lacinia mobilis with 2 larger teeth on either end and a row of smaller teeth in between, 2 spatulate spines or processes, some cilia and a reversed, elongately triangular, pars molaris.

The first maxilla (Fig. 20c) consists of a proximal endite; a distal endite armed with 5 serrated spines and 1 seta; and a palp of 2 segments, the distal one of which bears 3 setae.

The second maxilla (Fig. 20d) consists of 2 lobes, with 3 and 4 setae, respectively.

The maxilliped (Fig. 20e, f) has a finger-shaped endite, armed with 2 small setules. Distad of the endite, one can distinguish a uniramous "palp" consisting of 5 articles and a distal claw.

Coxal plates are present for all seven pairs of legs, but they are very small (*cp* in Fig. 18d).

Coxal gills are pear-shaped, and present on pereiopods 3, 4, and 5.

The first gnathopod (Fig. 18d) has a wide basis (*b*) and short meral and ischial articles (*m* and *i*). The carpus (*c*) is transformed into a hand (in other amphipods, the propodus has this function); it is elongately oval in outline; the palm bears a proximal triangular process, 2 palmar angle spines, 1 small midpalmar spine, and a small number (about 10) of setae. In its proximal half, the palm is produced into 3 small triangular processes. The propodus and dactylus (*p* and *d*) form together the claw; the propodus is distally produced into a finger-shaped process bearing 2 setules; the dactylus bears 3 slender teeth.

The second gnathopod (Fig. 18e) is constructed in a way homologous to that of the first gnathopod. The basis is more elongate, the carpus slightly less elongate; the palm of the latter is armed as follows: proximally a triangular process, a seta, and an outstanding,

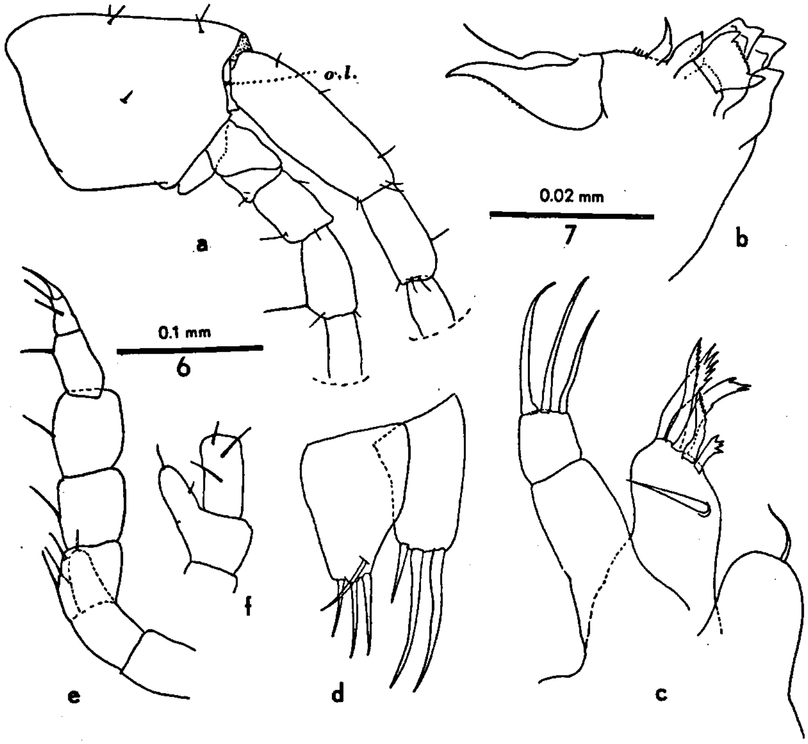

Fig. 20. *Ingolfiella putealis* n. sp., ♂ holotype. – a, head from the left (scale 6); b, mandible (7); c, first maxilla (7); d, second maxilla (7); e, maxilliped (5); f, basal part of maxilliped from under a different angle (5). [*o.l.* = ocular lobe].

pectinated, reversed spine; 1 heavy palmar angle spine and 1 smaller spine; a low number (about 5) of setae; a number (about 6) of small triangular projections. The propodus and dactylus show a similar armature as in gnathopod 1; the 2 proximal teeth on the dactylus are less slender.

The third pereiopod (Fig. 21a) has a narrow and slender basis; the carpus is elongated and bears 1 seta on its posterior margin; the narrow and slender propodus bears a row of minute spinules on its posterior margin, a mediodistal spine, and 2 laterodistal setae. The claw consists of a linear dactylus, distally produced into a sharp point, and a bifid, thin ungulus.

The fourth pereiopod is similar to the third.

The pereiopods 5 to 7 are reversed, in the sense that their dactyli point forward instead of backward (Fig. 18a). The fifth pereiopod (Fig. 21b) has a basis that is very narrow proximally, and that widens strongly distally; the carpus is short and wide, and also the propodus is much wider than in pereiopods 3 and 4. The claw is constructed in a way homologous to that in pereiopods 3 and 4.

