

Abscondicola humesi n. gen., n. sp. from the gill chambers of land crabs and the definition of the Cancrincolidae n. fam. (Copepoda, Harpacticoida) *

by Frank FIERS

Abstract

The harpacticoid copepod *Abscondicola humesi* n. gen., n. sp. is described from the gill chambers of terrestrial crabs recovered along the northern coast of Papua New Guinea. *Abscondicola* n. gen. is related to *Cancrincola* WILSON and *Antillesia* HUMES, also associates of semi- and terrestrial crabs, and is the first representative of this genus group in the Pacific Ocean. The genera *Cancrincola* and *Antillesia*, previously assigned to the Ameiridae, are together with *Abscondicola* n. gen. unified in the newly erected family Cancrincolidae n. fam. Relevant details of the adults of *Cancrincola jamaicensis*, *C. longiseta* and *Antillesia cardisomae* are summarized. In addition, the copepodid stages of the species studied herein are described and keys to the genera and species are provided.

Key-words : crab associates, Cancrincolidae n. fam., *Abscondicola*, n. gen., copepodids, checklist.

Résumé

Le copépode harpacticôïde *Abscondicola humesi* n. sp. est décrit des cavités branchiales des crabes terrestres découverts le long de la côte nord de la Papouasie Nouvelle Guinée. *Abscondicola* n. gen. est proche du *Cancrincola* WILSON et *Antillesia* HUMES, eux aussi associés des crabes terrestres et semi-terrestres; c'est le premier représentant de ce groupe dans l'Océan Pacifique. Les genres *Cancrincola* et *Antillesia*, attribués auparavant aux Ameiridae, sont regroupés avec *Abscondicola* n. gen. dans la nouvelle famille des Cancrincolidae n. fam. Des détails importants concernant les adultes de *Cancrincola jamaicensis*, *C. longiseta* et *Antillesia cardisomae* sont énumérés. En plus, on trouvera la description du développement des espèces étudiées ici, de même que les clés des genres et des espèces.

Mots-clefs : associés des crabes, Cancrincolidae n. fam., *Abscondicola*, n. gen., copepodites, liste faunistique.

Introduction

The earliest record of a harpacticoid associate living in the gill chambers of terrestrial decapod crabs is that of WILSON (1913). *Cancrincola jamaicensis* originally found on *Cardisoma guanhumii* (LATREILLE) collected at Montego Bay, Jamaica (WILSON, 1913) has been reported since then from many localities along the East Atlantic and West African coasts (see HUMES, 1958).

PEARSE (1930) discovered a second species, *C. wilsoni*, on two *Sesarma* species from Japan which he assigned to the genus *Cancrincola*. LANG (1948 : p. 842) doubted the designation of *C. wilsoni* while HUMES (1947) describing the closely related *P. orientalis* pointed to the differences with *Cancrincola* and erected the genus *Pholetiscus* to accommodate *C. wilsoni* and *P. orientalis*.

Actually, three genera of terrestrial crab associated copepods are known. *Cancrincola* and *Antillesia*, both widely distributed along the central atlantic coasts, have been attributed to the Ameiridae. The third genus, *Pholetiscus*, found on crabs in the Indian ocean and along the north-west pacific shorelines, belongs to the family Canthocampidae showing strong affinities with *Mesochra* and related genera (LANG, 1965).

The present contribution deals exclusively with the ameirid genera *Cancrincola* and *Antillesia*. A third and related genus, *Abscondicola* n. gen. is erected herein to accommodate *A. humesi* n. sp. found on two species of terrestrial crabs from Laing Island, Papua New Guinea.

The three genera share unique features justifying the removal of this group from the Ameiridae. The separate genital segments of the female, the sexual dimorphism and the unique shape of the male P₆ besides the particular behavior as associates of terrestrial crabs are the most important characteristics of the Cancrincolidae n. fam.

Furthermore, morphological details including descriptions of the copepodid stages of *Cancrincola jamaicensis*, *C. longiseta* and *Antillesia cardisomae* are given. Synonymies, location of type-material, lists of previous and new records are given for all known species while the diagnoses of the genera are updated in accordance with the results of the present study.

Materials and methods

During a short stay (9 - 18 Nov. 1986) at the Leopold III Biological Station (Laing Island, Madang Province, Papua New Guinea) terrestrial crabs were hand-collected, fixed in a buffered solution of 4 % formaldehyde and sent to Belgium. After arrival, the formaldehyde solution was replaced by 75 % ethylalcohol and filtered through a sieve

* Leopold III Biological Station, Laing Island, Contribution no. 190, Amsterdam Expeditions to the West Indian Islands, Report 60.

(mesh 39 μm). Only 4 specimens of *Abscondicola humesi* n. gen., n. sp. were in this residue.

The gill chambers of each crab were thoroughly rinsed above a sieve (mesh 39 μm) using a strong current created by a pipette connected to a water tap. The copepods were then picked from the residue collected from each individual crab and stored in 75 % ethylalcohol.

Crabs from the invertebrate collection were treated the same way. The preserving solution of these stored specimens has been filtered separately but no copepod specimens were found in the residues.

Since the copepod specimens strongly deform when transferred from alcohol to lactophenol, the specimens examined were kept in a drop of lactophenol for several days until their shape returned to normal. Dissected parts are mounted in lactophenol while preserved specimens are stored in 75 % ethylalcohol. Drawings were made using a camera lucida. Specimens deposited in the collections of the "Koninklijk Belgisch Instituut voor Natuurwetenschappen". Brussels, are numbered COP. Specimens collected during the West Indian Expeditions of the University of Amsterdam are labeled ZMA and deposited in the collections of the Taxonomic Institute, Amsterdam.

Systematics

Cancrincolidae n. fam.

Diagnosis :

Female : habitus cylindrical, almost vermiform; body segmentation obscure; first thoracic segment fused with the head; pleural regions and fringes absent; 6-th and 7-th (genital and first abdominal segments) separated; genital field (clasping organs and vulva) on the ventral surface of somite 6; copulatory pore on the ventral surface of the 6-th, close to the anterior part of the genital field or near the postero-ventral margin of the somite; both parts of the

genital complex internally connected with a receptaculum seminis; rostrum minute and fused with the head; antennule eight-segmented bearing an aesthetasc on segment 4 and 8; antenna with allobasis or semi-allobasis (one side fused, other side free); exopodite one-segmented; mandibular palp with endopodite, exopodite absent; basis without seta; exopodite of maxillule represented by a single seta; maxilla with two endites; maxilliped prehensile, without setae on the first endopodal segment; endopodite P₁ prehensile and two-segmented; exopodites of P₁-P₄ and endopodites of P₂-P₄ three-segmented; P₅ with baseoendopodite and exopodite, bearing respectively 2-5 and 4-5 setae.

Male : antennule six-segmented, sub-chirocer; distalmost inner spinule on the P₁ basis and outer subdistal spine of P₂ endopodite may be distinctly stronger than in female; P₃ with a curved inner apical seta instead of a long and feathered one; baseoendopodite of P₅ fused with the supporting segment; exopodite P₅ with 2 to 4 setae; P₆ without setae, situated in the middle of the ventral surface of the sixth segment, forming a single large median opening, closed with a large ovate plate.

Type-genus :

Cancrincola WILSON, 1913, here designated.

Besides the type-genus, the family comprises the genera *Antillesia* HUMES, 1958 and *Abscondicola* n. gen.

Discussion :

Originally, WILSON (1913) assigned *Cancrincola* to the Canthocamptidae but LANG (1936, 1948) who redefined the families, allocated the genus to the Ameiridae where it remained until now. The closely related genus *Antillesia* and three other cancrincolid species were described by HUMES (1957; 1958) who investigated numerous crabs from both sides of the Atlantic offering an outstanding contribution on the different species of this genus group. Actually, *Cancrincola* comprises four different species

Table 1 :

Chaetotaxy of the species of Cancrincolidae n. fam.

	P1	P2		P3		P4		P5		P5	
	Exo	Exo	End	Exo	End	Exo	End	Exo	Bas	Exo	Bas
<i>Cancrincola</i>											
<i>jamaicensis</i>	0-1-023	0-1-123	1-1-121	0-1-123	1-0,1-221	0-0-023	1-0-221	5	5	3,2	2
<i>longiseta</i>	0-1-023	0-1-223	1-1-121	0-1-223	1-0,1-221	0-0-123 *	1-0-221	5	5	2	2
<i>abbreviata</i>	0-1-023	0-1-123	1-1-121	0-1-123	1-0,1-221	0-0-023	1-0-221	5	5	2	2
<i>plumipes</i>	0-1-023	0-1-123	1-1-121	0-1-123	1-0-221	0-0-023	1-0-221	5	5	2	2
<i>Antillesia</i>											
<i>cardisomae</i>	0-0-023	0-1-123	1-1-121	0-1-123	1-1-221	0-1-123	1-1-221	5	5	4	0
<i>Abscondicola</i>											
<i>humesi</i>	0-0-022	0-0-022	1-1-121	0-0-022	1-0-121	0-0-122	1-1-121	4	2	3	0

* HUMES (1957) found specimens with 5 spines and setae instead of 6.

while *Antillesia* remains monotypic.

Abscondicola n. gen., defined below, has many features in common with both ameirid genera and should consequently join them in the Ameiridae. However, the three genera possess some unique and advanced characteristics indicating in the first place their common origin and suggesting that their presence in the family Ameiridae is questionable.

The main feature, excluding this genus group from the ameirids, is the morphology of the female genital segments. Cancrincolidae n. fam. show no trace of fusion between the sixth and seventh somite while all Ameiridae have completely fused genital and first abdominal segments forming the typical genital double segment. Separate genital segments are extremely rare Harpacticoida. The epimerae may be free to various degrees dorsally and/or laterally but the ventral sides of the sixth and seventh segment are always fused forming an entire rigid surface. The only exception is found in the Latiremidae (pers. obs.), a family whose affinities to other harpacticoid families is uncertain at the moment.

Separate genital and first abdominal segments are considered as a primitive state in copepods (BOXSHALL, *et al.*, 1984). Such character state has been frequently observed in the other orders (ex. Platycopioida and Misophrioida). However, the separated segments in Cancrincolidae n. fam. are not seen as ancestral but as an evolutionary novelty and as an apomorphy for this taxon. Indeed, all other features of the Cancrincolidae n. fam. — i.e. mouthparts, body shape and their association with terrestrial crabs — are advanced compared to the Ameiridae and related families.

The morphology of the mandibular palp of Cancrincolidae n. fam. is simple and contrasts with the homologous appendage of the Ameiridae in the chaetotaxy. In the former, this structure is composed of two small segments (basis and endopodite) without a seta or spine on the basal podomere. At first sight, the mandibular palp of Cancrincolidae and most Ameiridae resembles each other closely. However, the proximal podomere of ameirid species always bears setae or spines. Many highly advanced Ameiridae exhibit a very robust spine, in some species even larger than the entire palp.

Besides typical female and general characteristics, cancrincolid males show several very important diagnostic features. In contrast to the Ameiridae who have peculiar transformations of the inner spine of the P₁ basis, Cancrincolidae n. fam. exhibit no comparable modifications. The sole ameirid genus missing this feature is the genus *Karllangia*, but since it exhibits several other non-ameirid features, its presence in the family Ameiridae is questionable and should be reviewed in the future.

Amongst the Cancrincolidae n. fam., the genus *Cancrincola* clearly represents the less advanced branch. Of special interest in this group is the sexual dimorphism of the distalmost spinule (integumental structure) on the P₁ basis. Such modification resembles closely the transformation of the homologous spinule in the diosaccid genera related to *Amphiascus*. Moreover, the slightly sexual dimorphic

appearance of the endopodite P₂ in *Cancrincola* resembles closely more the Diosaccidae in which sexual dimorphism is exclusively exhibited on the P₂ endopodite. It is clear from the modification of the P₂ in *Cancrincola* is of a different nature than the P₂ transformations in the Diosaccidae. Apparently they are not the result of a common origin, but the presence of a dimorphic P₂ in Cancrincolidae n. fam. is undoubtedly an important diagnostic feature supporting the erection of this family.

Highly diagnostic for the Cancrincolidae n. fam. is the shape of the male P₆. Whereas the Ameiridae, including the most advanced species, bear a distinct socle with two or three setae on it, males of the Cancrincolidae n. fam. have only a single appendage without any armature. The margins of the male genital orifice of the present family are strongly sclerified while the orifice itself is closed with an ovate plate. The whole structure is situated near the centre of the ventral surface of the somite and forms the top of a slight elevation of the surface. In all other families, except for Canuellidae which have a highly specialized male genital orifice (petasma), the P₆ forms the posterior margin of the sixth somite. It seems clear that the specialized morphology of the P₆ in Cancrincolidae n. fam. is an important novelty influencing strongly the transport and behavior during the transmission of the spermatheca.

