STUDIES ON THE FAUNA OF CURAÇAO AND OTHER CARIBBEAN ISLANDS: No. 178

THE ZOOGEOGRAPHY OF THE CRUSTACEAN SUBORDER INGOLFIELLIDEA,
with descriptions of new West Indian taxa

by

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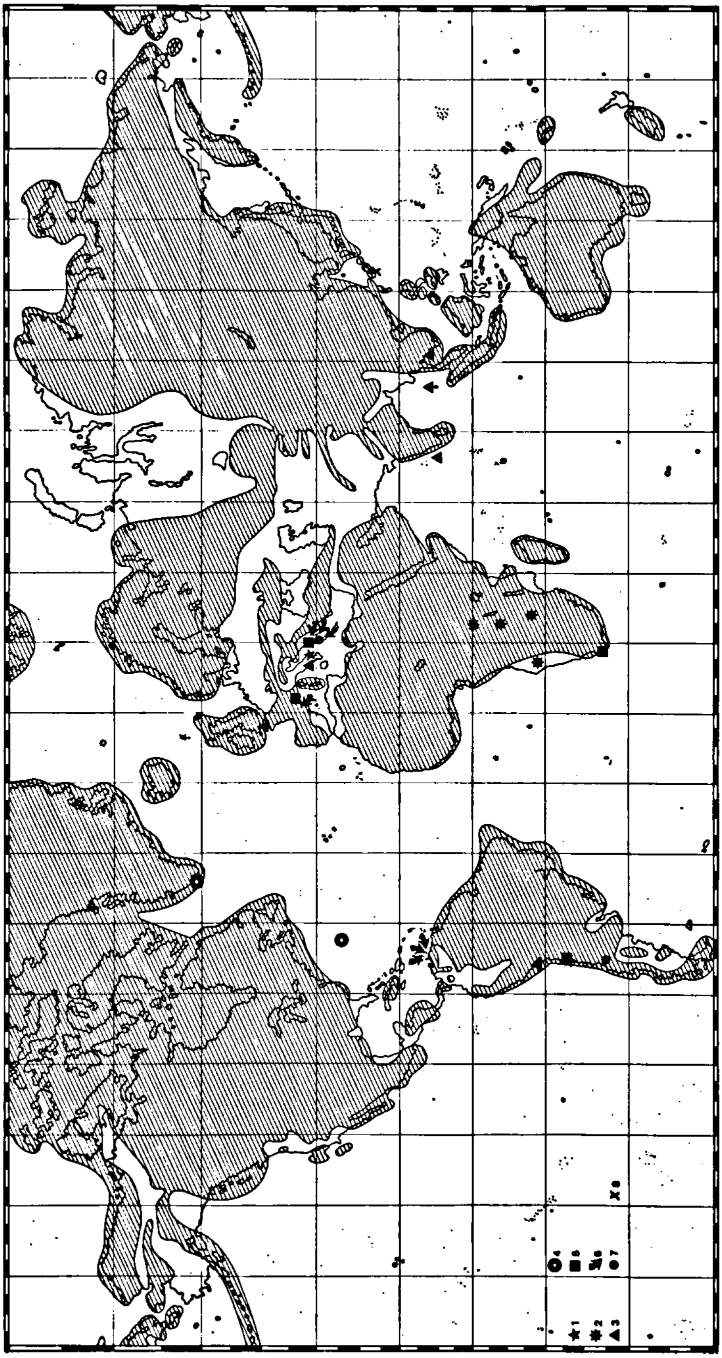
In a previous paper (STOCK, 1976b) I described, after a fortuitous find of a single specimen, an Ingolfiellid from a brackish well in Bonaire under the name of *Ingolfiella* (*Gevgeliella*) *putealis*. Financial support of the "Treub Maatschappij" (Utrecht) permitted me to revisit Bonaire in June 1976. At this occasion, a rich additional material of *I.* (*G.*) *putealis* could be collected in several brackish wells on the island; moreover, samples from a freshwater spring in Bonaire and from a marine interstitial habitat in Curaçao yielded Ingolfiellids as well, which proved to belong to undescribed species. This brings the total number of species known from the West Indies to three.

Thanks are due to Mr. P. HOETJES and Mr. E. WESTINGA, for attempts to collect additional material from several localities in Curaçao, and Mr. J. HERRERA, Kralendijk, Bonaire, for hospitality on his estates Fontein and Bacuna.