Pereiopod 6 is similar to pereiopod 5.

Pereiopod 7 (Fig. 21c) is more slender than pereiopods 5 and 6: the basis and ischium in particular are much more elongated. The claw is similar to that of the 5th pereiopod (Fig. 21d).

Three pairs of pleopods are present, all 3 a kind of leaf-like, roughly triangular in outline. The first pleopod (Fig. 21e) has a roundedly triangular posterior margin and bears 2 short distal setae. The second and third pleopods (Figs. 21f and g) have a small tooth marked by a notch on the posterior margin and are devoid of distal armature.

Three pairs of uropods are present. The first uropod (Fig. 19b) consists of a peduncle armed with 2 setae only, and of 2 rami: a short, 2-segmented exopodite, and a long 1-segmented endopodite. The exopodite is less than half as long as the endopodite; article 1 bears 1 seta, article 2 is tapering and unarmed. The endopodite bears a medial row of long setae, 5 on the one, 6 on the contralateral ramus; a long, subterminal and lateral seta is present; the distal end of the ramus is provided with 5 sharp, tooth-like projections.

The second uropod (Fig. 19c) is of about the same size as the first, but has a more robust peduncle armed, on the inner surface, with a proximal hooked spine, and with 3 rows of setae (the proximal row with 8 elements, the central row with 12, and the distal row with 10); on the outer surface, the peduncle bears 2 setae. Both rami are claw-like (unimerous, curved, tapering); the exopodite bears 2 shorter and 1 very long seta, the endopodite 2 shorter setae.

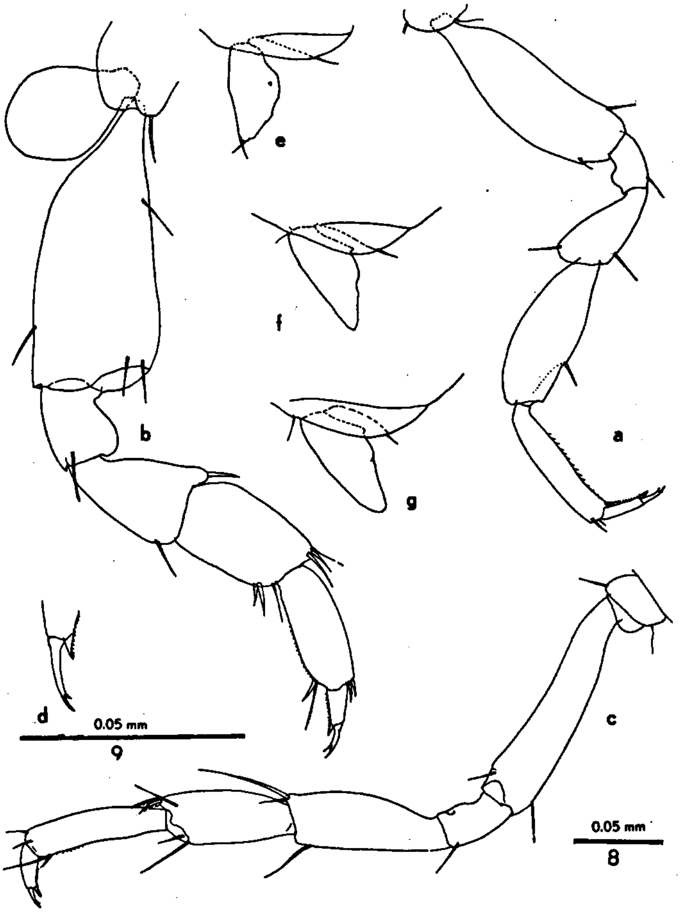

Fig. 21. *Ingolfiella putealis* n. sp., ♂ holotype. – a, third pereiopod (scale 8); b, fifth pereiopod (5); c, seventh pereiopod (8); d, claw of seventh pereiopod (9); e, first pleopod (4); f, second pleopod (4); g, third pleopod (4).

The third uropod (Fig. 18c) is rudimentary, consisting of a short 2-segmented bud, bearing 2 setules on article 1 and 1 long seta on article 2.

The telson (Fig. 18c) is a fleshy lobe, inbedded at its basis in the third urosomite, and provided with a pair of minute setules on either side and with a pair of longer dorsal setae.

Discussion. – The only available specimen is doubtless a male, as can be concluded from the presence of a reversed element on the carpus of gnathopod 2 and from the presence of setae on pleopod 1. I have attributed the Bonaire material to the subgenus *Gevgeliella* which is precisely characterized by these characters. Comparison with the other species in the same subgenus reveals that the Bonaire material constitutes a new species, called *I.* (*G.*) *putealis*, which differs from the other members of *Gevgeliella* as follows:

I. (*G.*) *petkovskii* and *I.* (*G.*) *vandeli* have a reversed element on gnathopod 2 of a different structure, viz. bag-like, stalked (instead of spiniform, pectinated); the first ♂ pleopod is finger-shaped (versus triangular).