Finally, the life-style of the Cancrincolidae n. fam. as associates of terrestrial and semi-terrestrial decapods, suggests a fundamental modification of structures. The vermiform body shape including the secondary articulation between the sixth and seventh somite in the female as well as the markedly developed prehensile P₁, furnished like the other natatorial legs with strongly armed spines, are considered as highly specialized modifications of the ancestral (harpacticoid - ameiomorph) body plan. Amongst the Ameiridae, at least three species live associated with invertebrates (*Nitocra bdelluriae*, *N. divaricata*, *N. medusaea*, see GOTTO, 1979). Regarding their morphology the three species exhibit no special structures which could be considered as specialized equipment for their behavior.

Nevertheless, Cancrincolidae n. fam., seems to retain the capacity for free living. At least two species, *Cancrincola jamaicensis* and *Antillesia cardisomae* have been found in sediment samples (PETKOVSKI, 1978, present contribution). As described in the following pages, both species were found in interstitial samples from inland waters showing a reduced salinity. It is possible that terrestrial crabs were nearby and that the associated harpacticoid species freely moved in and out the gill chambers. Future research on this matter will throw some light on these questions.

Features indicating relationships of the present family with the Ameiridae are obvious. The antennule in both sexes, morphology of the maxillule, maxille and maxilliped and the general shape of the genital field illustrate the phylogenetic proximity of the two families. From a phylogenetic point of view these shared features are not at odds with the above discussed diagnostic characteristics which distinctly separate the taxon Cancrincolidae n. fam. from the Ameiridae.

Key to the genera

- 1 - Furcal rami about 3 times as long as wide, bearing six setae; second exopodal segment P₁ without an inner seta; male exopodite P₅ with three setae at least: . . . 2
- Furcal rami at the most 1.5 times as long as wide, bearing seven setae; second exopodal segment P₁ with an inner seta; male exopodite P₅ with two setae at the most: . . .
 *Canacrincola*
- 2 - Ultimate exopodal segments P₁-P₄ with 3 outer spines; median exopodal segments P₂-P₄ with an inner seta; female P₅ with 5 setae on both rami: *Antillesia*
- Ultimate exopodal segments P₁-P₄ with 2 outer spines; median exopodal segments P₂-P₄ with an inner seta; female P₅ with 4 exopodal and two baseoendopodal setae: *Abscondicola*

Canacrincola WILSON, 1913*Diagnosis:*

Body fusiform compressed; furcal rami 1.5 times as long as wide and bearing seven setae; genital organ with a short bulbous receptaculum seminis with copulatory pore close to the vulva; ultimate exopodal segments P₁-P₄ with three outer spines; median exopodal segment P₁ with an inner seta; median exopodal and endopodal segments of P₄ without inner setae; baseoendopodite and exopodite of P₅ with five setae.

Male: basis P₁ bearing a dimorphic spinule; endopodite P₂ smaller than in the female and bearing a stronger subdistal outer spine; baseoendopodite and exopodite of P₅ with two setae.

Type-species:

Canacrincola jamaicensis WILSON, 1913 by designation.

Key to the species

- 1 - Third exopodal segment P₂ and P₃ with two inner setae, P₄ with one inner seta: *C. longiseta*
- Third exopodal segments P₂ and P₃ with one inner seta, of P₄ without setae: 2
- 2 - Inner seta of the first endopodal segment P₁, reaching beyond the second segment: *C. jamaicensis*
- Inner seta of the first endopodal segment P₁ reaching the articulation with the second segment only: 3
- 3 - Exopodite P₅ at least twice as long as wide; baseoendopodite without spinules along the inner margin:
 *C. abbreviata*
- Exopodite P₅ ± 1.5 times as long as wide; baseoendopodite with spinules along the inner margin: *C. plumipes*

Canacrincola jamaicensis WILSON, 1913

Figs. 1 - 6

Synonymy:

Canacrincola jamaicensis, new species: WILSON, 1913, pp. 264-268, Pl. 50 (281), 51 (282, 283), 52 (290-302); WIL-

SON, 1935, pp. 347; LANG, 1948, pp. 842-843, Fig. 338 (1); HUMES, 1957, pp. 180-183, Pl. 1 (1-13), Pl. 2 (14-17); HUMES, 1958, pp. 77-80, Fig. 1-6; PETKOVSKI, 1973, pp. 140; PETKOVSKI, 1978, pp. 103-109, Fig. 1-9; non PEARSE, 1951, pp. 342.

Type-locality:

Jamaica, Montego Bay: from the gill chambers of *Cardisoma guanhumii* LATREILLE (Decapoda, Gecarcinidae).

Type-material:

Originally deposited in the United States National Museum (no. 43506: holotype, female and no. 43596: paratypes) but dried up (HUMES, 1958). One topotypic female designated by HUMES (1958, p. 77).

Material:

Amsterdam Expeditions to the West Indian Islands.

- Sta 80-16. Aruba, well at Daimari (12°31'56"N 69°56'30"W), in coconut plantation, dry "aroya" (torrent bed); water table at 1.3 m, water depth 0.30 m; temp. 28.9° C; chlorinity 2,804 mg/l; black sediment, 23 May 1980. Leg. L. BOTOSANEANU & J. NOTENBOOM. Three females, one Cop male and one Cop V female, preserved (ZMA Co 102.833). One male dissected, mounted on three slides (Cop 2917a, b, c).
- Sta 80-31. Bonaire. Small cave very close to "Boca Onima" (12°15'35"N 68°18'37"W) in cave pool (description in WAGENAAR HUMMELINCK, 1979). Chlorinity 3,514 mg/l, 28 May 1980. Leg. L. BOTOSANEANU & J. NOTENBOOM. One female (ZMA Co 102.830).
- On *Cardisoma armatum* HIRKLOTS (female, carapax width: 49 mm) from Zaire, Banana, caught on the beach along the riverside of the creek, IG. 16808, leg. A. Capart, 30 April 1949. 18 females (12 ovig.), 7 males, 1 Cop V, 1 Cop IV, 1 Cop III, 1 Cop II, preserved in alcohol (COP 2912), one ovig. female and one male dissected (Cop 2913a, b, c and Cop 2914a, b, c).
- On *Cardisoma armatum* HIRKLOTS (male, carapax width: 54 mm), same locality as above. Dissected copepodids: 2 Cop I (Cop 2918, 2920); Cop II (Cop 2921); Cop III (Cop 2919); Cop IV female (Cop 2923), male (Cop 2922); Cop V female (Cop 2925), male (Cop 2924). Preserved specimens: 2 females (ovigerous), 4 males, 2 Cop V, 3 Cop IV, 3 Cop II, 2 Cop I (Cop 2926).

Previous reports:

Since the reports of *C. jamaicensis* by PEARSE (1951) are based on misidentifications or are not identifiable anymore, these locations are omitted as proposed by HUMES (1958).

- On *Cardisoma guanhumii*: Bahamas, Bimini; Barbados, St. James; Brazil, Cannavieiras and Pernambuco; Cuba, Bahia Honda; Haiti, Grand Anse; Jamaica, Montego Bay (type-locality, WILSON, 1913; HUMES, 1958), Port Henderson; St. Kitts; Swan Island; U.S.A., Vero Beach (Fla) (HUMES, 1958).

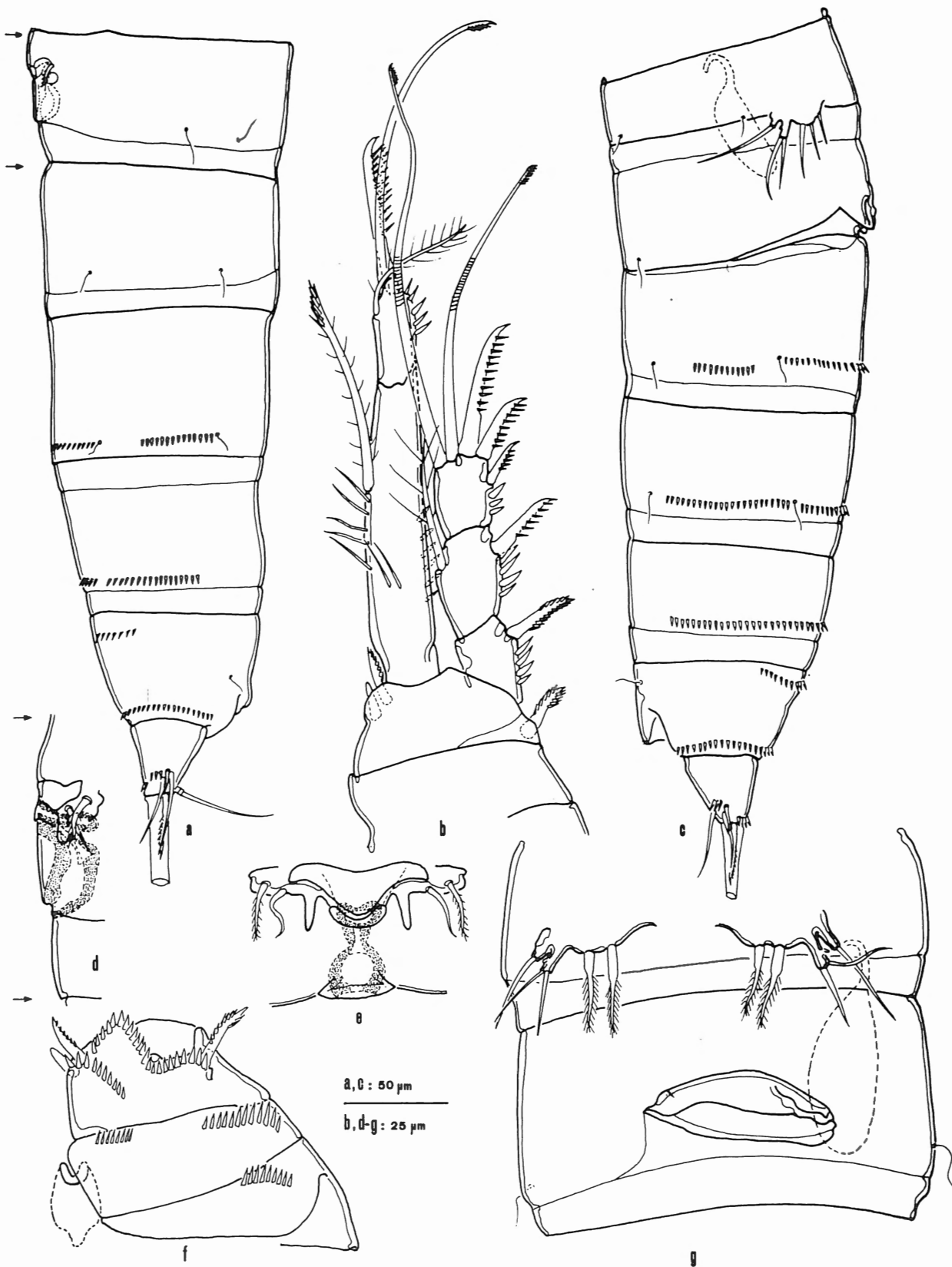


Fig. 1. - *Cancrincola jamaicensis*: a. Female abdomen, lateral view; b. P₁ of the male (posteriad); c. Male abdomen, lateral view; d. Female genital field in lateral view (arrows indicating enlarged region in a); e. Female genital field in ventral view; f. Protopodite P₁, male; g. P₅ and P₆ of the male, in situ.

