AMSTERDAM EXPEDITIONS TO THE WEST INDIAN ISLANDS, REPORT 2*)

NEW DATA ON TAXONOMY AND ZOOGEOGRAPHY OF INGOLFIELLID CRUSTACEA

by

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ABSTRACT

Groundwaters (in wells, springs, caves, macroporous interstitia...) of 29 Caribbean islands have been investigated. Only on the four islands off the coast of Venezuela (viz., Aruba, Curaçao, Bonaire, and Margarita) members of the suborder Ingolfiellidea (Crustacea, Amphipoda) have been encountered, altogether six species, of which three are described here for the first time. The zoogeographical implications of this limited range in the West Indies is discussed.

ZOOGEOGRAPHY OF THE INGOFIELLIDEA

The Ingofiellidea form a suborder of the Amphipoda, with a limited number (by this time 27) of species allocated to two families, together with three genera and five subgenera. The great interest of the suborder lies in the fact that its ecological amplitude is so large: its members are distributed from the deepsea to fresh stygobiotic habitats. The geographic distribution is equally large: world-wide for certain taxa of the genus-group.

In two previous papers (Stock, 1976, 1977), I have described the first West Indian members of the suborder (two species from Bonaire and one from Curaçao). The older of these two papers contains a review of the entire suborder and a revision of the taxonomy on generic and subgeneric level. The second paper gives a survey of the distribution of the Ingolfiellidea, from which it is concluded that the suborder must be a very old one, having reached a world-wide distribution already before the break-up of the continental plates. A similar conclusion was reached by Delamare Deboutteville (1960), although he based his view on only 6 species, the number known at that time, instead of the 24 used in my 1977 paper. Dahl (1977) recently independently summarized the evidence and likewise thinks that (:227) "indirect evidence... tends to place Peracarid origin and radiation earlier than has generally been supposed."

A new thread of evidence, indirect again since there is no fossil record of the Ingolfiellidea, is added to the general texture in the present paper.

In the period 1973-1978 we have explored 29 islands of the Antillean chain for the presence of stygobionts, such as Ingolfiellidea. Consistently, the same methods were used in all islands. Table I and fig. 1 show the islands sampled; the number of hypogean (groundwater) samples obtained in each island and the number of samples containing Ingolfiellidea, are also shown in the table. Far over 1000 stations were visited, and in 580 of these stygobionts were obtained. This rather intensive sampling program has yielded only four islands with Ingolfiellidea: Aruba (with one species, which also occurs on Curaçao), Curaçao (with three species of which two endemic), Bonaire (with two species, both endemic), and Margarita (with one endemic species). In my opinion, it cannot be accidental that these four islands happen to be situated close to the Venezuelan mainland, in fact all four islands off the coast of South America (the Leeward group in the terminology of Hummelinck, 1953) sampled during our program yielded Ingolfiellidea. The other 25 islands, at a greater distance of the continent, did not reveal any members of the suborder.

I explain this phenomenon by assuming that the ingolfiellids were already widely spread over the ancient landmass of Pangaea. Like I showed in my 1977 paper, this assumption is based on the observation that several ingolfiellid taxa are, at

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TABLE	I
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Island group	Island (V=predominantly volcanic; C=pre- dominantly calcareous)		No. of ground- water samples containing stygobionts	No. of samples with Ingolfiel- lidea (No. of species in parentheses)
GREATER ANTILLES	1.	. Hispaniola (C/V)	48	0(0)
	2.	Mona (C)	4	0(0)
	3.	Puerto Rico (C/V)	4	0(0)
LESSER ANTILLES (Windward Group)	4.	Vieques (C)	11	0(0)
	5.	Culebra (C)	13	0(0)
	6.	St. Thomas (C)	2	0(0)
	7.	St. John (C)	10	0(0)
	8.	St. Croix (C)	15	0(0)
	9.	Tortola (incl. Beef		
		Isl. and Frenchman's		
		Cay) (C)	23	0(0)
	10.	Virgin Gorda (C)	18	0(0)
	11.	Anegada (C)	16	0(0)
	12.	Anguilla (C)	17	0(0)
	13.	St. Martin (C/V)	45	0(0)
	14.	Tintamarre (C)	1	0(0)
	15.	St. Barths (V)	16	0(0)
	16.	Saba (V)	6	0(0)
	17.	St. Eustatius (V)	20	0(0)
	18.	Barbuda (C)	16	0(0)
	19.	Antigua (C/V)	15	0(0)
	20.	Guadeloupe (C/V)	15	0(0)
	21.	Marie-Galante (C)	4	0(0)
	22.	Dominica (V)	5	0(0)
	23.	Martinique (V)	6	0(0)
	24.	St. Lucia (V)	5	0(0)
	25.	Barbados (C)	32	0(0)
(Leeward Group)	26.	Margarita (V/(C))	13	1(1)
	27.	Bonaire (C)	53	5(2)
	28.	Curaçao (C/(V))	111	6(3)
	29.	Aruba (C)	36	1(1)