ZOOGEOGRAPHY

All three species now known from the two of the three Leeward Islands of the Netherlands Antilles (and, for that matter from the entire West Indian region) belong to the subgenus *Gevgeliella* of the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genus *Ingolfiella*, and form even within this subgenus a closely cohaerent and well-distinguished group. It is quite interesting to note that the three Antillean members of *Gevgeliella* represent the complete salinity range from marine to limnic, being a reflection of the marked euryhalinity of the entire suborder. In addition to euryhalinity, members of the suborder are also eurythermal and eurybathic. There are few groups of animals in which the marine ancestors and the limnic descendants are morphologically still so closely related: from its discovery in 1903 up to S. KARAMAN's first attempt towards a subdivision in 1959, all members of the group were considered to belong to a single genus, *Ingolfiella*, known from the deep-sea in the North Atlantic to shallow coral flats in the Indian Ocean, and from marine sands to fresh subterranean waters far inland.

A distribution map of the Ingolfiellid taxa (Fig. 55) known at present (23 species distributed over 2 families, with 7 genera and subgenera, vide STOCK, 1976b) shows clearly that the members of this suborder have a distribution pattern different from that of several other "old" groups, such as the Isopod family Microparasellidae (STOCK, 1977a), Hadziid amphipods (STOCK, 1977b), or the order Thermosbaenacea (STOCK, 1976a). For these three groups, it was supposed that their members were once widely distributed in the former Tethys Sea, and that they "stranded" at the end of the Tethys period (Oligocene-Miocene) due to sea-level regressions and uplifting of landmasses. Their actual distribution still coincides perfectly with the extension of Tethyan waters. All places where they occur now in inland waters, were under sea-level in the late Oligocene.

The Ingolfiellidea on the other hand do not show a distribution

Fig. 55. – The extension of the TETHYS SEA in the Oligocene (sea areas white, land masses hatched), after DE LATTIN. 1967. For orientation purposes, the actual distribution of sea and land is also shown. – The actual distribution of the Ingolfiellidea (2 families, 7 genera and subgenera, 23 described species) is plotted: 1 = species of *Metaingolfiella*. 2 = species of *Trogloleleupia*. 3 = species of *Hanseniella*. 4 = species of *Ingolfiella* s, str. 5 = species of *Trianguliella*. 6 = species of *Gevgeliella*. 7 = species of *Balcanella*. 8 = unidentified ingolfiellids. Note there is no match between the distribution pattern and the Oligocene shorelines.

pattern that matches the Oligocene extent of the Tethys Sea (Fig. 55). Although several localities, e.g. in the Balkans, lay in regions formerly innundated by Tethyan waters, several other localities are situated in areas that never have been under the Tethyan sea-surface or not even near its shore-lines (e.g. the central African and South American localities). Unlike Hadziids, Microparasellids, and Thermosbaenaceans, the Ingolfiellids comprise also a small number of deep-sea species.

As the distribution map shows, the continental waters of Africa harbour an endemic genus, *Trogloleleupia*, but South America has no endemic taxa of the genus-group. All South American subgenera are also known from the northern Mediterranean belt.

The marine shallow-water subgenus *Hanseniella* may well represent the most generalized Ingolfiellid unit actually known, from which other subgenera radiated in various biotopes: the deep-sea subgenus *Ingolfiella* s. str., the interstitial (coastal and limnic) subgenera *Trianguliella* and *Gevgeliella*, and the limnic subgenus *Balcanella* (cf. STOCK, 1976b, fig. 17). The African inland genus *Trogloleleupia* clearly is related to this group (there is also an African marine Ingolfiellid known, belonging to the subgenus *Trianguliella* which is widely distributed from the northern Mediterranean to South America).

The only way to explain properly the close relationship (on subgeneric level) between the African, South American and Mediterranean forms, appears to be the assumption that the subgenera had already occupied the major part of their actual range before the separation between the South American plate and the landmasses of Europe and Africa took place (see MONOD, 1975, for similar cases). On the other hand, I believe that several brackish water or limnic Ingolfiellids originated (from marine ancestors) in later, perhaps even much later times than the Mesozoic, the era in which the break-up of the continents is supposed to have taken place. In fact, the invasion of – or the adaptation to – inland waters has been and is probably a process still continuously going on. An indication in favour of this supposition is found in the very close relationship between the three Antillean species recorded in the present paper. *Ingolfiella* (*Gevgeliella*) *tabularis* from Curaçao still is a marine meiofaunal element; *I.* (*G.*) *putealis* from Bonaire occurs in oligo- and mesohaline subterranean waters, whereas, *I.* (*G.*) *fontinalis* lives in a freshwater spring in a cave on Bonaire. The available "adaptation time", for the series marine → limnic is in good agreement with the geological data for Bonaire (DE BUISONJÉ, 1974, map 4). The locality where the limnic species (*fontinalis*) was found, viz. the Spring of Fontein, is situated in the area characterized by the Washikemba formation consisting of Cretaceous or even older limestones. This area was not innundated by sea water in the late Tertiary, Pleistocene, or Neogene, so it is quite possible that limnic elements had a long period available for adaptation to freshwater conditions and for evolution. The localities in which the mixohaline species (*putealis*) was found, all are situated in the area of Bacuna/Rooi Lamunchi, which was under sea-level in the Pleistocene. This makes it improbable that any freshwater element survived in that area; in fact, I assume that *putealis* evolved, from a marine ancestor, when the area emerged after the Pleistocene regressions.