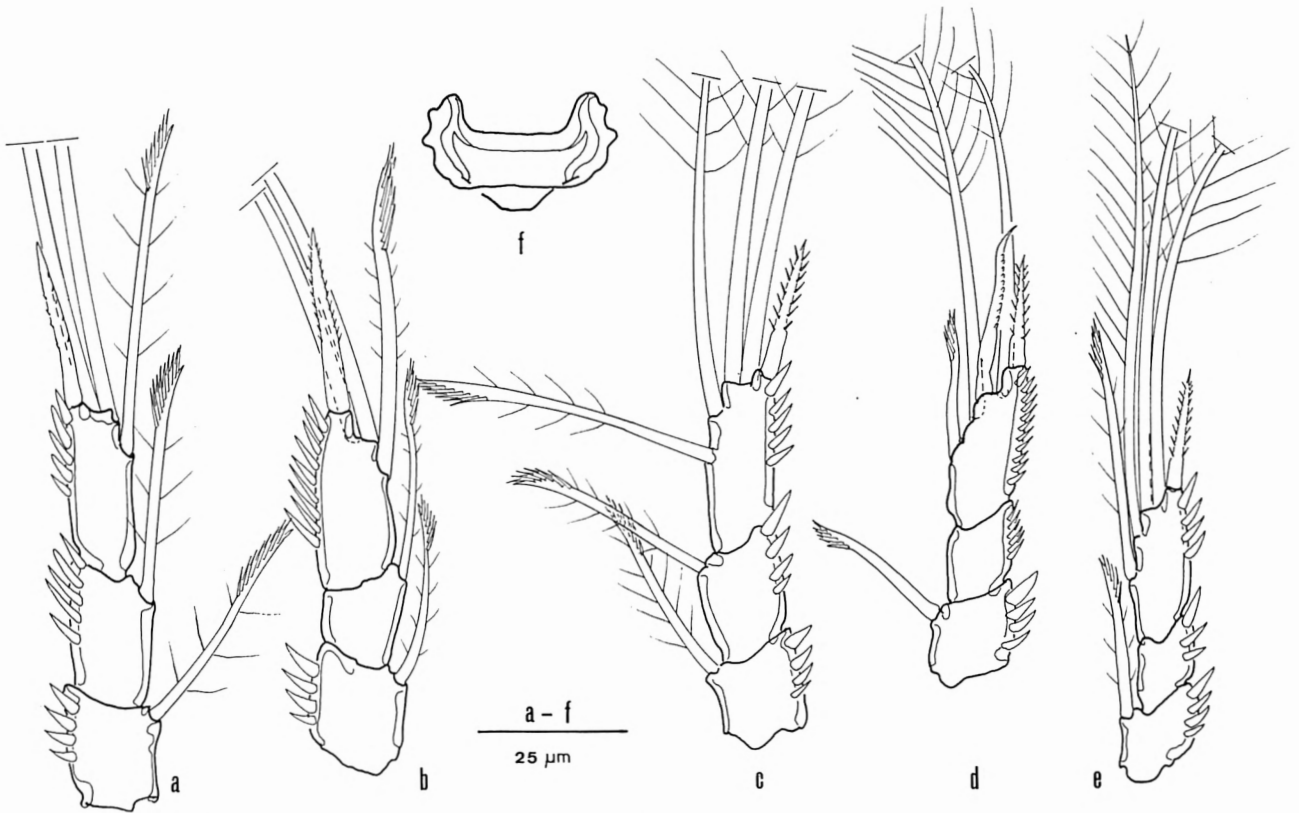


Fig. 2. - *Cancrincola jamaicensis*: a. Endopodite P_2 , female; b. Endopodite P_2 , male; c. Endopodite P_3 , female; d. Endopodite P_3 , male; e. Endopodite P_4 , male; f. Intercoxal plate, P_3 .

— On *Cardisoma armatum*: Ghana, Accra; Ivory Coast, Koumassi (Abidjan); Nigeria, near Lagos; People's Republic of the Kongo, Pointe Noire; Senegal, N'Gor (Dakar) and Joal; Sierra Leone, near Freetown; (HUMES, 1957).

— On *Sesarma huzardi*: Sierra Leone, near Freetown: 1 specimen among 100 specimens of *Cancrincola abbreviata* (HUMES, 1957).

Description:

Full descriptions of this species can be found in WILSON (1913) and HUMES (1957, 1958). Some amendments are given below which are relevant in the context of the present study.

Female: second and third abdominal segments furnished with a spinulose row on the lateral and ventral surface of the somites near the posterior margin (Fig. 1a); anal segment with a row of spinules in the anterior half of the ventral side and along the articulation with the furcal rami. Genital organs (Fig. 1d and e): receptaculum seminis short and bulbous, having thick margins; posterior part of the receptaculum rounded in anterior view; vulva flattened and ovate in anterior view.

P_1 : inner seta of first endopodal segment reaching the apical margin of the ramus; feathered along the stem and pectinate near the tip; exopodal spines of second and third segments strongly armed along the outer margin but spines on basis and first segment spinulose along both sides; apicalmost setae of the exopodite and endopodite slightly geniculated and pectinate near the tip.

P_2 - P_4 (Fig. 2a, c, respectively): inner endopodal setae of the proximal and middle segments feathered and pectinate; inner endopodal seta of third segment P_2 and proximal endopodal setae of the third segments of P_3 and P_4 feathered and pectinate; distal inner setae of the third endopodal segments of P_3 and P_4 and apical setae of P_2 - P_4 feathered only; outer distal spine of P_2 armed with a few minute spinules, of P_3 and P_4 normally spinulose; intercoxal plate (Fig. 2f) wide.

Male: general appearance as in the female; first, second and third abdominal segments with combs along the lateral and ventral margins; anal segment as in the female.

P_1 (Fig. 1b, f): rami, prae-coxa and coxa as in the female; basis with a distinctly larger spinule situated on the posterior surface near the implantation of the inner spine.

P_2 - P_3 (Fig. 2b, d, e, respectively): outer distal spines of endopodites P_2 and P_3 implanted on a distinct socle; median endopodal segment of the endopodites lower than in the female; endopodite P_4 and P_2 with the same chaetotaxy as in the female; endopodite P_3 without an inner seta on the median segment, with a much smaller proximal seta on the third segment and a curved, armed spinulosa inner distal seta.

P_6 (Fig. 1g) ovate with a strongly sclerified left margin.

Variability:

The P_5 of the male sometimes bears three baseendopodal setae instead of two. Some females lack an inner seta on the median endopodal segment of the P_3 .

Table II :

Chaetotaxy of the copepodids of Cancrincola jamaicensis (notation of setal formula as in HUMES and HO, 1969).

	Cop I	Cop II	Cop III	Cop IV	Cop V
P ₁ exo	0,2,IV	0,I-0,2,III	=	0,I-1,2,III	0,I-1,2,IV
end	0,2I,0	1,0-0,2I,0	=	1,0-0,2I,0	1,0-0,2I,0
P ₂ exo	0,2,III	0,I-1,2,II	0,I-1,2,III	0,I-2,2,III	0,I-2,2,IV
end	0,2,I	1,0-0,2,I	1,0-1,2,1	1,0-1,2,I	1,0-2,2,I
P ₃ exo	3	0,2,III	0,I-1,2,II	0,I-1,2,III	0,I-2,2,IV
end		0,2,I	1,0-1,2,I	1,0-2,2,I	1,0-2,2,I
P ₄ exo		3	0,2,III	0,I-0,2,III	0,I-1,2,IV
end			0,2,I	1,0-2,2,I	1,0-2,2,I
P ₅ exo			3	4/3 *	5/2 *
bas				2/0	5/2
P ₆				—	—

* Female/male chaetotaxy; —means leg not present.

COPEPODID DEVELOPMENT

Copepodid I

Body (Fig. 3a) with five segments; length, 345 µm; rostrum fused and prominent; anal segment with a transverse row of spinules on the ventral surface and near the implantation of the furcal rami (Fig. 3b); furcal rami tapering in posterior direction and about as long as wide; principal furcal setae fused; dorsal surface with two setae: one articulating on two basal parts and one directly implanted on the ramus; three lateral setae; ventral distal margin of each ramus set with large spinules.

Antennule (Fig. 3f) four-segmented; aesthetasc on the second and fourth segments; aesthetascs tubular, showing no differentiation.

Antenna with allobasis; general shape of the antenna as in the adult except for the large exopodite (Fig. 3e), bearing five setae and having curved margins.

Mouthparts as in the adult.

P₁ (Fig. 3c): protopodite with distinct parts and furnished with the adult pattern of spinules; inner distal spine of the basis absent; exopodite and endopodite one-segmented; spines and setae with adult appearance.

P₂ (Fig. 3d): parts of protopodite distinct, integumental structures present; exopodite and endopodite one-segmented; chaetotaxy in table II.

P₃ (Fig. 3b): represented as a small socle, bearing three setae and situated on the ventral surface of the third somite.

Copepodid II

Habitus (Fig. 4a): body with six segments, more or less fusiform; length, 370 µm; anal segment as in Cop I; shape of the setae on furcal rami as in the adult (Fig. 4e).

Antennule (Fig. 5a) five-segmented with aesthetasc on the second and fifth segments; aesthetasc of second segment widened near the middle; aesthetasc of segment five, tubular.

Antenna (Fig. 5a) five-segmented with aesthetasc on the second and fifth segments; aesthetasc of second segment widened near the middle; aesthetasc of segment five, tubular.

Antenna (Fig. 4j) and mouthparts as in the adult.

P₁ (Fig. 4b): protopodite as in the preceding stage but with an inner distal spine on the basis; exopodite and endopodite two-segmented; chaetotaxy in table II; inner seta on the first endopodal segment short, thick and setulose.

P₂ (Fig. 4c) with adult protopodite; exopodite and endopodite two-segmented; chaetotaxy in table II.

P₃ (Fig. 4d): protopodite with distinct parts; rami one-segmented, setal formula shown in table II.

P₄ (Fig. 4i): as P₃ in Cop I: represented as three setae.

Copepodid III

Habitus and furcal rami as in Cop II except for an additional body somite; length, 465 µm.

Antennule (Fig. 5b) five-segmented; differs from the antennule of Cop II in proportional lengths of the segments and the number of setae on the second segment.

P₁ as in Cop II; P₂ with an additional seta on the inner margin of the second endopodal segment and an additional spine on the outer margin of the second exopodal segment; P₃ (Fig. 4h) resembles the P₂ closely but differs in chaetotaxy of the exopodite (table II).

P₅ (Fig. 4k) present on the ventral surface of the fifth somite and represented as a small socle, bearing three setae.

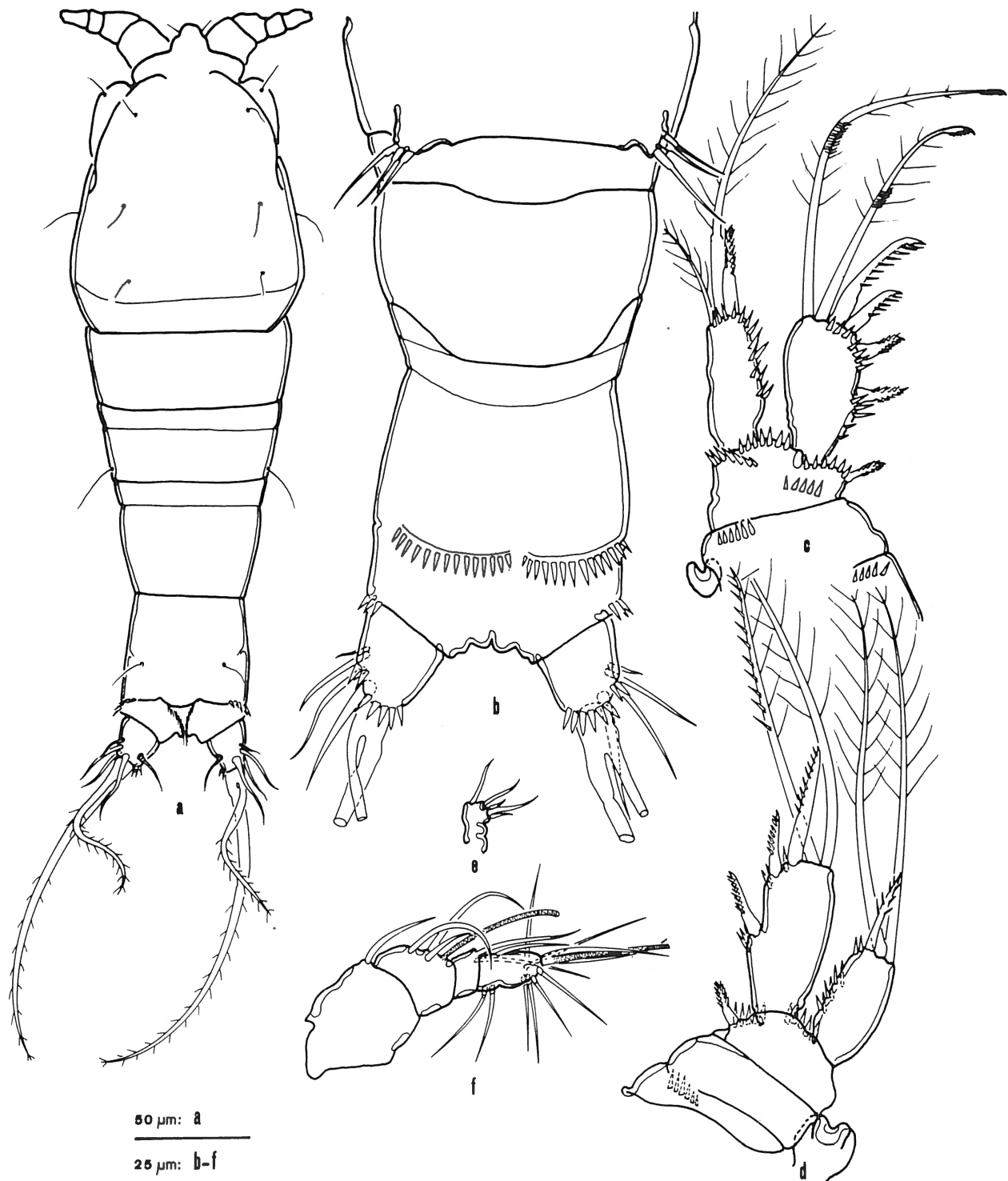


Fig. 3. - *Cancrincola jamaicensis*: copepodid I: a. Habitus; b. Third to fifth somite, with P₃, in ventral view; c. P₁; d. P₂; e. Exopodite of the antenna; f. Antennule.