Caribbean islands investigated during the Amsterdam Expeditions to the West Indian Islands, 1973-1978.

subgeneric level, still identical in South America and Europe. Apparently, as Remane (1952) and Delamare Deboutteville (1960) stressed, stygobionts as ingolfiellids, have great difficulty in spreading over larger stretches of open sea. Under the assumption that they were already present in continental subterranean waters of South America before this plate got separated, it will be clear that most attempts to spread any further into the much more recently emerged Caribbean islands, must have failed due to their inability of crossing open ocean. Only the islands near the coast of Venezuela could be reached. Aruba is a mere 27 km N of the Venezuelan peninsula of Paraguana, and on the South American continental shelf; Curaçao is about 64 km offshore, and separated by abyssal depths from the continent; Bonaire is 87 km remote from the continent, likewise separated by a deep trench from the mainland; Margarita is closest to the coast, only 22 km N of Venezuela and on its continental shelf (data based on Hummelinck's, 1940, treatment of the islands).

The two islands lying on the Venezuelan shelf (Aruba and Margarita) have one species of Ingolfiellidea each (that on Aruba is not even endemic to the island). It is hard to decide whether it is coincidental that the two other islands, not lying on the shelf (Curaçao and Bonaire) have three and



Fig. 1. Map of the Caribbean, showing (dotted) the 200 m line being the edge of the continental shelf. The groundwaters of 29 islands have been sampled. The numbers of the islands correspond with those in table I. Only in four islands (encircled on the map) of the Leeward group, Ingolfiellidea have been found.

two species of Ingolfiellidea, respectively. Although it must be admitted that Curaçao is intensively sampled (explaining in part the greater number of species), the situation might be indicative of multiple invasion as well.

Since all four West Indian islands from which ingolfiellids are presently known are arid, they have no really fresh surface or subsurface waters (defined as waters with a low ion content, salinity, S <500 mg/l); both by evaporation at the surface and by sodium ions carried in by the constant trade winds, the groundwaters of the islands usually are oligonaline (S = 500-5000 mg/l) or even mesohaline (S = 5000-18000 mg/l) in the terminology of the Venice System. Nevertheless, we have found an almost complete range of salinity conditions in the six species known from the four islands off the Venezuelan coast. These conditions vary from fully marine (Ingolfiella Juadridentata), through marine-polyhaline (I. tabularis, I. grandispina) and mesohaline (I. putealis) to oligohaline/limnic (I. fontinalis, I. margaritae), showing - even in the limited area of these four small islands — the complete ecological spectrum that is so characteristic of the entire suborder. I have no doubt, that certain members of this group are still in the process of invading the continental waters via the mixohaline interstitial waters of sandy beaches, etc. Although the ways of dispersal over stretches of open ocean appear to be very limited, the marine/polyhaline forms have the greatest chance to be distributed over more than one island (I. tabularis from Curacao and Aruba represents such a case), whereas the chances for the oligohaline/limnic species must be considered very slight indeed. At any rate, the slow dispersion rate is reflected in the rather pronounced degree of endemism showed by the ingolfiellid taxa (at species level), as well as by their incapability of reaching the more offshore Caribbean islands.



Fig. 2. Ingolfiella (Gevgeliella) tabularis Stock, 1977, Q juv. from the left, from Sjingot cave, Curaçao. Natural size (total body length) 1.37 mm.



Fig. 3. Ingolfiella (Gevgeliella) tabularis Stock, 1977, 9 juv. from Sjingot cave, Curaçao. a, first antenna (scale AC); b, second antenna (AC); c, endite of maxilliped (AD); d, first gnathopod (AD); e, second gnathopod (AD); f, first uropod (AD); g, third uropod (AD). For scales see fig. 8.



Fig. 4. Ingolfiella (Gevgeliella) tabularis Stock, 1977, ? juv. from Sjingot cave, Curaçao. a, third pereiopod (scale AC); b, dactylus and ungulus of third pereiopod (AE); c, fourth pereiopod (AC); d, fifth pereiopod (AC); e, dactylus and ungulus of fifth pereiopod (AE); f, distal segments of sixth pereiopod (AE); g, seventh pereiopod (AC); h, first pleopod (AD); i, second pleopod (AD); j, third pleopod (AD); k, second uropod (AD). For scales see fig. 8.