A closer micro-biogeographic survey of the Dutch Leeward Antilles (such as has been done for the Hadziid amphipods in Curaçao, vide STOCK, 1977b) would be necessary for the Ingolfiellidea to prove, or disprove, an eventual correlation between the last submergence under seawater and the evolution of the group. Such a survey would not be that easy, since Ingolfiellids are of so small a size that they are not usually captured by ordinary collecting methods. Moreover they have the awkward habit of floating on the water, or on preservation fluids like formalin, or even alcohol, so that they adhere to nets, vials, stoppers, petri dishes, etc, and are hard to detect.

Summarizing, I presume that from some plesiomorph marine shallow water Ingolfiellid (e.g. of the *Hanseniella* type), freshwater forms developed already in Mesozoic times in the still cohaerent Pangaean landmass. This explains the similarity between the European and South American taxa. In several other areas that were submerged in the Mesozoic and/or in the older Tertiary, several populations got to fresh waters; they descended from littoral populations that stranded during the late-Tertiary sea-level regressions (good examples being some of the Balkan taxa). Even in areas that emerged in or shortly after the Pleistocene, Ingolfiellids got established, presumably again originating from a marine source (an example is shown by the Bacuna area of Bonaire where *I. putealis* is found).

A distribution pattern quite similar to that described above for the Ingolfiellidea, is found in the amphipod family Bogidiellidae (STOCK, 1977c). It is assumed that the Bogidiellid taxa reached their actual distribution along the very same lines as postulated above for the Ingolfiellids.

Ingolfiella (Gevgeliella) putealis Stock, 1976

(Fig. 56)

Ingolfiella (*Gevgeliella*) *putealis* STOCK, 1976b: 66–71, figs. 18–21.

MATERIAL. – BONAIRE:

- 33 specimens; Sta. *76–13*, estate Bacuna, Pos di Cerca, a cemented well with two openings leading to a natural crevice, surrounded by troughs for cattle; water level at 6 m; position 12°07′35″ N 69°12′31″ W; temperature 29.5°C; chlorinity 2350 mg/l; June 13, 1976; accompanying fauna *Microcharon herrerai* Stock, 1977 (Isopoda), some cyclopoid copepods. (This locality is some 700 m SSW of the type-locality.)
- 37 specimens; Sta. *76–14*, Bacuna, Pos di Molina, a round cemented well on a natural crevice, about 300 m SW of former station, with ruined wind-mill; water level at 5½ m; 12°07′29″ N 68°12′38″ W; temp. 27.7°C; chlor. 1250 mg/l; June 13, 1976; accompanying fauna *Microcharon herrerai* (Isopoda).
- 7 specimens; Sta. *76–34*, coastal plain E. of Mal Hasi estate, circular well, recently constructed on a natural crevice; water level at 4 m; 12°09′38″ N 68°12′13″ W; temp. not recorded; chlor. 3450 mg/l; June 15, 1976; accompanying fauna *Microcharon herrerai* (Isopoda).

REMARKS

This species was based on a single male specimen found in a well, Pos di Wayaká, on the Bacuna estate in Bonaire. The present three records are from the same general area in Bonaire (photographs of some of the wells from which this species was recorded, can be found in STOCK, 1977a). The chlorinities at which the species was found range from 800 mg/l (type-locality) to 3450 mg/l (present records). At renewed search on June 13, 1976, the type-locality, Pos di Wayaká, showed a chlorinity of 4600 mg/l, but did not yield any further specimens of *I.* (*G.*) *putealis*, although it did reveal several addition-