Copepodid IV: female

Body with eight somites; length, 445-455 μm; general shape as in the preceding stage.

Antennule (Fig. 5c) six-segmented, bearing an aesthetasc on segment three and six.

P₁-P₄ (Fig. 6a-d): ornamentation and setation resembling

closely the adult morphology but still having two-segmented rami and lacking still an outer spine on the exopodite.

P₅ (Fig. 6f) with two baseoendopodal and four exopodal ones; exopodal segment not separate; baseoendopodal setae rather spiniform.

P₆ not present.

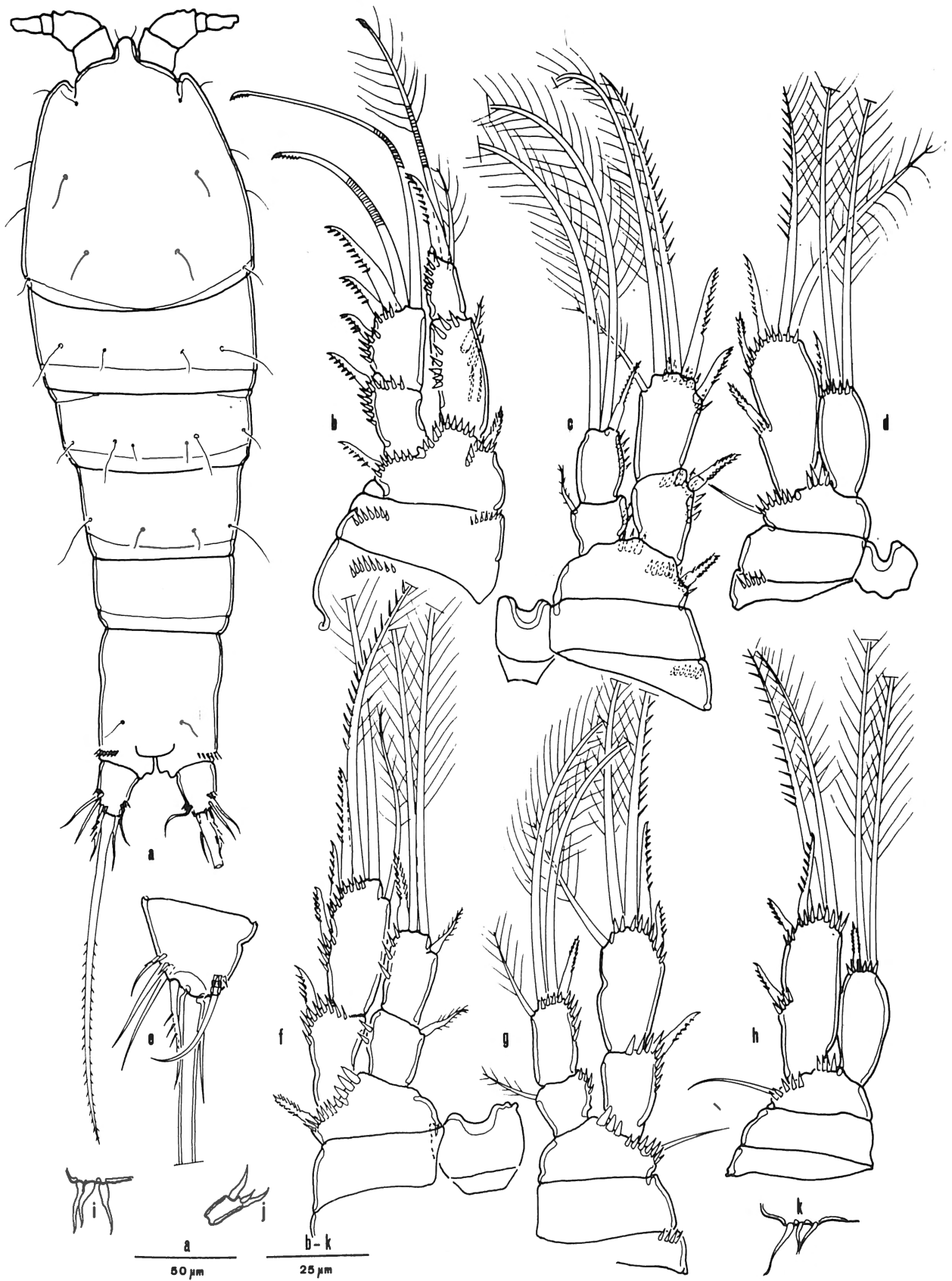


Fig. 4. - *Cancrincola jamaicensis*: copepodid II: a. Habitus; b. P₁; c. P₂; d. P₃; e. Furcal ramus, in dorsal view; copepodid III; f. P₂; g. P₃; h. P₄; copepodid II; i. P₄; j. Exopodite antenna, copepodid III; k. P₅.

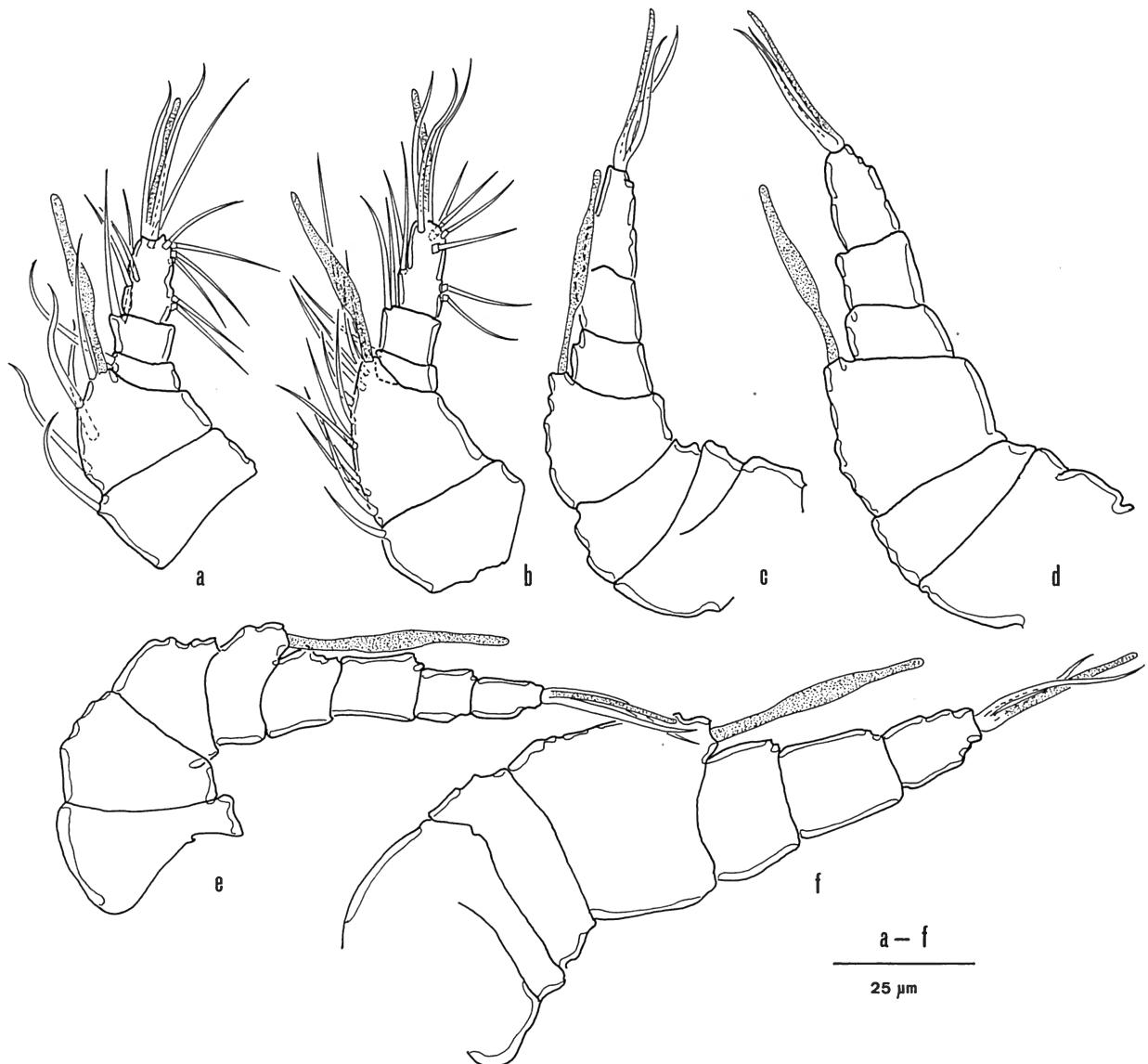


Fig. 5. - *Cancrincola jamaicensis* : a. Antennule, Cop II; b. Antennule, Cop III; c. Antennule, female Cop IV; d. Antennule, male Cop IV; e. Antennule, female Cop V; f. Antennule, male Cop V.

Copepodid IV : male

Differs from the opposite sex in the antennule and the shape of the P_5 .

Antennule (Fig. 5d) six-segmented as in the female but proportional lengths of segments distinctly different.

P_5 (Fig. 6e) nearly identical as in the Cop III but with more pronounced elevation bearing the three setae.

P_6 not present.

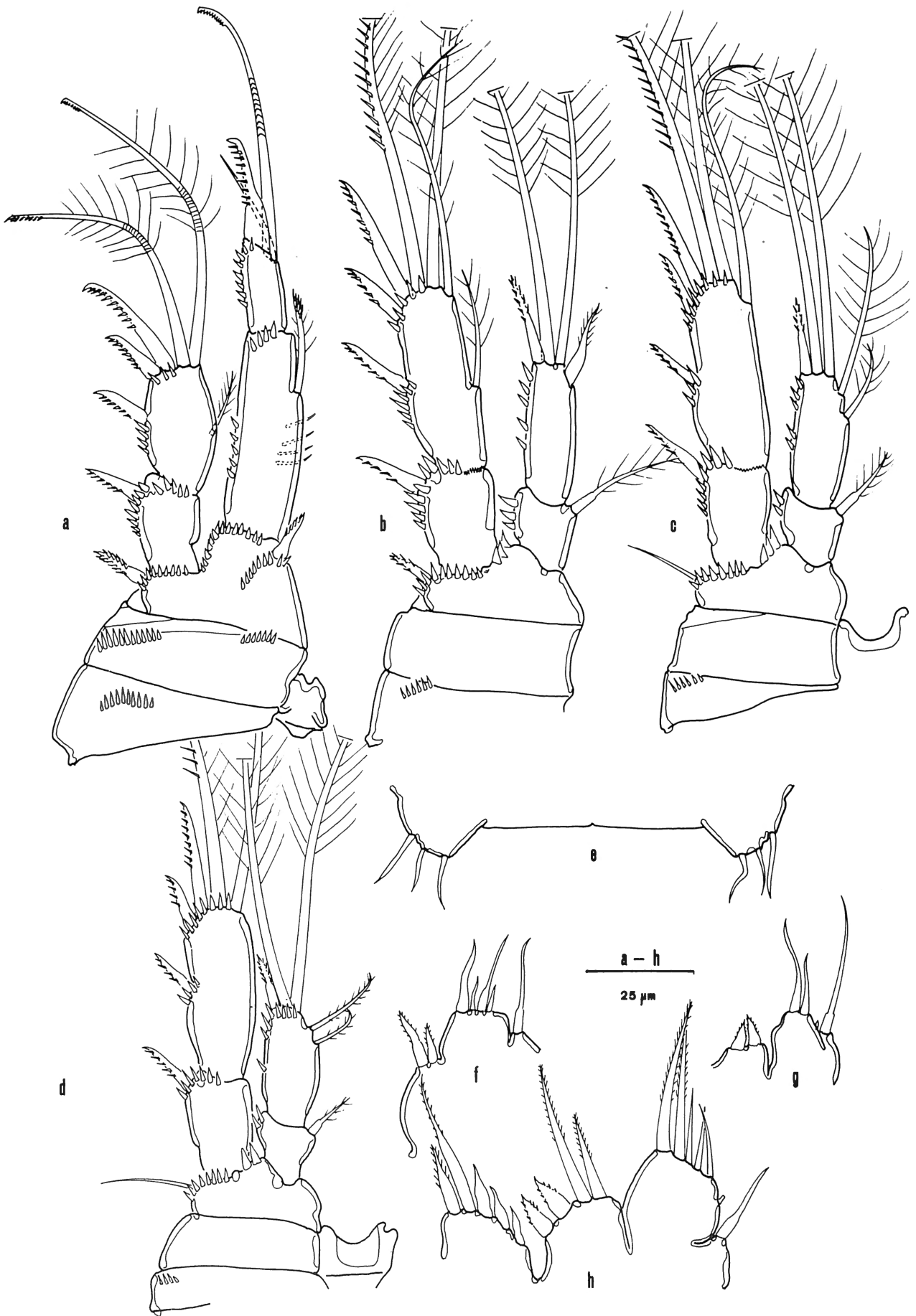
Copepodid V : female

Habitus as in Cop IV but with an additional somite; length, 675-695 μm ; integumental structures on the abdominal segments as in the adult.