TAXONOMIC NOTES ON CERTAIN WEST INDIAN SPECIES

Ingolfiella (Gevgeliella) tabularis Stock, 1977. Figs. 2-4, 5t.

Ref. — Stock, 1977: 142-145, fig. 59.

Material. — CURAÇAO, 1 \Im : Sta. 78/280, Cave of Sjingot, Hato plain (approx. 12°13'12"N 68°59'58"W); Cvetkov net used by a skin diver in anchihaline lake of the cave; red loam, calcite crystals on water surface; semi-dark; depth 2-3 m; chlorinity 1480 mg/l at the moment of observation (measurements at other days indicate fluctuations of 1400-2800 mg/l); 14 May 1978.

CURAÇAO, 35 specimens of both sexes: Sta. 78/305, phreato-biological pump in dry rain gully, just below the entrance of Boca Tabla sea cave (approx. 12°22'19"N 69°06'49"W), about 1 m above sea-level, rarely reached by the waves; coarse sand and gravel, loam; chlorinity 4990 mg/l; 19 May 1978.

CURAÇAO, 1 \Im : Sta. 78/306. As 78/305, but just above sea-level, regularly flooded by the waves; coarse sand, loam; full marine salinity.

ARUBA, 2 3, 5 9: Sta. 78/295, Cave of Andicuri (12°32'26''N 69°57'04''W), anchihaline subterranean pools, depth 0-2 m; loam; semi-dark; chlorinity 4000 mg/l; 17 May 1978.

Accompanying fauna: At Sta. 78/280, the species has been found together with hadziid Amphipoda, *Typhlatya* (Macrura), anthurid Isopoda, Harpacticoida, Cyclopoida. At Sta. 78/295 it was accompanied by *Microcharon* (Isopoda), Harpacticoida, Cyclopoida, *Pyrgophorus* (Gastropoda), Oligochaeta. At Stas. 78/305 and 306 it lives together with *Microcerberus* and *Microcharon* (Isopoda), *Halosbaena* (Thermosbaenacea), Ostracoda, Cyclopoida, Harpacticoida, *Caecum* (Gastropoda), and Oligochaeta.

All these localities are anchihaline. In one locality (Boca Tabla) the species is more abundant at a certain distance of the high tide mark (Sta. 78/ 305) than closer to the sea (Sta. 78/306 and Sta. 76/2 of Stock, 1977).

Remarks. — This species shows distinct sexual dimorphism in the following appendages: (a) second gnathopod; (b) first pleopod; (c) second uropod.

The second gnathopod bears in the male a strongly developed, reversed, spiniform element on the posterior margin of the carpus; this element is lacking in the female. The palma of the carpus of this appendage bears 6 triangular tooth-like processes in the male, 7 in the female. These processes have been given numbers (1 to 6 — or 7 — in distal to proximal direction; see Stock, 1977: 138, footnote). In the male, teeth 1 and 2 are strongly enlarged, whereas teeth 3 to 6 are closely set; in the female, teeth 1 and 2 are not much enlarged, and there is an open space between teeth 3 and 5.

The first pleopod of the male bears two distal setae, that of the female is unarmed.

The second male uropod bears a subbasal peduncular hook, absent in the female.

The present collection shows a strikingly high number of females (nearly half of the females examined) that have a male type of first pleopod. Such a specimen is represented in figs. 2 to 4. Apart from the two setae on the pleopod, such females differ in nothing from "normal" females of the species. It is provisionally assumed that such females are subadult (their incubatory plates are small or lacking) and will loose the setae during the next moult.

The abundant material provides the opportunity to study the variability of the species. The shape and shortness of the dactylus of the 6th pereiopod, considered a salient feature in the original description, is slightly variable. The distal triangular process of the dactylus is always short (never so elongate as in *I. fontinalis* Stock, 1977); the ratio length propodus/length dactylus is 3.2-3.4 in *tabularis*, against 2.5-2.6 in the type specimens of *fontinalis*. The propodus often looks more elongated in the present specimens of *tabularis* than in the types, but it is still markedly shorter than in *fontinalis*.



Fig. 5. Palma of second gnathopod, \mathcal{Q} , of paratypes of *Ingolfiella (Gevgeliella) fontinalis* Stock, 1977 (*f*, from Fontein cave, Boniare), and *I. (G.) tabularis* Stock, 1977 (*t*, from sands near the entrance of Boca Table sea cave, Curaçao). Both figures same scale.