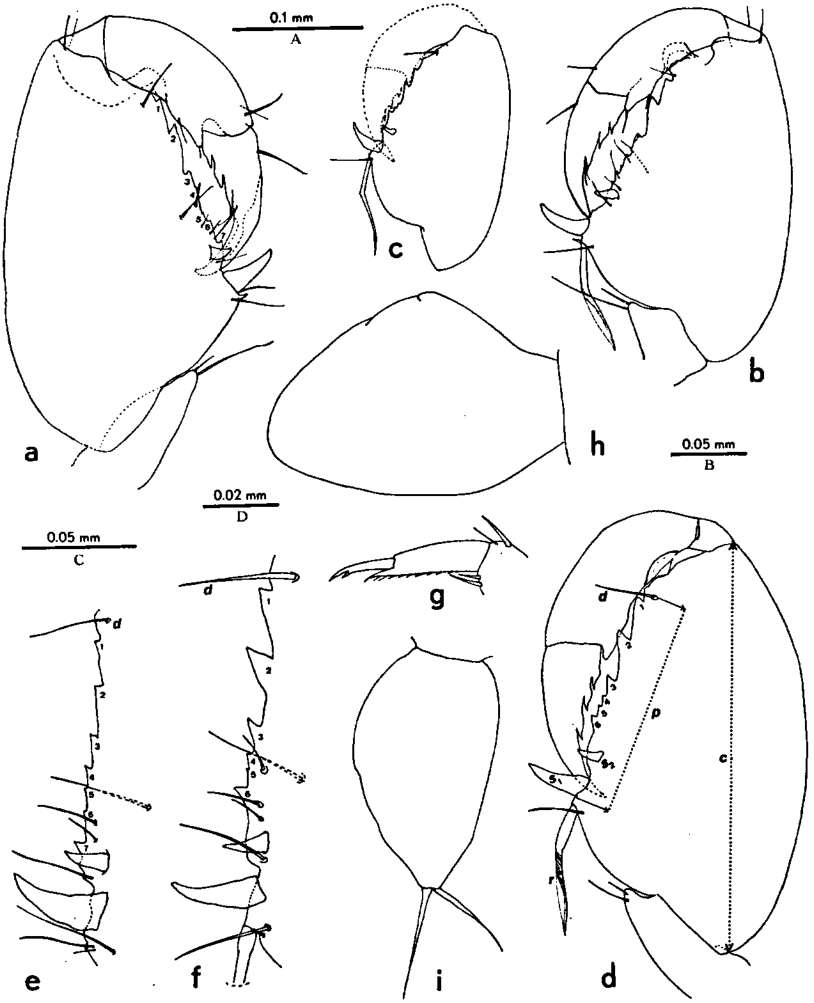

Fig. 56. – *Ingolfiella* (*Gevgeliella*) *putealis* Stock, 1976 (from wells at Bacuna, BONAIRE).

a, distal segments of second gnathopod, adult ♀ (scale A); b, same of adult ♂ (scale A); c, same juvenile ♂, semi-diagrammatic, most setae omitted (scale B); d, same of another adult ♂, semi-diagrammatic, most setae omitted (scale B); e, palmar margin of second gnathopod, adult ♀ (scale C); f, same of adult ♂ (scale C); g, distal segments of third pereiopod, adult ♂ (scale D); h, first pleopod, ♀ (scale C); i, same of ♂ (scale C).

[*c* = length of carpus; *d* = distal palmar seta; *p* = length of palma; *r* = reversed spine of male; s_1 = larger palmar angle spine; s_2 = smaller palmar angle spine; 1 through 7 = palmar teeth].

al specimens of *Microcharon herrerai*, a microparasellid isopod usually associated with the ingolfiellid.

The 1976 collections contained the hitherto unknown female of *I.* (*G.*) *putealis*, and thus provided an opportunity to make some additional descriptive notes.

The length of adult specimens ranges from 1.9 to 3.0 mm (♀, ♂). The colour of live specimens is white. The secondary sexual differences are limited to the carpus of gnathopod 2, the first pleopod, and the 2nd uropod.

Gnathopod 2: In the female, the palmar angle is armed with a large spine, a spiniform process, and 2 setae (Fig. 56a). In the male, one of these setae is replaced by a reversed, bent, ciliated element of considerable length (*r* in Fig. 56d). The palmar edge bears a number of serrations*); in both sexes, the distal three teeth (nrs. 1 to 3 in Figs. 56a, d, e, f) are large and distinct, the proximal teeth (four in female, the nrs. 4 to 7 in Fig. 56e; three in male, the nrs. 4 to 6 in Fig. 56f) are smaller.

Pleopod 1: The male first pleopod has a distal armature consisting of 2 setae (Fig. 56i); in female these setae are lacking (Fig. 56h). In one female specimen, a first pleopod with 1 distal seta has been observed.

Uropod 2: The peduncle bears a basal hook-shaped element in male (see Stock, 1976b, fig. 19c) which is absent in female.

The armature of the carpus (palmar margin) of a juvenile male (Fig. 56c) is fundamentally similar to that of the adult male.

Ingolfiella (Gevgeliella) fontinalis n. sp.