Antennule (Fig. 5e) eight-segmented with shape and number of setae as in the adult female.

P_1 - P_4 : chaetotaxy, ornamentation and proportional lengths of the rami as in the adult; rami still two-segmented; future articulation between the second and third segments of the rami indicated anteriorly with the adult spinulation; inner seta of the first endopodal segment of P_1 and inner setae of the endopodite P_1 pectinate but shorter than in the adult. P_5 (Fig. 6h) resembles the adult leg closely but exopodite still fused with the baseendopodite and setae markedly shorter and stouter; baseendopodal lobe normally bearing five setae, one specimen found with four setae (left baseendopodal lobe in illustration).

Fig. 6. - *Cancrincola jamaicensis*, copepodid IV : a. P_1 ; b. P_2 ; c. P_3 ; d. P_4 ; e. Male P_5 ; f. Female P_5 ; copepodid V : g. Male P_5 ; h. Female P_5 .



Copepodid V : male

Resembles the female in all details except for the antennule, the P₅ and body length (595-610 µm).

Antennule (Fig. 5f) six-segmented; aesthetascs on segments three and six; proportional lengths of the entire antennule and the separate segments clearly otherwise than in the female.

P₅ (Fig. 6g) : baseoendopodite distinct, bearing two spiniform setae; exopodite conical, reaching far beyond the endopodal process and having two smooth setae.

P₆ not present.

Cancrincola abbreviata* HUMES, 1957Synonymy :*

Cancrincola abbreviata n. sp. : HUMES, 1957, pp. 185-189, Pl. III (23-38).

Type-locality :

Ivory Coast, embankment at Koumassi, between the entrance to Abidjan aerodrome and the village Vridi. Found in the gill chambers of *Sesarma huzardi* (Desma-rest).

Type-material :

Holotype, allotype and paratypes (100 specimens) in the collections of the Museum National d'Histoire Naturelle, Paris. Other paratypes deposited in the U.S. National Museum, Washington, in IFAN, Dakar, and in the collection of HUMES (Woods Hole).

Previous reports :

- On *Sesarma huzardi* : Ivory Coast, near Adiopodoumé and near Abidjan (type-locality); Nigeria, near Lagos; People's Republic of the Kongo, Pointe Noire and the mouth of the Loeme River; Sierra Leone, near Freetown (HUMES, 1957).
- On *Sesarma angolense* : People's Republic of the Kongo, mouth of the Loeme River (HUMES, 1957).
- On *Sesarma curvatum* : Sierra Leone, near Freetown; People's Republic of the Kongo, mouth of the Loeme River (HUMES, 1957).

***Cancrincola longiseta* HUMES, 1957**

Figs. 7 - 11

Synonymy :

Cancrincola longiseta n. sp. : HUMES, 1957, pp. 183-185, Pl. II (18-22), III (23-29); HUMES, 1958, pp. 82.

Type-locality :

Sierra Leone, mangrove area at Rokupa near Freetown. Found in the gill chambers of *Goniopsis cruentata* (LATREILLE, 1803).

Type-material :

Holotype, allotype and paratypes deposited in the collections of Museum National d'Histoire Naturelle, Paris. Paratypes also in the collections of the U.S. National Museum, Washington and of IFAN, Dakar, and in the collection of HUMES (Woods Hole).

Material :

- On *Goniopsis cruentata*, male (carapax width 49 mm), from Zaire, Banana. Leg. A. Capart, 20 May 1950, IG. 17.622. One male preserved in alcohol (Cop 2929).
- On *Goniopsis cruentata*, male (carapax width 43 mm), from Zaire, Banana : Ile de Rosa (Lemba). Leg. A. Capart, 23 July 1955, IG. 20.403. Dissected specimens : two females (Cop 2931, 2933), two males (Cop 2932, 2935), two Cop I (Cop 2934, 2937), two Cop II (Cop 2938, 2939), three Cop III (Cop 2940, 2941, 2942), two Cop IV females (Cop 2943, 2945), one Cop V male (Cop 2944), one Cop V female (Cop 2947) and one Cop V male (Cop 2946). Preserved specimens : 16 females (6 ovigerous), 13 males, 13 Cop I, 14 Cop II, 12 Cop III, 17 Cop IV, 9 Cop V, labeled Cop 2948.

Previous reports :

- On *Goniopsis cruentata* : Brazil, Caruca, Victoria, Santa Clara, Pernambuco, Rio de Janeiro; Bermuda; Haiti, Jeremie; Ivory Coast, near Adiopodoumé; Nigeria, near Lagos; Panama (Atlantic coast); People's Republic of the Kongo, Songolo and Loeme River; Sierra Leone, near Freetown (type-locality) (HUMES, 1957; 1958).
- On *Sarmatium curvatum* : People's Republic of the Kongo, Loeme River, one specimen among 57 of *Cancrincola abbreviata* (HUMES, 1957).
- On *Sesarma huzardi* : People's Republic of the Kongo, Loeme River, one specimen among 50 of *Cancrincola abbreviata* (HUMES, 1957).

Description :

Descriptions of all appendages are given by HUMES (1957). The attention here is focused on some details thought to be relevant in the present study.

Female : habitus (Fig. 7a) : body fusiform depressed; lateral margins of cephalothorax strongly tapering over the entire length; largest width near the posterior margin of the cephalothorax and the second thoracic segment; abdominal segments with nearly parallel margins; rostrum prominent and smooth.

Furcal rami (Fig. 7d) with strongly sclerified lateral margins and a remarkable depression on the dorsal surface; three lateral setae implanted in the posterior third of the outer margin; outer apical and inner apical setae small and smooth; dorsal seta implanted close to the inner apical edge and articulating on two basal elements; principal seta bulbous near the implantation and finely armed in the second half of the stem.

Genital organ (Fig. 8g, h) : external part with two sclerified lips and two setae; receptaculum seminis short, bulbous

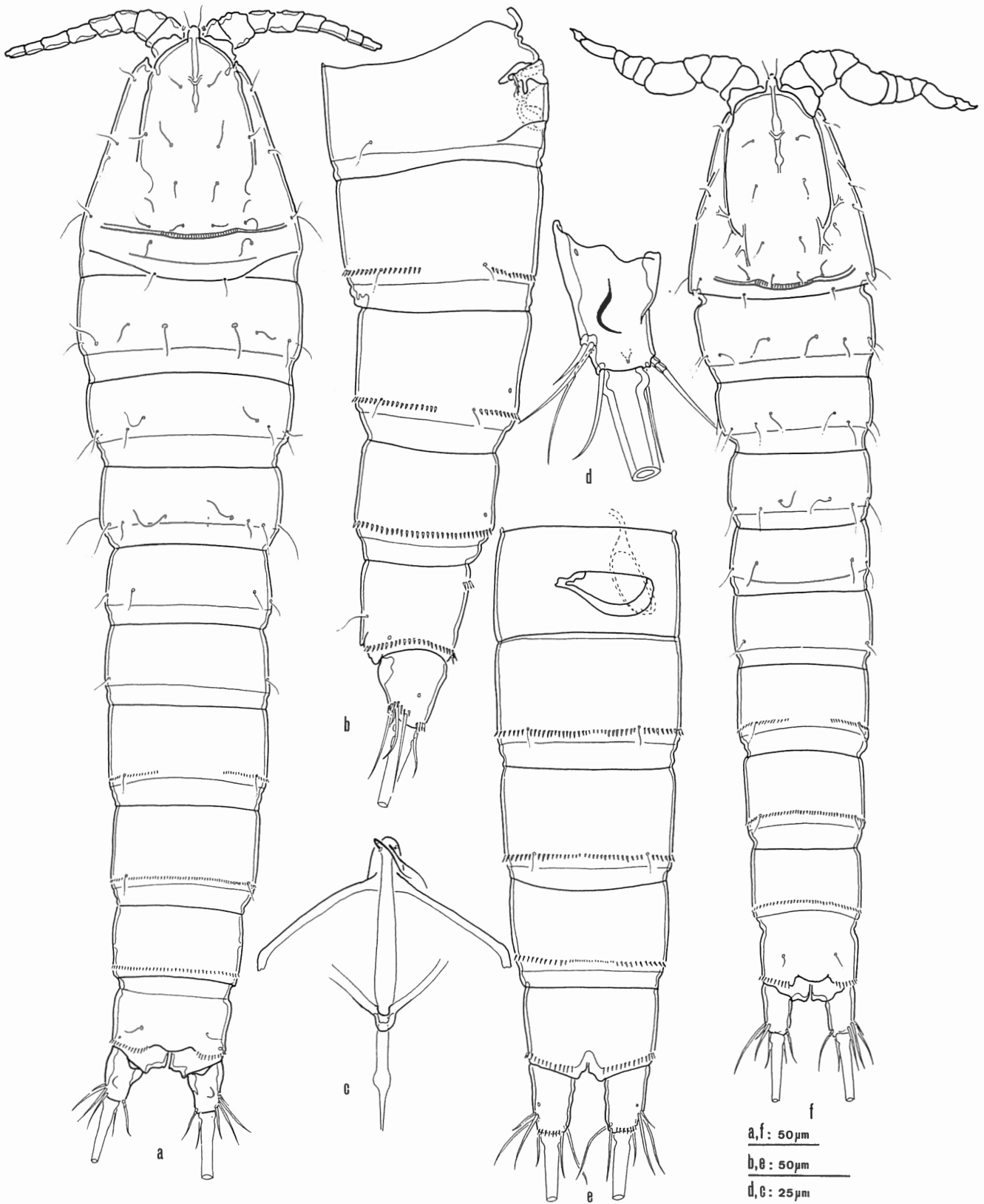


Fig. 7. - *Cancrincola longiseta* : a. Habitus, female ; b. Female abdomen, lateral view ; c. Rostrum and anterior part of the cephalothorax ; d. Left furcal ramus, female ; e. Male abdomen, ventral view ; f. Habitus, male.