Not mentioned in the original description are the differences in carpal armature (\mathcal{P}) of the second gnathopod (fig. 5). In *I*. (*G*.) tabularis the palmar tooth 3 is larger than tooth 4, teeth 6 and 7 are inserted close to one another, 4 and 5 are widely spaced. In *I*. (*G*.) fontinalis teeth 3 and 4 are subequal, 6 and 7 are widely spaced, whereas 4 and 5 are implanted close to each other.

Though *fontinalis* and *tabularis* are closely related, as is in particular clear from the morphology of the second male gnathopod, the differences mentioned above appear to be pretty constant, and justify, along with the notably different microhabitat (*fontinalis* in almost fresh, running springs; *tabularis* in macroporous marine or polyhaline interstitia and in anchihaline cave waters) the specific distinction between the two taxa.

Ingolfiella (Gevgeliella) margaritae n. sp. Figs. 6-8.

Material. — ISLA DE MARGARITA (Venezuela), 1 & (holotype): Sta. 78/341, La Plaza, covered well (approx. 11°05'53"N 63°51'35"W); water level at 9 m, water depth 4 m; Cvetkov net; chlorinity 480 mg/l; 1 June 1978. (ZMA Amph. 106.443-444).

Accompanying fauna: Bogidiellidae (Amphipoda), Isopoda, Cyclopoida, Harpacticoida, Annelida.

The locality can be characterized as permanently fresh; its water is used in large quantities (tankcars) for water supply of the islanders.



Fig. 6. Ingolfiella (Gevgeliella) margaritae n. sp., & holotype, from La Plaza, Isla de Margarita. a, first antenna (scale AB); b, second antenna (AB); c, maxilliped (AD); d, first gnathopod (AC); e, second gnathopod (AC); f, palma of second gnathopod (AD); g, fifth pereiopod (AC); h, dactylus and ungulus of fifth pereiopod (AE). For scales see fig. 8.

Description. — Body length (frontal margin cephalosomite to tip telson) 2.07 mm. First antenna slender (fig. 6a), similar to other species of *Gevgeliella*, in particular *putealis*. Second antenna (fig. 6b) without particularities. Maxillipedal endite (fig. 6c) as in *I*. (*G*.) *tabularis*; distal claw of "palp" longer than penultimate segment.

First gnathopod (fig. 6d) with almost vertical palm; claw with 3 inner teeth. Second gnathopod (fig. 6e) distinctive: carpus with a strong, flanged, reversed spine (subgeneric character), and two palmar angle spines, one of which is very heavy; the palma (fig. 6f) is armed with the usual 6 triangular teeth; tooth 2 is hardly larger than tooth 1; tooth 4 is only slightly smaller than tooth 3; there is no large open stretch between teeth 4 and 5; teeth 4, 5 and 6 are of equal size; the claw bears 3 inner teeth. The c/p index (for definition see Stock, 1977: 139) is 2.1 and is similar in this

respect to that of fontinalis and tabularis.

The third pereiopod (fig. 7a) has a very slender dactylus and a slender, bifid ungulus (fig. 7b). The fourth pereiopod is similar to the third. The fifth pereiopod (fig. 6g) has a slender dactylus, produced into a lanceolate distal process and a slender, bifid ungulus (fig. 6h). The sixth pereiopod resembles the fifth (figs. 7c, d). The seventh pereiopod (fig. 7e) is longer than the others; the dactylus is very slender, produced into a tall distal process (fig. 7f); the slender ungulus is bifid.

The first pleopod (fig. 8a) is narrowly triangular, with 2 short apical setae; pleopods 2 and 3 are broadly triangular, unarmed (figs. 8b, c).

Uropod 1 (fig. 8d): pedunculus longer than the rami; outer ramus slightly less than half as long as the inner ramus, armed with 1 seta; inner ramus with 5 bifid dorsal setae, 1 long ventral seta, and 2 dorsodistal teeth.



Fig. 7. Ingolfiella (Gevgeliella) margaritae n. sp., 3 holotype, from La Plaza, Isla de Margarita. a, third pereiopod (scale AC); b, dactylus and ungulus of third pereiopod (AE); c, sixth pereiopod (AC); d, dactylus and ungulus of sixth pereiopod (AE); e, seventh pereiopod (AC); f, dactylus and ungulus of seventh pereiopod (AE). For scales see fig. 8.



Fig. 8. Ingolfiella (Gevgeliella) margaritae n. sp., & holotype, from La Plaza, Isla de Margarita. a, first pleopod (scale AD); b, second pleopod (AD); c, third pleopod (AD); d, first uropod (AC); e, second uropod (AC); f, last urosomite, third uropod and telson, from the right (AC).