(Figs. 57–58)

MATERIAL. – BONAIRE:

- 1♂ (holotype), 1♀ (allotype), 1♂ and 5♀ (paratypes; Sta. *76–9*, estate Fontein, in a small artificial cave (almost completely dark) from which the spring of Fontein

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*) For descriptive purposes, the serrations (or teeth) are numbered (Figs. 56d, e, f) in a somewhat unusual way, viz. starting with nr. 1 for the tooth just proximal of the distal palmar seta (*d* in the figures), the next tooth is nr. 2, and so on in proximal direction to the tooth next to the palmar angle spine (s_2); the latter tooth is nr. 7 in ♀, or nr. 6 in ♂. In this way, the teeth 1 to 3 are homologous in male and female, whereas the series from 4 upward is variable.

originates; washed from sand and calcareous gravel in the fast-flowing water; 12° 14′34″ N 68°17′54″ W; temperature 29.1°C; chlorinity 370 mg/l; June 13, 1976; accompanying fauna Polychaeta and *Pyrgophorus* spec. (Gastropoda). The type-material has been preserved in the Zoölogisch Museum, Amsterdam, under Amph. nr. 106.106.

DESCRIPTION

Length (♀, ♂) 2.0–2.5 mm. Body shape and most appendages very similar to those of *I.* (*G.*) *putealis*. Small ocular lobe (Fig. 57a) present.

First antenna (Fig. 57b) slightly less slender than in *putealis*. Second antenna (Fig. 57c) also slightly less slender, but otherwise very similar to that of *putealis*. Mouth-parts identical. Maxilliped (Fig. 57d) having a rectangular endite (rounded in *putealis*).

First gnathopod (Figs. 57e, f) resembling that of *putealis*. Second gnathopod showing the most obvious distinctions: the carpus (♀, ♂) has a slightly different shape, more in particular because the palmar edge is shorter than in *putealis*. Figs. 56d and 57h show how the length of the palmar edge (*p*) has been measured, viz. from the proximal point of insertion of the larger palmar margin spine (s_1) to the insertion of the distal palmar seta (*d*). The length of the carpus (*c*) has been measured as indicated in the same figures. The ratio c/p gives an indication of the relative length of the palmar edge. This ratio is identical in both sexes; in *fontinalis*, 6 measurements showed a range of 2.11 to 2.40; in 8 specimens of *putealis* a range of 1.83 to 1.94 was found (a juvenile male of *putealis* fell within this range with a ratio of 1.90). The serration of the palmar margin forms another clear-cut distinction. In the male, both *putealis* (Figs. 56d, f) and *fontinalis* (Figs. 57g, h, j) have 6 serrations. However, in *fontinalis*, teeth 3, 4, 5, and 6 are densely crowded (4 and 5 being almost vestigal), whereas in *putealis* these teeth are well-separated. Tooth 2 of *fontinalis* ♂ is tall, higher than wide, almost isoscleles; in *putealis* ♂ this tooth is strongly scalene, wider than high. For tooth 1 the same holds true, be it less pronounced so. In the female, the palmar margin bears 7 serrations (Figs. 57i, k); teeth 1 and 2 are almost isosceles in *fontinalis*, strongly scalene in *putealis*. The carpus of the female has two simple setae of equal length near the palmar corner,