I. (*G.*) *catalanensis* resembles the present species in the configuration of the 2nd gnathopod: the carpus, of the male only, has a backward directed strong spine. Differences exist in the dactylus (= distal claw segment) of the 2nd gnathopod, which is slenderer in *catalanensis*; in the ornamentation of the palm of the first gnathopod (without triangular projections in *catalanensis*); in the unarmed and very short outer ramus of the first uropod in *catalanensis*; in the short rami and the low number of setae on the 2nd uropod of *catalanensis*; in a more slender 5th pereiopod and more slender claws in the 5th to 7th pereiopods of *catalanensis*; and in the absence of pleopods 2 and 3 in the male of *catalanensis*, whereas the first male pleopod is finger-shaped.

Since in a number of other species of *Ingolfiella* the male is unknown, it was thought justifyable to differentiate *I.* (*G.*) *putealis* also from the other species of the genus *Ingolfiella*, although not belonging to the subgenus *Gevgeliella* as far as our knowledge reaches.

I. (*I.*) *abyssi* has simple claws on pereiopods 5 to 7 (bifid in *putealis*); uropod 2 bears 4 rows of setae on the inner surface of the peduncle (3 in *putealis*); the exopodite of uropod 1 is longer than half the endopodite (shorter in *putealis*); the claw of the first gnathopod is untoothed (toothed in *putealis*), etc.

I. (*I.*) *atlantisi* has the ungulus of the 7th pereiopod very slender and as long as the dactylus (shorter than the dactylus in *putealis*); the claws in the 5th to 7th pereiopods are simple (bifid in *putealis*); and the dactylus of gnathopods 1 and 2 bears 4 teeth (3 in *putealis*).

I. (*H.*) *littoralis* has simple and quite robust claws on pereiopods 5 to 7 (bifid and more slender in *putealis*), and lacks teeth on the claw of the first gnathopod (present in *putealis*).

I. (*H.*) *britannica* has a very slender ungulus, as long as the dactylus, on the 7th pereiopod (in *putealis* the ungulus is much shorter than the dactylus); the second gnathopod has a broadly triangular carpus (rectangular to ovate in *putealis*); the dactylus of gnathopods 1 and 2 bears 4 teeth (3 in *putealis*).

I. (*H.*) *ruffoi* lacks setale on the first male pleopod (present in *putealis*); has only 2 articles in the accessory flagellum of the first antenna (3 in *putealis*); and has 4 teeth on the dactylus of gnathopod 2 (3 in *putealis*).

I. (*H.*) *xarifae* bears 4 teeth in the dactylus of the 2nd gnathopod (3 in *putealis*); the peduncle of uropod 2 is much shorter than in *putealis*; the 3rd article of the 2nd antenna is longer than the 4th (shorter in *putealis*); the first article of antenna 1 is much more slender than in *putealis*.

I. (*H.*) *kapuri* has a broadly triangular carpus in the 2nd gnathopod (rectangular to ovate in *putealis*); the dactylus of gnathopods 1 and 2 bears 4 teeth (3 in *putealis*); the first and second antennae resemble those of *xarifae* and differ consequently from the corresponding appendages of *putealis*.

I. (*H.*) *ischitana* has likewise a broadly triangular carpus in the 2nd gnathopod, the palm of which is armed with 2 tooth-like projections (6 in *putealis*); the claws on the posterior pereiopods are simple instead of bifid.

I. (*T.*) *manni* lacks bifid claws on the posterior pereiopods, it has a finger-shaped first pleopod like *I.* (*G.*) *petkovskii*, and a broadly triangular Gn. 2 carpus like *I.* (*T.*) *macedonica*.

I. (*T.*) *macedonica* has a broadly triangular carpus in the second gnathopod (versus rectangular to ovate in *putealis*), and simple claws on pereiopods 5 to 7 (versus bifid).

I. (*T.*) *thibaudi* has an undifferentiated 2nd male gnathopod (no reversed element on the carpus); the first male pleopod is finger-shaped, the 2nd and 3rd male pleopods are lacking.

I. (*T.*) *berrisfordi* lacks bifid claws on the posterior pereiopods; the peduncle of uropod 2 bears 5 rows of setae (3 in *putealis*); the armature of the carpus of gnathopod 2 differs also in certain details.

I. (*B.*) *acherontis* is a poorly known species, which has apically pointed pleopods (rounded in *putealis*) and 4 aesthetes on the first antenna (3 in *putealis*).

I. (*B.*) *uspallatae* differs clearly from *I. putealis* in its simple claws on the posterior pereiopods, the unarmed exopodite in the 2nd uropod, the presence of 4 rows of setae on the peduncle of the 2nd uropod, and the presence of only 1 distal seta on the palp of maxilla 1.

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