Uropod 2 (fig. 8e): pedunculus with 3 rows, of 9 to 10 setae each; rami subequal; outer ramus with 1 very long and 2 shorter setae; inner ramus with 2 shorter setae. Subbasal, hook-shaped spine on peduncle (sexual character).

Uropod 3 and telson (fig. 8f) without particularities.

Remarks. — All members of the subgenus Gevgeliella resemble each other closely. However, the European species (*petkovski* Karaman, 1957; catalanensis Coineau, 1963; vandeli Bou, 1970) differ from the neotropical species in the first male pleopod which is finger-shaped instead of triangular. I. (G.) *petkovski* has a reserved element on the carpus of gnathopod δ of a special shape ("French letter"), whereas in vandeli it is pedunculate; catalanensis is characterized by an oblong carpus in gnathopod 2 and a very short outer ramus in uropod 1.

The three neotropical species (*putealis* Stock, 1976, *tabularis* Stock, 1977, and *fontinalis* Stock, 1977) are very similar to the present species. The pereiopodal dactyli of the new species are very slender, as is especially clear in comparison with P7 of *I*. (*G*.) *putealis* and of P5 and P6 in *I*. (*G*.) *tabularis*. The main differences, however, between the four neotropical species are found in the shape and mutual distance of the teeth on the palmar margin of gnathopod 2. It is unfortunate that only the male of the new species is known, because (as we have seen above for the closely related species *tabularis* and *fontinalis*) the female palmar margin may offer some good distinctions as well.

I. (G.) putealis (δ) from Bonaire has tooth 5 very small (this tooth is as large as teeth 4 and 6 in margaritae); I. (G.) fontinalis, likewise from Bonaire, and tabularis, from Curaçao and Aruba, have tooth 2 very elongate and slender, teeth 3 to 6 densely crowded, and teeth 4 and 5 much smaller than teeth 3 and 6 (in margaritae, tooth 2 is not elongate, teeth 3 to 6 are well-spaced and of similar size).

Ingolfiella (Trianguliella?) grandispina n. sp. Figs. 9-11.

Material. — CURAÇAO, 1 9 (holotype): Sta. 78/308, pumped (with phreatobiological pump) from gravel and sand in front of the lower entrance of the cave of Blauw Baai (12°08'20"N 68°59'05"W); chlorinity 18840 mg/l; 20 May 1978. (ZMA Amph. 106.441-442).

Accompanying fauna: *Caecum* (Gastropoda), *Cyathura, Microcerberus* and *Microjaera* (Isopoda), Tanaidacea, hadziid Amphipoda, bogidiellid Amphipoda, *Halosbaena* (Thermosbaenacea), Ostracoda, Harpacticoida, Cyclopoida, Annelida (div. fams.).

The locality is of a definite anchihaline nature. In periods of heavy rain, oligo- and mesohaline elements (e.g. *Metaniphargus*) predominate; during periods of drought, polyhaline or marine elements (*Halosbaena*, Polychaeta) get more abundant. The ingolfiellid described here belongs to the latter category.

Description. — Body length (frontal margin cephalosomite to tip telson) 2.28 mm. First antenna (fig. 9b) with slender peduncle; segment 1 elongate; aesthetes, on distal three flagellum segments, very broad. Second antenna (fig. 9c) with 5- or 6-segmented flagellum. Between the insertion of the first and second antenna a distinct, articulated, triangular structure is found, the so-called ocular lobe (fig. 9a).

First maxilla (fig. 9d): proximal endite with 4 setae, distal endite with 1 combed spine, 1 heavy tricuspidate spine, 2 bicuspidate spines, and 2 'normal' spines; palp 2-segmented, with 4 distal setae.

Second maxilla (fig. 9e) bilobed, each lobe with 4 distal elements.

Maxillipedal endite (fig. 9f) wide, armed with 1 distal and 1 medial spine; "palp" with a slender distal claw and a subequal seta.

First gnathopod (fig. 9g) with elongate carpus; palmar angle armed with 1 spiniform process, 1 small and 1 large spine; palmar margin slightly sinuous, without teeth, but provided with 5 bifid spines and some setules. Propodus with a pointed disto-internal process, armed with a setule. Dactylus with 3 pointed internal teeth.