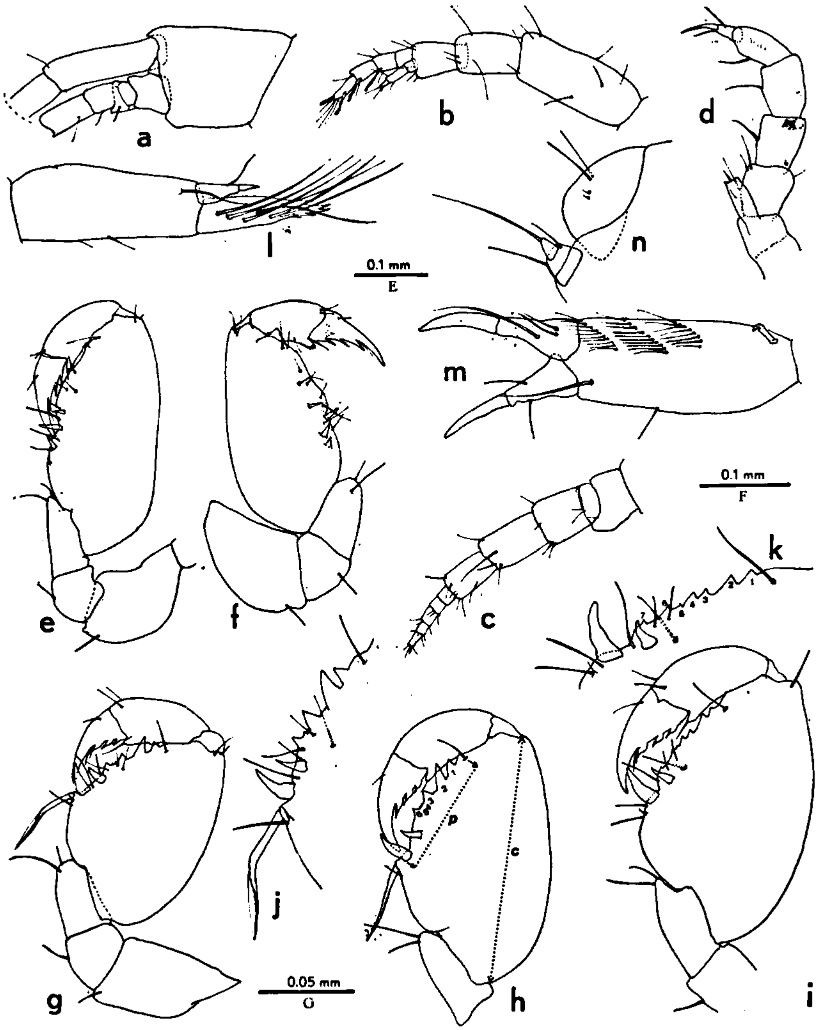

Fig. 57. – *Ingolfiella* (*Gevgeliella*) *fontinalis* n. sp. (from Fontein, BONAIRE; b, c, d, f, g, j, l, m, n after the holotype; a, e, h, i, k after paratypes).
a, head, from the left, ♀ (scale E); b, first antenna, ♂ (scale F); c, second antenna, ♂ (scale F); d, maxilliped, ♂ (scale G); e, f, first gnathopod, ♂ (scale A); g, second gnathopod, ♂ (scale A); h, same of another ♂, semi-diagrammatic, most setae omitted (scale B); i, second gnathopod, ♀ (scale B); j, palmar margin of second gnathopod, ♂ (scale G); k, same of ♀ (scale C); l, first uropod, ♂ (scale B); m, second uropod, ♂ (scale B); n, third uropod and telson, ♂, from the left (scale B).
[*c* = length of carpus; *p* = length of palma; 1 through 7 = teeth on palmar margin].

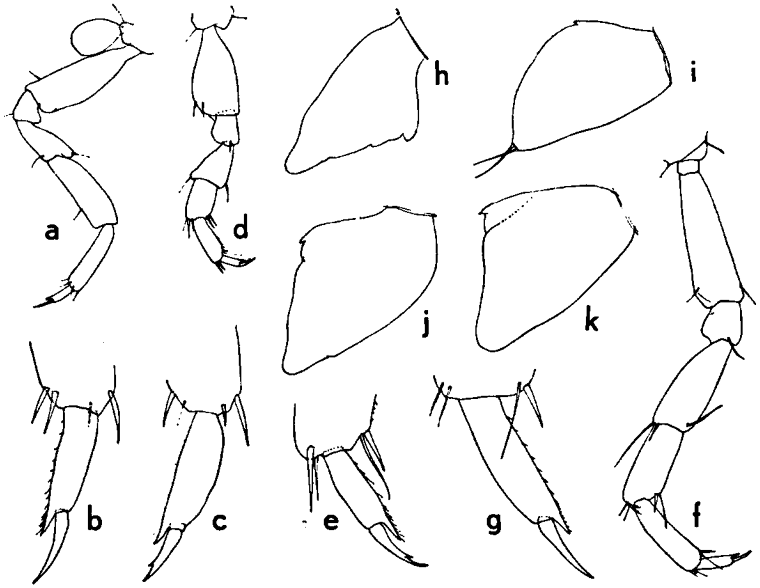

Fig. 58. – *Ingolfiella* (*Gevgeliella*) *fontinalis* n. sp. (from Fontein, BONAIRE; c, and h after paratype ♀, rest after holotype ♂).
a, third pereiopod, ♂ (scale E); b, distal segments of same (scale D); c, distal segments of third pereiopod, ♀ (scale D); d, sixth pereiopod, ♂ (scale E); e, distal segments of same (scale D); f, seventh pereiopod, ♂ (scale F); g, distal segments of same (scale D); h, first pleopod, ♀ (scale C); i, first pleopod, ♂ (scale C); j, second pleopod, ♂ (scale C); k, third pleopod, ♂ (scale C).

in the male one of these assumes a reversed direction and is strongly developed, just as in *putealis*. Another sexual difference is found in the shape of tooth nr. 2 (higher than wide in ♂, slightly wider than high in ♀).

The pereiopods 3 to 7 (Figs. 58a–g) are very similar to those of *putealis*, with one exception: The ungulus of P3, P4, and P7 often, but certainly not always, lacks a bifid tip. The holotype (a male, Figs. 58b, g) has a simple ungulus in P3, P4, and P7, but a paratypic female has a bifid ungulus in P3, and a simple one in P4 and P7, whereas a paratypic male has a bifid ungulus in P7 and simple ones in P3 and P4. Pereiopods 5 and 6 always seem to have bifid unguli in this species. In *putealis* all unguli are, without exception, bifid.