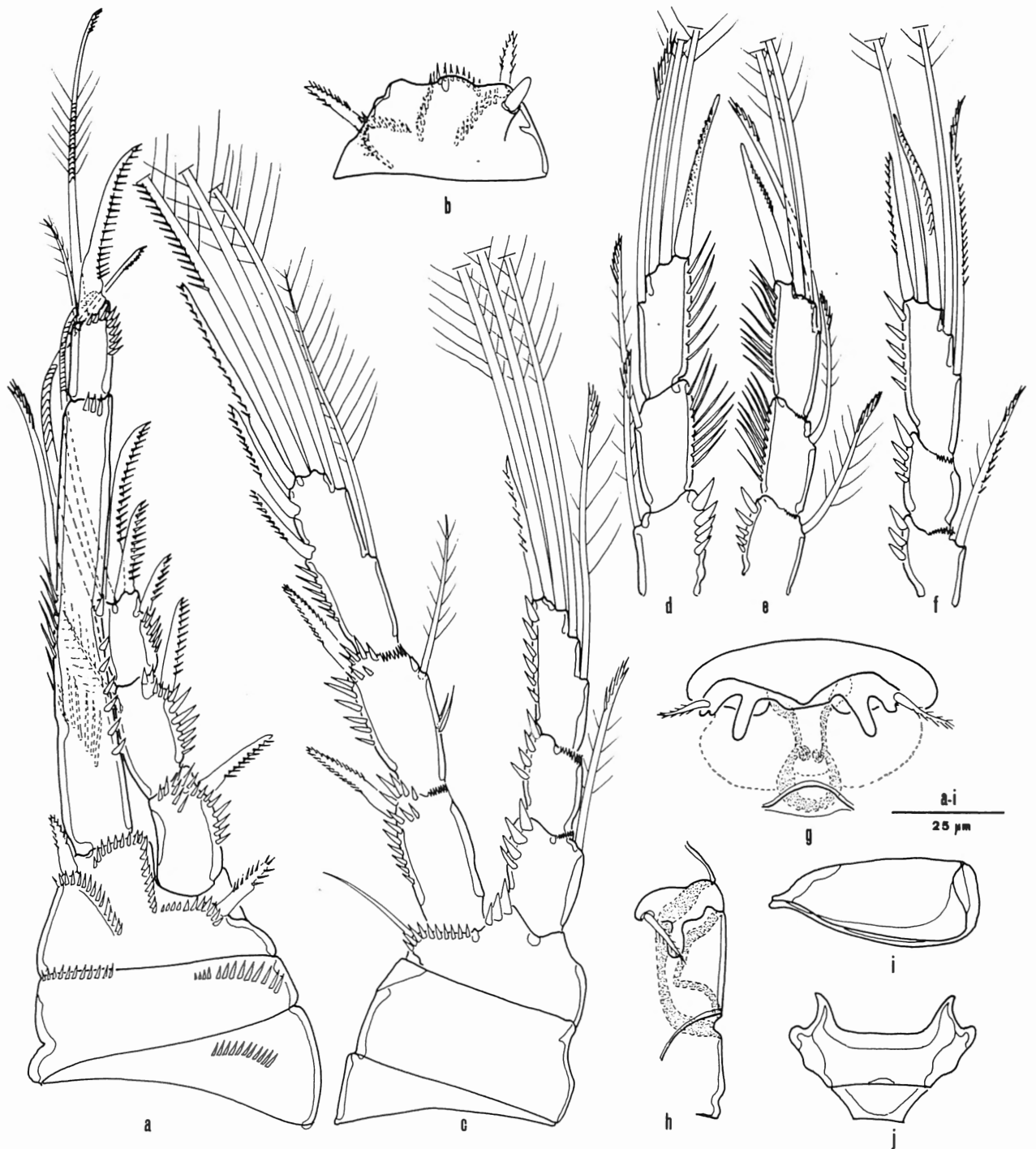


Fig. 8. - *Cancrincola longiseta*: a. P_1 , female; b. Basis P_1 of male; c. P_3 , female; d. Endopodite P_2 , female; e. *Idem*, male; f. Endopodite P_3 , male; g. Female genital field, ventral view; h. *Idem*, lateral view; i. P_6 , male; j. Intercostal plate of P_3 .

and having thick walls; vulva ovate in frontal view. Integumental structures: cephalothorax with two sclerified strips running parallel with the lateral margins; median anterior part of the head with a strong integumental strip, connected with a pore orifice and running towards the rostral tip (Fig. 7c); head also with a transverse striated strip in the posterior region; integument of the somites smooth except for a spinulose comb along the posterior margin of the abdominal segments; anal segment with spinules near the implantation of the furcal rami and in

the anterior half of the ventral surface; furcal rami with some spinules along the apical margin of the ventral side. P_1 (Fig. 8a): exopodite reaching the middle of the first endopodal segment; outer spines of the exopodite armed along one side of the stem; apical setae of the third exopodal segment geniculated and pectinate; inner seta of the first endopodal segment and inner apical seta of the second segment pectinate; the former reaching just beyond the articulation between the first and second segment. P_2 (Fig. 8c): protopodite with smooth surfaces except for

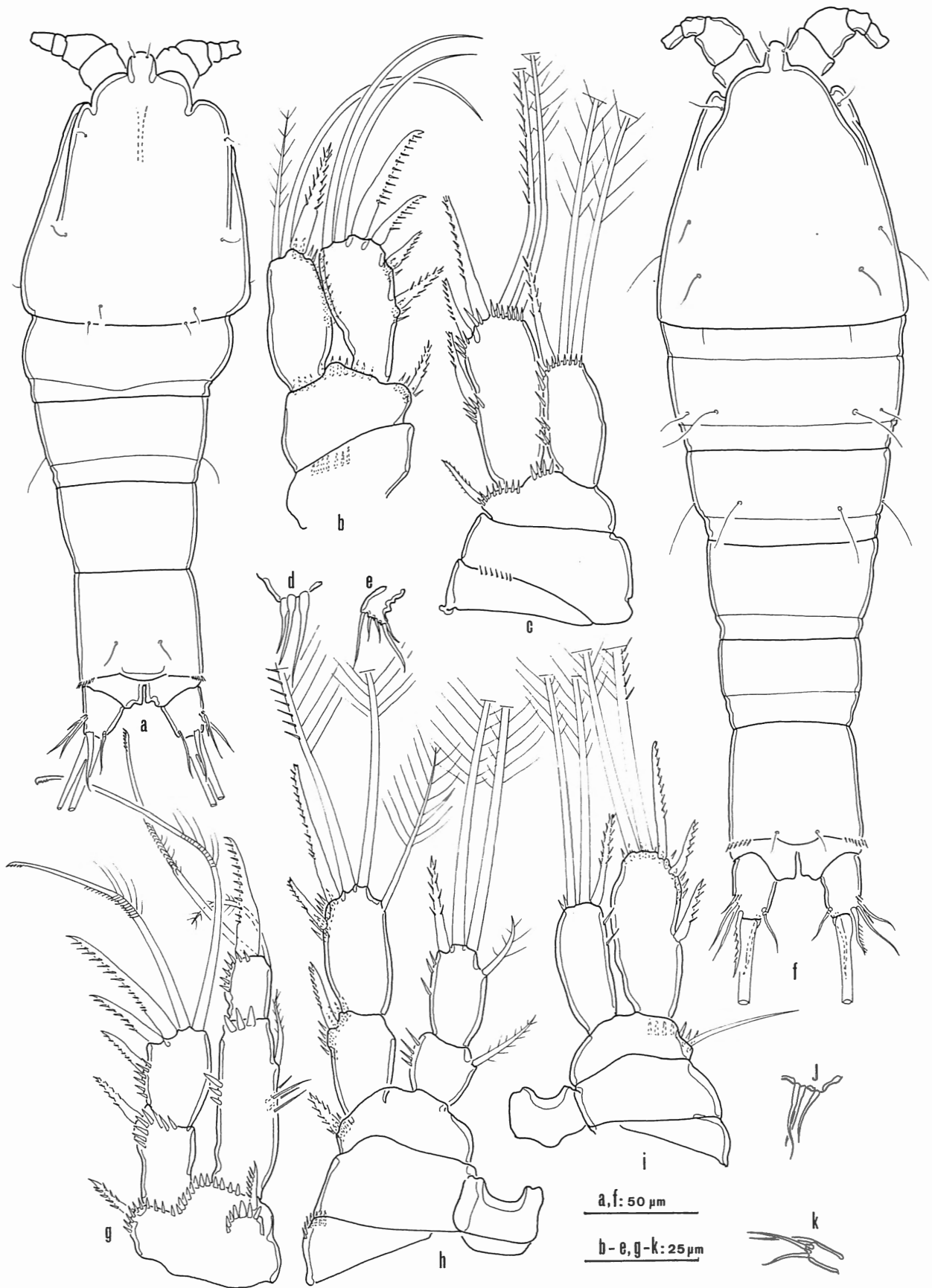


Fig. 9. - *Cancrincola longiseta*, copepodid I : a. Habitus; b. P₁; c. P₂; d. P₃; e. Exopodite antenna; copepodid II : f. Habitus; g. P₁; h. P₂; i. P₃; j. P₄; k. Exopodite antenna.

Table III :

Chaetotaxy of the copepodids of *Cancrincola longiseta* (notation of setal formula as in HUMES and HO, 1969).

	Cop I	Cop II	Cop III	Cop IV	Cop V
P ₁ exo	0,2,IV	0,I-0,2,III	=	0,I-1,2,III	0,I-1,I-0,2,III
end	0,2I,0	1,0-0,2I,0	=	1,0-0,2I,0	1,0-0,2I,0
P ₂ exo	0,2,III	0,I-1,2,II	0,I-1,2,III	0,I-3,2,III	0,I-1,I-2,2,III
end	0,2,I	1,0-1,2,I	1,0-1,2,1	1,0-1,2,I	1,0-1,0-1,2,I
P ₃ exo	3	0,2,III	0,I-1,2,II	0,I-2,2,III	0,I-1,I-2,2,III
end		0,2,I	1,0-1,2,I	1,0-2,2,I	1,0-0,0-2,2,I
P ₄ exo		3	0,2,III	0,I-0,2,III	0,I-0,I-1,2,III
end			0,2,I	1,0-2,2,I	1,0-0,0-2,2,I
P ₅ exo			3	4/3 *	5/2 *
bas				2/0	5/2
P ₆				-	-/-

* Female/male chaetotaxy; - means leg not present.

a single row of spinules on the basis; morphology as in HUMES, 1957 but third exopodal segment with three outer spines instead of two.

Male : habitus (Fig. 7f) generally as in the female but with a marked slender thorax and abdomen; furcal rami less sclerified and without a dorsal depression.

Integumental organs and structures as in the female.

P₁ (Fig. 8b) as in the female except for the much stronger spinule on the inner apical edge of the basis.

P₂-P₄ (Fig. 8e, f, respectively) : protopodite and exopodite as in the female; endopodite P₂ with a stronger armed apical spine on the third segment; P₄ endopodite as in the female but the inner pectinate setae having an additional row of spinules along the inner side of the stem; proportional lengths of the endopodal segments equal in male and female.

P₆ (Fig. 8i) typical; left margin less strongly sclerified than in *C. jamaicensis*.

COPEPODID DEVELOPMENT

Copepodid I

Habitus (Fig. 9a) : body with five segments; length : 250 µm; greatest width near the posterior margin of the cephalothorax; integument smooth except for a ventral row of spinules on the anal segment and a lateral row near the articulation with the furcal rami.

Furcal rami : with smooth margins, slightly conical; seven setae : three lateral, two dorsal and two apical ones; the latter fused near their implantation.

Antennule (Fig. 11a) four-segmented, bearing an aesthetasc on the second and fourth segment; aesthetascs tubular.

Antenna : general shape as in the adult but exopodite (Fig. 9e) proportionally larger, with bent margins and bearing

three lateral and two apical setae; other mouthparts as in the adult.

P₁ (Fig. 9b) : protopodite present and divided in three parts; inner spine of the basis absent; exopodite and endopodite one-segmented; chaetotaxy in table III; apical setae not geniculated or pectinate.

P₂ (Fig. 9c) : resembles P₁ closely but lacking an outer spine on the exopodite.

P₃ (Fig. 9d) : represented as a small socle, bearing three setae, on the ventral side of the third somite.

Copepodid II

Habitus (Fig. 9f) : body with six segments, resembling the preceding stage closely; integumental structures as in Cop I; length : 385-395 µm.

Furcal rami : differing from Cop I as follows : one dorsal seta; three lateral ones; inner apical seta present; outer apical seta armed and not fused with the principal one.

Antennule (Fig. 11b) : five-segmented; aesthetascs on segments two and five; the former widened, the latter tubular. Antenna and mouthparts as in the adult.

P₁ (Fig. 9g) : basis with an inner spine; rami two-segmented; apical setae of exopodite and apical inner seta of endopodite geniculate and pectinate; inner seta of first endopodal segment short and feathered.

P₂ (Fig. 9h) : rami two-segmented; inner setae of the endopodal segments feathered.

P₃ (Fig. 9i) : prae-coxa, coxa and basis present; rami one-segmented; chaetotaxy in table III.

P₄ (Fig. 9j) : represented as three setae on a small socle.

Copepodid III

Habitus as in the preceding stage but with an additional somite; length : 420-435 µm.