Second gnathopod (fig. 10a): carpus oval; palmar angle marked by a single, huge spine; palmar margin with 2 sharp spines and 2 clubshaped spines and a few setae, distal end of margin with 2 large triangular teeth. Propodus robust, disto-internal process bluntly rounded. Dactylus



Fig. 9. Ingolfiella (Trianguliella?) grandispina n. sp., 9 holotype, from Blauw Baai cave, Curaçao. a, head and ocular lobe from the right (scale AB); b, first antenna (AB); c, second antenna (AB); d, first maxilla (AE); e, second maxilla (AE); f, maxilliped (AD); g, first gnathopod (AC). For scales see fig. 8.

long, overreaching the palmar angle spine; inner margin with 3 sharp teeth.

Third pereiopod (fig. 10b) rather slender; dactylus rectangular (fig. 10c), with a distoposterior, elongated, triangular process; ungulus straight, thin, denticulate. Oöstegite short, fingershaped, with one very long distal seta.

Fourth pereiopod resembling the third.

Fifth pereiopod (fig. 10d) rather slender; carpus with a disto-anterior transformed spine (a slender spine on a pyramidal socle). Dactylus and ungulus robust, curved (fig. 10e). Sixth pereiopod similar to the fifth, likewise with a transformed spine on the carpus.

Seventh pereiopod (fig. 11a) very slender; posterodistal angle of carpus with 2 transformed spines (combed and hook-shaped, fig. 11b). Ungulus short, indistinctly separated from the dactylus (fig. 11c). Pleopods 1 to 3 (figs. 10f-h) similar in shape (at least in the only known sex, \Im): trapezoidal, outer margin with 2 teeth.

First uropod (fig. 11d) with short peduncle; endopodite nearly as long as peduncle, distally armed with 7 teeth arranged in 2 rows; laterally armed with 16 long setae, arranged in 6 transverse rows (1 to 3 setae per row); exopodite about half as long as endopodite, armed with 2 setae.

Second uropod (fig. 11e): peduncle with 5 transverse rows of setae; in fourth row also 3 spines; endopodite 2-segmented with 2 setae; exopodite slightly overreaching the endopodite, 2segmented, proximal segment with 6 setae.

Third uropod (fig. 11f) with pointed distal segment; 3 short setae on basal segment, 1 long seta on distal segment. Telson (fig. 11f) without particular characters.



Fig. 10. Ingolfiella (Trianguliella?) grandispina n. sp., 9 holotype, from Blauw Baai cave, Curaçao. a, second gnathopod (scale AC); b, third pereiopod (AB); c, dactylus and ungulus of third pereiopod (AD); d, fifth pereiopod (AB); e, dactylus and ungulus of fifth pereiopod (AD); f, first pleopod (AC); g, second pleopod (AC); h, third pleopod (AC). For scales see fig. 8.

Remarks. - Species with more than 3 rows of setae on the peduncle of uropod 2 are rare: apart from in the new species, this character is encountered only in Ingolfiella (Trianguliella) macedonica Karaman, 1959, I. (T.) thibaudi Coineau, 1968, and in I. (T.) berrisfordi Ruffo, 1974. The number of setal rows in I. (Hanseniella) ischitana Schiecke, 1973, is not mentioned in the description; this species may (judging from Schiecke's figures) well be rather similar to the new species, but it differs from it in having the palmar angle spine of gnathopod 2 and the dactylus of the same appendage of "normal" size, and not enlarged. The same characters separate also macedonica and thibaudi at once from the new species. I. (T.)berrisfordi on the other hand agrees with the new species in the exaggerated elongation of both the palmar angle spine and the dactylus (the proposed

specific name for the n. sp. alludes to the former of these two characters).

As point of fact, I consider the new species so closely related to I. (T.) berrisfordi (a form from intertidal sands of Table Bay, South Africa), that I have attributed it provisionally to the subgenus Trianguliella, although no proof for such an allocation is available (Trianguliella is characterized by secondary sexual differences of the male, and this sex is unknown in the new species). A number of small differences with berrisfordi exist, such as the presence of 4 setae on the proximal endite of maxilla 1 (2 in berrisfordi), the presence of inner setae on the dactylus of P5 to P7 (absent in berrisfordi), dactylus and ungulus of P5 to P7 separated (fused in berrisfordi), transformed spines on carpus of P7 pectinate and hook-like (pedunculate like in P5 and P6 in berrisfordi).



Fig. 11. Ingolfiella (Trianguliella?) grandispina n. sp., \mathcal{Q} holotype, from Blauw Baai cave, Curaçao. a, seventh pereiopod (scale AB); b, transformed spine of carpus of seventh pereiopod (AE); c, dactylus and ungulus of seventh pereiopod (AD); d, first uropod (AC); e, second uropod (AC); f, third uropod and telson, from the right (AC). For scales see fig. 8.