The first pleopod is sexually dimorphic: in male it bears 2, very rarely 3, distal setules, lacking in female (Figs. 58h, i). All three pleopods (Figs. 58i, j, k) have a more or less triangular shape, with a straight or feebly curved medial margin, and a lateral margin produced into a projection (least marked in pleopod 1, ♂).

The first uropod (Fig. 57l) resembles that of *putealis*, except for the endopodal setae that tend to be arranged in 2 rows. The second uropod (Fig. 57m) has a basal hook in ♂, and is similar to that in *putealis*, except in that exo- and endopodite both are clearly 2-segmented (segmentation obscure to absent in *putealis*).

The third uropod and the telson (Fig. 57n) do not differ from those in *putealis*.

REMARKS

Though closely related to *I.* (*G.*) *putealis*, the new species is sufficiently distinct morphologically (especially in the ornamentation of the carpus of gnathopod 2) to warrant a separate taxonomic rank. Also ecologically there are differences: *putealis* occurs in oligo- and mesohaline stagnant groundwater, whereas *fontinalis* has been found in fresh, fast-running waters of a spring. It is assumed that both species inhabit the interstitia of coarser sediments.

The proposed specific name, *fontinalis*, alludes to the name of the type-locality, Fontein, in Bonaire.

Ingolfiella (Gevgeliella) tabularis n. sp.

(Fig. 59)

MATERIAL. – CURAÇAO:
- 1♂ (holotype), 1♀ (allotype): Sta. *76–2*, Boca Tabla (12°22′19″ N 69°06′49″ W); in coarse sand, particle size 1 to 5 mm, of a dry rain gully (a so-called "rooi"), just below the entrance of the Boca Tabla sea cave; marine salinity; June 11, 1976; accompanying fauna *Microcerberus* spec. (Isopoda), *Caecum* spec. (Gastropoda). The type-material has been preserved in the Zoölogisch Museum, Amsterdam, cat. nr. Amph. 106.107.

DESCRIPTION

Body length of the male 1.9 mm, of the female 1.5 mm. Ocular lobe minute.

First antenna: peduncle clearly more slender than in *I.* (*G.*) *fontinalis* (in the male specimen both antennulae are broken off, but there is no reason to assume that the female antennula illustrated in Fig. 59a differs in any way from the corresponding male appendage).

Second antenna (Fig. 59b) clearly more slender than in *fontinalis* and slightly more slender than in *putealis*, but otherwise very similar in structure.

The maxillipedal endite (Fig. 59c) is slender, almost finger-shaped, and is distally armed with 2 spiniform processes and 1 setule.

The first gnathopod (Fig. 59d) resembles that of *putealis* most. The carpus is more elongated than in *fontinalis*.

The second gnathopod resembles strongly that of *fontinalis*. The carpus is sexually dimorph. In the male (Fig. 59e), one of the palmar angle setae is transformed into a strongly developed, reversed element. Between the smaller palmar angle spine and the distal palmar seta, the usual 6 teeth arise (Fig. 59f). The mutual distance and the size of these teeth resemble the condition found in *fontinalis* i.e., tooth nr. 2 is very tall, almost isosceles, teeth 3 to 6 are very crowded, 4 and 5 being minute).

In the female (Fig. 59g) the carpus of gnathopod 2 bears 7 teeth on the palmar margin (Fig. 58h), arranged and shaped as in *fontinalis*. The ratio carpal length/palmar length (*c*/*p*) is 2.14–2.15 for both sexes, thus resembling the *fontinalis* condition. The projection at the inner distal end of the propodus is terminally truncated.

All pereiopods have bifid unguli. The dactylus and ungulus of the 3rd (Fig. 59i) and 4th pereiopods are perhaps a trifle less slender than in *fontinalis*. The dactylus of the 5th (Fig. 59k) and in particular the 6th pereiopods (Fig. 59m) offers the main distinction to separate the present species from *fontinalis*: the dactylus is very short (and not at all elongated as in *fontinalis*), its inner distal corner is produced into a low, rounded, triangular projection (a long sharp point in *fontinalis*). As a matter of fact the entire P5 and P6 (Figs. 59j, l) are more robust than in *fontinalis*.

The 7th pereiopod (Fig. 59n) is as slender as in *fontinalis*, although the distal inner process on the dactylus (Fig. 59o) is triangular (elongate and more spiniform in *fontinalis*).