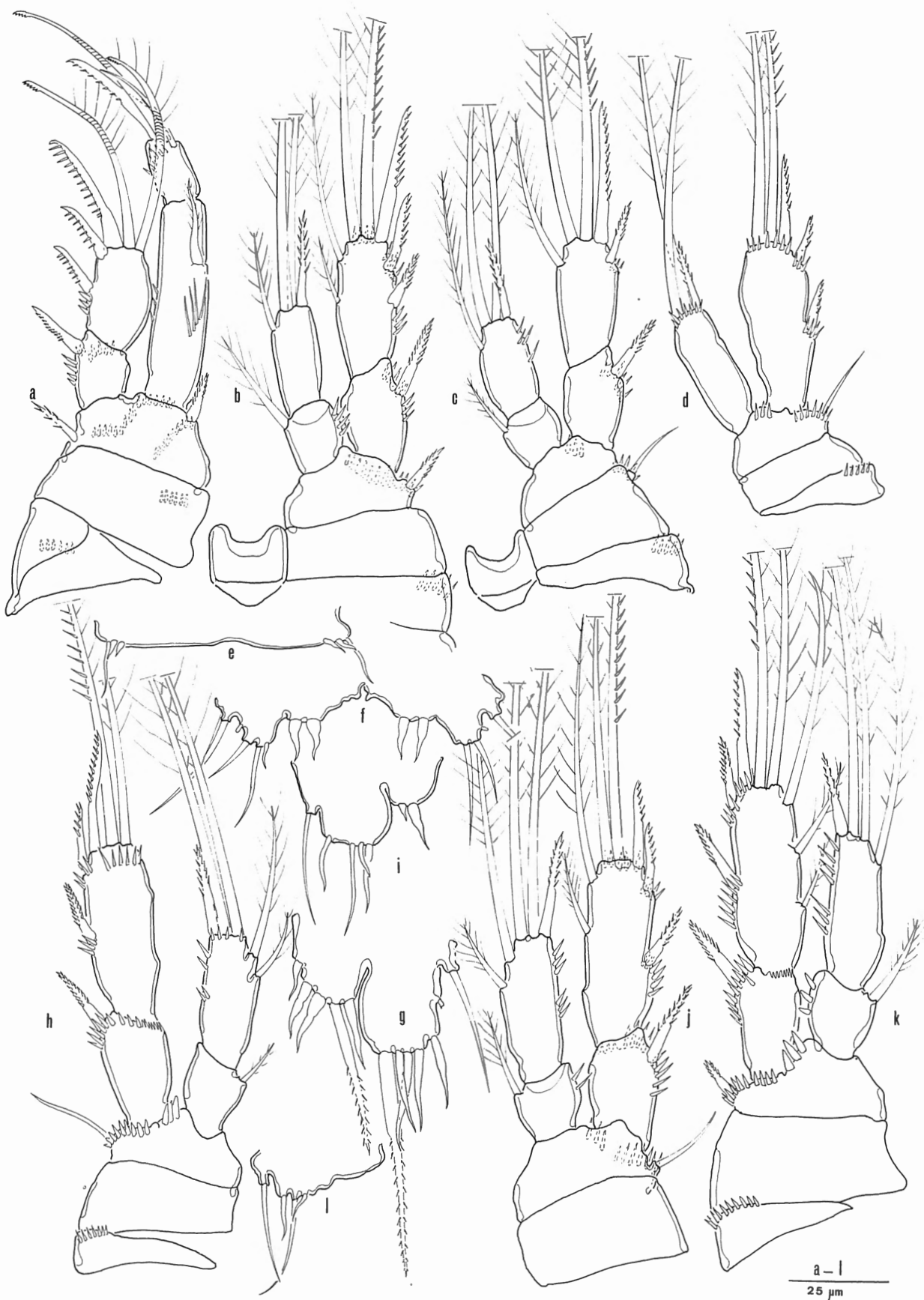


Fig. 10. - *Cancrincola longiseta*, copepodid III : a. P_1 ; b. P_2 ; c. P_3 ; d. P_4 ; e. P_5 ; copepodid V : f. P_5 (male); g. P_5 (female); copepodid IV : h. P_4 ; i. P_5 (female); j. P_3 ; k. P_2 ; l. P_5 (male).

Antennule (Fig. 11c) : five-segmented with aethetasc on the second and last segments; proportional lengths and number of setae differing from the preceding stage.

P₁ (Fig. 10a) : rami two-segmented; setal ornamentation and arrangement as in Cop II.

P₂-P₃ (Fig. 10b, c, respectively) : both with two-segmented rami; chaetotaxy of endopodite P₂ remaining the same; exopodite P₂ and both rami of P₃ with additional setae and spines, see table III.

P₄ (Fig. 10d) with one-segmented rami and P₅ (Fig. 10e) represented by three setae.

Copepodid IV : female

Habitus as in the Cop III but body with eight segments; length : 475-495 µm; antennule (Fig. 11e) six-segmented, bearing an aesthetasc on the third and ultimate segments; chaetotaxy of the segments as in the adult female.

P₁ as in Cop III but with an inner seta on the second exopodal segment; P₂-P₄ (Fig. 10k, j, h, respectively) with two-segmented rami; chaetotaxy in table III.

P₅ (Fig. 10i) with exopodal and baseoendopodal lobe bearing four and two setae respectively.

P₆ not present.

Copepodid IV : male

Differs from the female copepodid in the length (460-475 µm), the antennule and the P₅.

Antennule (Fig. 11d) six-segmented but with other proportional lengths than in female; P₅ (Fig. 10l) represented as a small lobe showing the outer baseoendopodal seta and three exopodal ones; inner part of baseoendopodite not differentiated.

P₆ not present.

Copepodid V : female

Habitus as in the preceding stage but with nine segments; length, 640-690 µm.

Antennule (Fig. 11g) eight-segmented with appearance and chaetotaxy as in the adult.

P₁-P₄ with an adult chaetotaxy and with three-segmented rami; inner setae of the endopodites P₂-P₃ still rather strong and feathered, not pectinate.

P₅ (Fig. 10g) : exopodal and baseoendopodal lobe much more pronounced than in the Cop IV; both rami with five setae.

P₆ not present.

Copepodid V : male

Habitus as in the female; length 620-655 µm; antennule (Fig. 11f) six-segmented, bearing an aesthetasc on the third and sixth segments; proportional lengths of the segments considerably different from those of the female.

P₁-P₄ as in the female; P₅ (Fig. 10f) with a small baseoendopodal and exopodal lobe, bearing respectively two and

three setae; specimens with two exopodal setae common. P₆ not present.

***Cancrincola plumipes* HUMES, 1941**

Synonymy :

Cancrincola plumipes, new species : HUMES, 1941, pp. 379-385, fig. 18a-m; HUMES, 1958, pp. 80, 82, fig. 7-10, 11-17.

Type-locality :

U.S.A., Louisiana : Grand Isle, from the gill chambers of two specimens (one male, one female) of *Sesarma reticulatum* (SAY).

Type-material :

U.S. National Museum : no. 79347 (holotype), 79348 (allotype), 79349 (paratypes, 20 spec.).

Previous reports :

— On *Sesarma reticulatum* : U.S.A., Grand Isle (La., type-locality), Alligator Harbor (Fla.), Tiverton (R.I.) (HUMES, 1941; 1958).

— On *Sesarma cinereum* : U.S.A., Wadmalaw Island (S.C.), Alligator Harbor (Fla.), Jacksonville (Fla.) (HUMES, 1958).

***Antillesia* HUMES, 1958**

Diagnosis :

Body vermiform; furcal rami three times as long as wide, bearing six setae; genital organ with a long curved receptaculum seminis with copulatory pore near the postero-ventral margin; ultimate exopodal segments P₁-P₄ with three outer spines; median exopodal segments of P₂-P₄ with an inner seta; P₅ with five baseoendopodal and exopodal setae.

Male : No sexual dimorphism on P₁ and P₂; sexual dimorphism of P₃ typical; baseoendopodal P₅ without setae, exopodite with four setae.

Type-species :

Antillesia cardisomae HUMES, 1958 by designation.

***Antillesia cardisomae* HUMES, 1958**

Fig. 12

Synonymy :

Cancrincola jamaicensis WILSON, PEARSE, 1951, pp. 342 [part]; *Antillesia cardisomae*, n. sp. : HUMES, 1958, pp. 82-89, figs. 18-46; PETKOVSKI, 1978, pp. 101.

Type-locality :

Jamaica, mud flat at Port Henderson, St. Catherine. In the gill chambers of *Cardisoma guanhumi* LATREILLE.

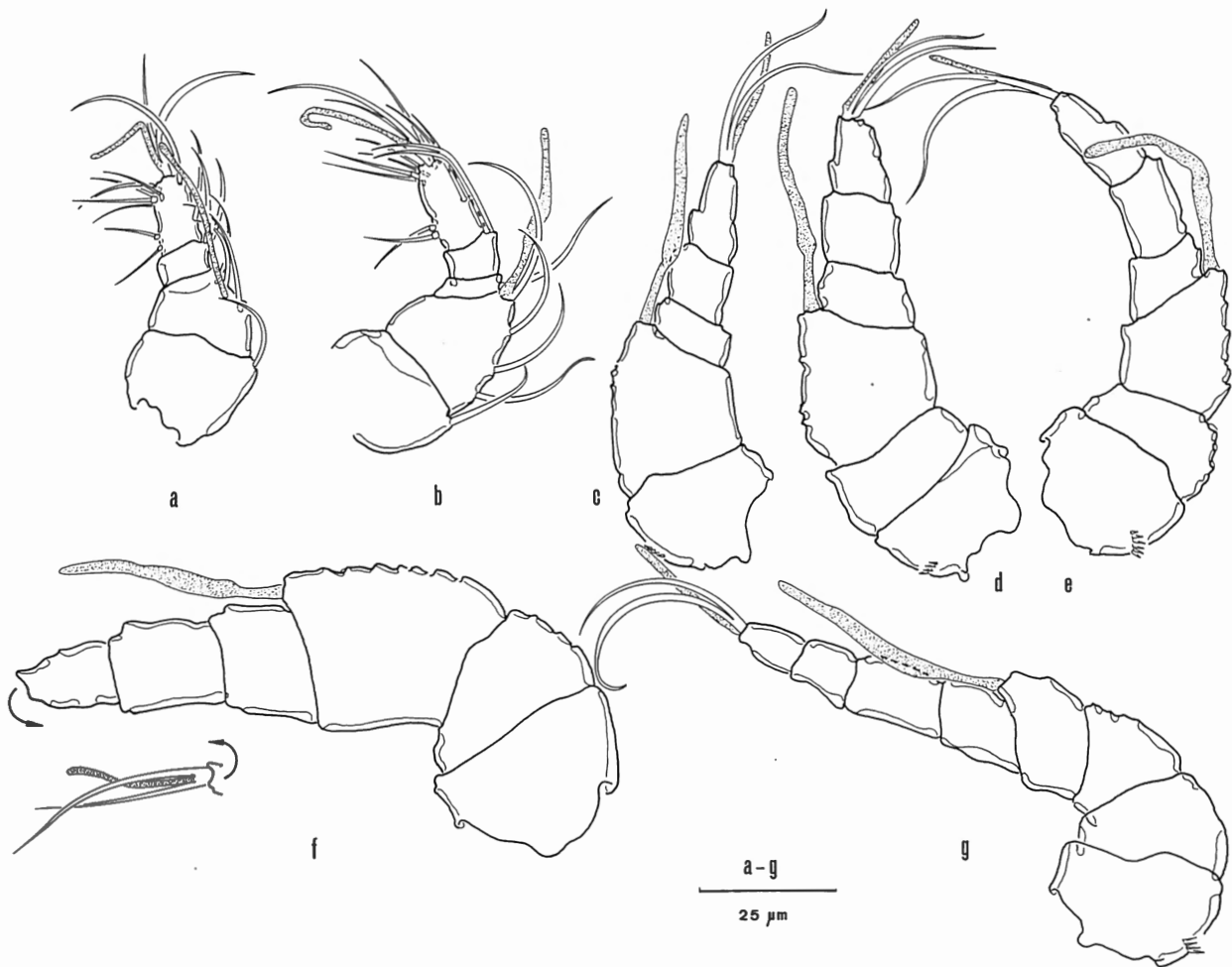


Fig. 11. - *Cancrincola longiseta*: a. Antennule Cop I; b. Antennule Cop II; c. Antennule Cop III; d. Antennule Cop IV, male; e. Antennule Cop IV, female; f. Antennule Cop V, male; g. Antennule Cop V, female.

Type-material :

Holotype, allotype and paratypes (28 specimens) deposited in the collections of the U.S. National Museum.

Material :

Amsterdam Expeditions to the West Indian Islands.

— Sta. 80-15. Aruba, well at Daimara ($12^{\circ}31'56''N$ $69^{\circ}56'30''W$) in coconut plantation, c. 150 m from the shore; water table at 2 m, water depth 0.20 m. Temp. $28.9^{\circ}C$; chlorinity 2,768 mg/l, 23 May 1980. Three females, one male and one Cop V preserved (ZMA Co 102.829, Cop 2911), one female dissected, mounted on one slide, Cop 2905.