Ingolfiella (Hanseniella?) quadridentata n. sp. Figs. 12-14.

Material. — CURAÇAO, 1 \Im (holotype), 1 \Im (paratype): Sta. 78/315, c. 500 m W of Piscadera (approx. 12°07'42''N 68°58'18''W), from coarse coral sand of a submarine flat 1), depth 4 m, full marine salinity; washed from the top 30 cm of the sand; 22 May 1978. (ZMA Amph. 106.445-446).

Accompanying fauna: *Caecum* (Gastropoda), Macrura, oculate Amphipoda, Microparasellidae (Isopoda), Thermosbaenacea, Cumacea, Harpacticoida, Cyclopoida, *Amphioxus*, flatworms.

Description. — Female 1 (paratype, dissected and illustrated) is 1.26 mm long (frontal margin cephalosomite to tip of telson); female 2 (holo-type, not dissected) is 1.58 mm long.

¹) In the diagram of the Curaçao reef (Bak, 1975, fig. 1) this habitat corresponds with zone 3 ("the barren zone"). The habitat, and the collecting method, are also shown in fig. 15 in the present paper.

Ocular lobe (fig. 12a) well-developed, triangular.

First antenna (fig. 12b) with elongate first peduncle segment. Second antenna (fig. 12c) rather robust; flagellum of 5 segments.

Maxilliped (fig. 12d) with tapering, fingershaped endite, armed with 1 proximal and 1 distal seta. The "palp" ends into 2 very inequal elements: 1 long and claw-like, 1 short and setiform.

First gnathopod (fig. 12e) with slender, tapering carpus, armed with only 1 palmar spine (and without triangular process); palmar margin sinuous, with 1 small tooth; propodus with a triangular disto-internal process; dactylus with 4 sharply pointed internal teeth (fig. 12f).

Second gnathopod (fig. 13a) with triangular carpus. Palmar margin (fig. 13b) with 9 teeth, the distal teeth (nrs. 1 and 2) very low; palmar corner with a heavy, bifid spine and a smaller, BIJDRAGEN TOT DE DIERKUNDE, 49(1) - 1979



Fig. 12. Ingolfiella (Hanseniella?) quadridentata n. sp., 9 paratype, from submarine sands, Piscadera, Curaçao. a, head with ocular lobe, from the right (scale AC); b, first antenna (AC); c, second antenna (AC); d, maxilliped (AE); e, first gnathopod (AC); f, distal segments of first gnathopod (AE); g, first uropod (AD); h, second uropod (AC). For scales see fig. 8.

simple spine. Propodus robust, disto-internally produced into a short, blunt, setiferous process. Dactylus with 4 sharp teeth.

Third pereiopod (fig. 13c) with slender dactylus; ungulus (fig. 13d) feebly curved, very elongate and slender, with inner row of spinules. Fourth pereiopod similar to the third. Oöstegites found on third and fourth pereiopods only (fig. 13c), curved, truncate at tip, provided with 3 apical teeth, but without setae. Coxal gills (fig. 13c) ovate.

Fifth pereiopod (fig. 13e) robust; ungulus (fig. 14a, representing P6, which is similar to P5) distally bifid.

Seventh pereiopod (fig. 14b) more slender than the others; carpus posterodistally with 2 modified spines (one comb-like, one bifid, cf. fig. 14b, detail). The dactylus (fig. 14c) is rather elongate; the ungulus is distally bifid. The pleopods 1, 2, and 3 are similar, at least in the female (only sex known): triangular to trapezoidal, without distal armature (figs. 14d, e).

Uropod 1 (fig. 12g) has a robust peduncle, armed with 3 long setae; the exopodite is about half as long as the endopodite, pointed, tapering, armed with 2 short setae; the endopodite is wider than the exopodite, distally provided with 5 to 6 slender teeth, laterally armed with 5 long setae, not arranged in a row.

Uropod 2 (fig. 12h) with short, broad peduncle, ornamented with 3 rows of short setae and several isolated longer setae. Rami subequal, curved, pointed; exopodite with 4 setae, endopodite with 2 setae.

Uropod 3 (fig. 13f) and telson of "normal" shape.

Remarks. — In absence of the male sex, it is not possible to attribute the present species with ab-

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Fig. 13. Ingolfiella (Hanseniella?) quadridentata n. sp., \mathcal{P} paratype, from submarine sands, Piscadera, Curaçao. a, second gnathopod (scale AC); b, palma, propodus, and dactylus of second gnathopod (AE); c, third pereiopod (AC); d, dactylus and ungulus of third pereiopod (AE); e, fifth pereiopod (AD); f, last urosomite, with telson and third uropod, from the right (AD). For scales see fig. 8.