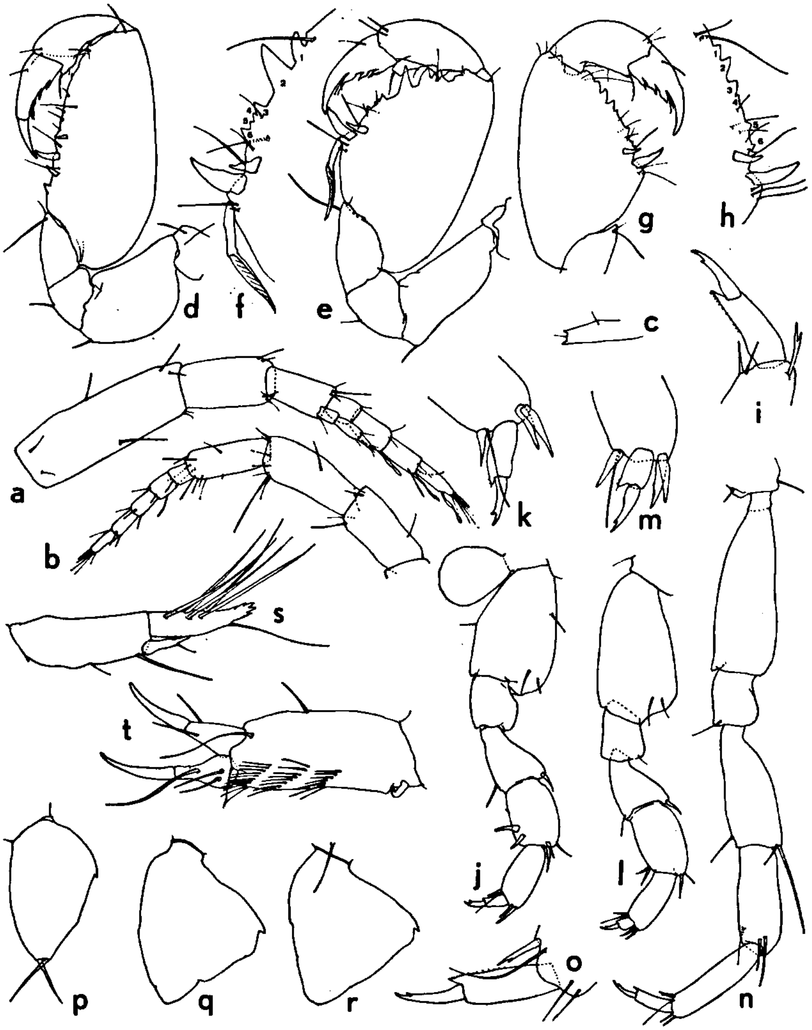

Fig. 59. – *Ingolfiella* (*Gevgeliella*) *tabularis* n. sp. (from Boca Tabla, CURAÇAO; ♂ holotype, ♀ allotype).

a, first antenna, ♀ (scale B); b, second antenna, ♂ (scale B); c, endite of maxilliped, ♂ (scale C); d, first gnathopod, ♂ (scale B); e, second gnathopod, ♂ (scale B); f, palmar margin of same, the numerals denote the teeth (scale C); g, second gnathopod, distal segments, ♀ (scale B); h, palmar margin of same, the numerals denote the teeth (scale C); i, distal part of third pereipod, ♂ (scale D); j, fifth pereiopod, ♂ (scale B); k, distal part of same (scale D); l, sixth pereiopod, ♂ (scale B); m, distal part of same (scale D); n, seventh pereiopod, ♂ (scale B); o, distal part of same (scale D); p, first pleopod, ♂ (scale C); q, second pleopod, ♂ (scale C); r, third pleopod, ♂ (scale C); s, first uropod, ♂ (scale B); t, second uropod, ♂ (scale B).

The first pleopods are sexually dimorph: in male (Fig. 59p) they are provided with 2 distal setules, which are lacking in female. Pleopods 2 and 3 (Figs. 59q, r) are very markedly triangular in outline, relatively wider than in *fontinalis* and *putealis*.

The first uropod (Fig. 59s) has a distally serrated endopodite; the margins of the endopodite bear 1 and 3 + 2 setae, respectively.

The second uropod (Fig. 59t) bears a proximal peduncular hook in male, which is lacking in female. There are 3 rows, of 7, 8, and 11 setules, respectively, on the peduncle. The rami are slender, curved, distinctly 2-segmented. The distal exopodite article in particular is much more slender than in *fontinalis*.

The third uropod and the telson are as in *fontinalis*.

REMARKS

The short dactylus in the 6th pereiopod distinguishes this species at once from the two related taxa from Bonaire, *I.* (*G.*) *putealis* and *I.* (*G.*) *fontinalis*. The palmar armature resembles strongly that of *fontinalis*, but the more slender antennae form an additional distinctive character from that species.

The three Antillean species of the subgenus *Gevgeliella* form a closely cohaerent group, distinguished from the three other (European) species, *petkovskii*, *vandeli*, and *catalanensis*, by having triangular (instead of finger-shaped) first male pleopods.

The proposed specific name alludes to the type-locality, Boca Tabla.

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