Fig. 14. Ingolfiella (Hanseniella?) quadridentata n. sp., 9 paratype, from submarine sands, Piscadera, Curaçao. a, distal segments of sixth pereiopod (scale AE); b, seventh pereiopod (AC); c, dactylus and ungulus of seventh pereiopod (AE); d, first pleopod (AD); e, second pleopod (AD). For scales see fig. 8.



Fig. 15. The habitat of Ingolfiella (Hanseniella?) quadridentata n. sp.: the sands of the so-called barren zone at a depth of about 4 m on the Curaçao reef. The animals are collected by scooping the top layer of the sand; the sand is washed out at the surface on board of the ship. From a colour slide, photo E. S. W. Weinberg.

solute certainty to any particular subgenus of the genus Ingolfiella, since these subgenera are characterized by male features. The present material certainly does not belong to the subgenus Ingolfiella s. str. (which is diagnosed by the shape of the distal segments of gnathopod 2 in both sexes). Neither does it belong to the subgenus Balcanella, which has symmetrical, spoon-shaped female pleopods. The other subgenera (Hanseniella, Trianguliella, and Gevgeliella) remain as possible seat for the present species. The presence of a well-developed ocular lobe, as well as the habitat (in submarine sands), seem to indicate that the best provisional place for the present species will be in the subgenus Hanseniella. At any rate, the new species will be compared in the next lines not only with the other members of Hanseniella, but also with those of Trianguliella and Gevgeliella.

Ingolfiella quadridentata has, as suggested by

the specific name, four teeth on the inner margin of the dactylus of gnathopods 1 and 2. In most other species there are 0 to 3 (usually 3) teeth; this is the case in I. (Hanseniella) littoralis Hansen, 1903, I. (H.) ischitana Schiecke, 1973, I. (H.) xarifae Ruffo, 1966, I. (Trianguliella) manni Noodt, 1961, I. (T.) thibaudi Coineau, 1968, I. (T.) berrisfordi Ruffo, 1974, and all species of the subgenus Gevgeliella. The following taxa share the 4-toothed condition with the new species: I. (H.) britannica Spooner, 1960, I. (H.) ruffoi Siewing, 1960, I. (H.) kapuri Coineau & Rao, 1972, and I. (T.) macedonica Karaman, 1959. The following differences distinguish I. quadridentata from these species: britannica possesses a distal maxilliped armature consisting of 2 setiform elements of equal size, and has very long unguli in P6 and P7; ruffoi lacks transformed spines on the carpus of P7, the entire P7 is more slender and the exopodite of uropod 1 is shorter;

macedonica has a rich setal armature on the endopodite of uropod 1, whereas the palma of gnathopod 2 is devoid of teeth. Most similar to the new species appears to be I. (H.) kapuri from littoral sands in the Andaman Islands. This Indian Ocean species differs from the Caribbean material in certain details of the armature of the palma of the second gnathopod (proximal spine the smallest in kapuri, the largest in quadridentata), the slenderness of the dactylus of the third pereiopod (twice as long as wide in kapuri, almost three times as long as wide in quadridentata), and the ungulus of the third pereiopod (trifid in kapuri, multidenticulate in quadridentata).

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REFERENCES

- BAK, R. P. M., 1975. Ecological aspects of the distribution of reef corals in the Netherlands Antilles. Bijdr. Dierk., 45 (2): 181-190.
- DAHL, E., 1977. The amphipod functional model and its bearing upon systematics and phylogeny. Zool. Scr., 6: 221-228.
- DELAMARE DEBOUTTEVILLE, Cl., 1960. Biologie des eaux souterraines littorales et continentales. Actualités sci. indust., **1280**: 1-740 (Hermann, Paris).
- HUMMELINCK, P. WAGENAAR, 1940. Studies on the fauna of Curaçao, Aruba, Bonaire and the Venezuelan islands,
 1. General information. Stud. Fauna Curaçao, 1: 1-57.
- ----, 1953. Description of new localities. Stud. Fauna Curaçao, 4: 1-108, pls. I-VIII.
- REMANE, A., 1952. Die Besiedlung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. Verh. deuts. zool. Ges., **1951**: 327-359.
- STOCK, J. H., 1976. A new member of the crustacean suborder Ingolfiellidea from Bonaire. Stud. Fauna Curaçao, 50: 56-75.
- —, 1977. The zoogeography of the crustacean suborder Ingolfiellidea with descriptions of new West Indian taxa. Stud. Fauna Curaçao, 55: 131-146.

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