— Sta. 80-16. See *C. jamaicensis*. Three females, 1 Cop V male, two Cop IV females, 3 Cop III, all preserved (ZMA Co 102.828). One female dissected, mounted on three slides (Cop 2916a, b, c) and one male dissected, mounted on two slides (COP 2927a, b), abdomen and P_5 preserved (Cop 2928).

— Sta. 80-31. See *C. jamaicensis*. One female (ZMA Co 102.830).

— Sta. 82-02. Venezuela, Tortuga Island : western extre-

mity, E. of Punta Arenas ($10^{\circ}55'29''N$, $65^{\circ}25'05''W$), method Karaman-Chappuis, ca 50 cm above the water-line (high tide), rather coarse sand (burrows of *Upogebia*, polychaetes, isopods and amphipods) chlorinity 23,928 mg/l, 17 Feb. 1982. One copepodid CV (ZMA Co 102.831).

Previous reports :

— On *Cardiosoma guanhum*: Bahamas, Bimini; Barbados, St James; Cuba, Bahia Honda; Haiti, Grand Anse; Jamaica, Port Henderson and Montego Bay; Swan Island; U.S.A., Key West (Fla.); Venezuela, Guenta (HUMES, 1958).

Description :

A. cardisomae was entirely described and figured by HUMES (1958). Some minor details, of importance for the present contribution, are briefly added here.

Female : genital complex (Fig. 12a, b, c) having a long U-shaped receptaculum seminis forming a distinctly thickened posterior part; vulva large with thickened lateral margins.

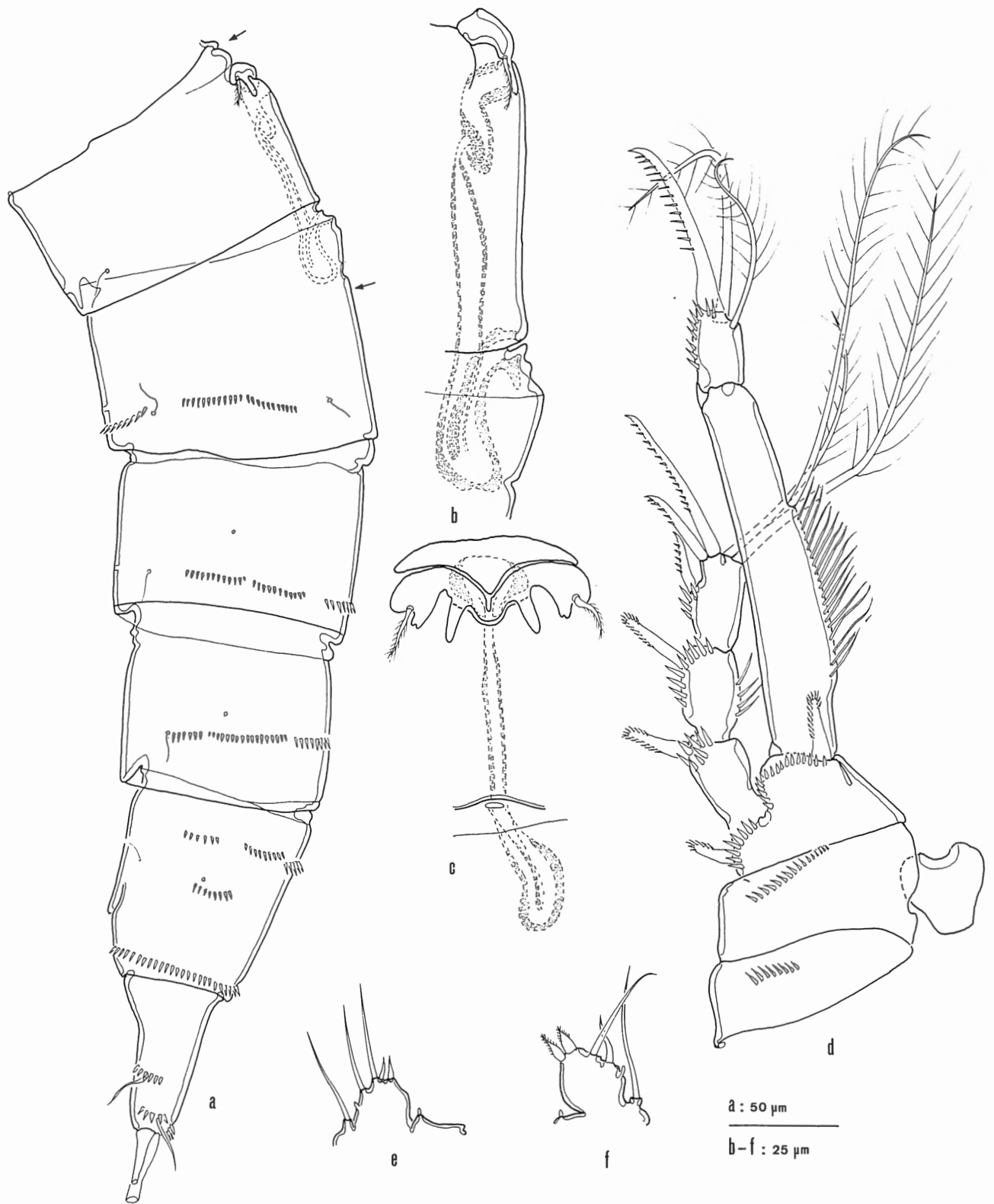
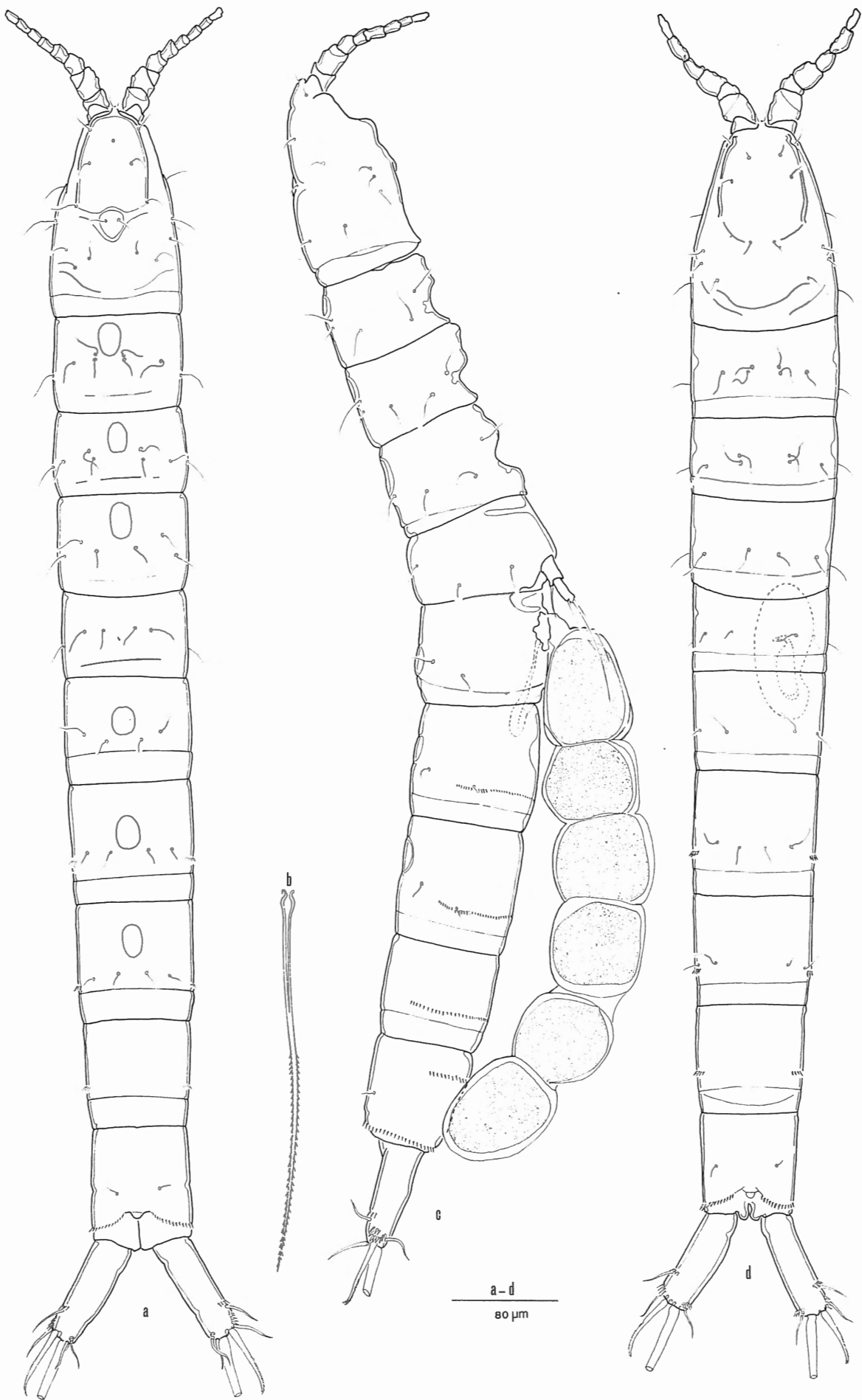


Fig. 12. - *Antillesia cardisomae*: a. Female abdomen in lateral view; b. Female genital field (arrows indicating enlarged region of a); c. Female genital field in ventral view; d. Male P₁; e. P₅ of a female copepod IV; f. P₅ of a male copepod V.

Fig. 13. - *Abscondicola humesi* n. gen., n. sp.: a. Habitus of the female; b. Principal furcal seta of a; c. Female in lateral view; d. Habitus of the male. ▷



P₁ : setae on the ultimate exopodal and on both endopodal segments feathered along the entire stem; apical parts of the setae not transformed in a comb-shaped structure.

P₂-P₄ : inner setae of the third exopodal segments of P₂ and P₃ feathered along their stem; inner exopodal seta of P₄ pectinate and smooth as well as the setae of first and second endopodal segments; inner seta of the third endopodal segments pectinate near their tip and heathered along the stem.

Male : P₁ (Fig. 12d) without sexual dimorphism of the spinules of the basis.

COPEPODIDS

The collection at hand comprises only three copepodid stages. Hence the omission of a detailed description of them but some interesting aspects of Cop III, Cop IV and Cop V are given below.

Copepodid III

Body with seven segments; length, 500 µm; furcal rami as in the adult; ventral surface of the anal segment with a transversal row of spinules, in the anterior third of the segment.

Antennule six-segmented, bearing aesthetascs on the second and last segments.

P₁-P₃ with two-segmented rami, P₄ with one-segmented rami; chaetotaxy of the legs as in Table II.

P₅ represented as three setae on a slightly elevated socle.

Copepodid IV : female

Body with eight segments; length, 585 µm; anal segment as in Cop III.

Antennule seven-segmented with an aesthetasc on the third and seventh segments; general appearance of the antennule as in the adult.

P₁-P₄ with two-segmented rami; chaetotaxy comparable to Cop IV of *C. jamaicensis* but : exopodite P₁ without inner seta and second endopodal segments of P₂-P₄ with two inner setae.

P₅ (Fig. 12e) : exopodal lobe with four setae; baseoendopodal lobe without setae but with a distinct hyaline pore tube.

Copepodid V : male

Body as in the preceding stage but with one additional somite; length, 770 µm.

Antennule six-segmented bearing an aesthetasc on the third and sixth segments; appearance of the antennule as in male Cop V of *C. jamaicensis*.

P₁ as in the adult; P₂-P₄ with three-segmented rami showing an adult female chaetotaxy; P₅ (Fig. 12f) having a rounded exopodal lobe, bearing four setae; baseoendopodite obsolete, indicated by a hyaline tube : P₆ not present.

Abscondicola n. gen.

Diagnosis :

Body vermiform; furcal rami three times as long as wide, bearing six setae; genital organ with a long and curved receptaculum seminis and copulatory pore near the postero-ventral margin; median exopodal segments P₁-P₄ without an inner seta; ultimate exopodal segments P₁-P₄ with two outer spines; baseoendopodite P₅ bearing two setae, exopodite four setae. Male : no sexual dimorphism on P₁ and P₂; endopodite P₃ with typical dimorphism; P₅ with three exopodal setae but without endopodal ones.

Type-species :

A. humesi n. sp., here designated.

Etymology :

The generic name is a conjunction of the Latin words *abscondere* (hidden) and *cola* (inhabitant). The gender is feminine.

Discussion :

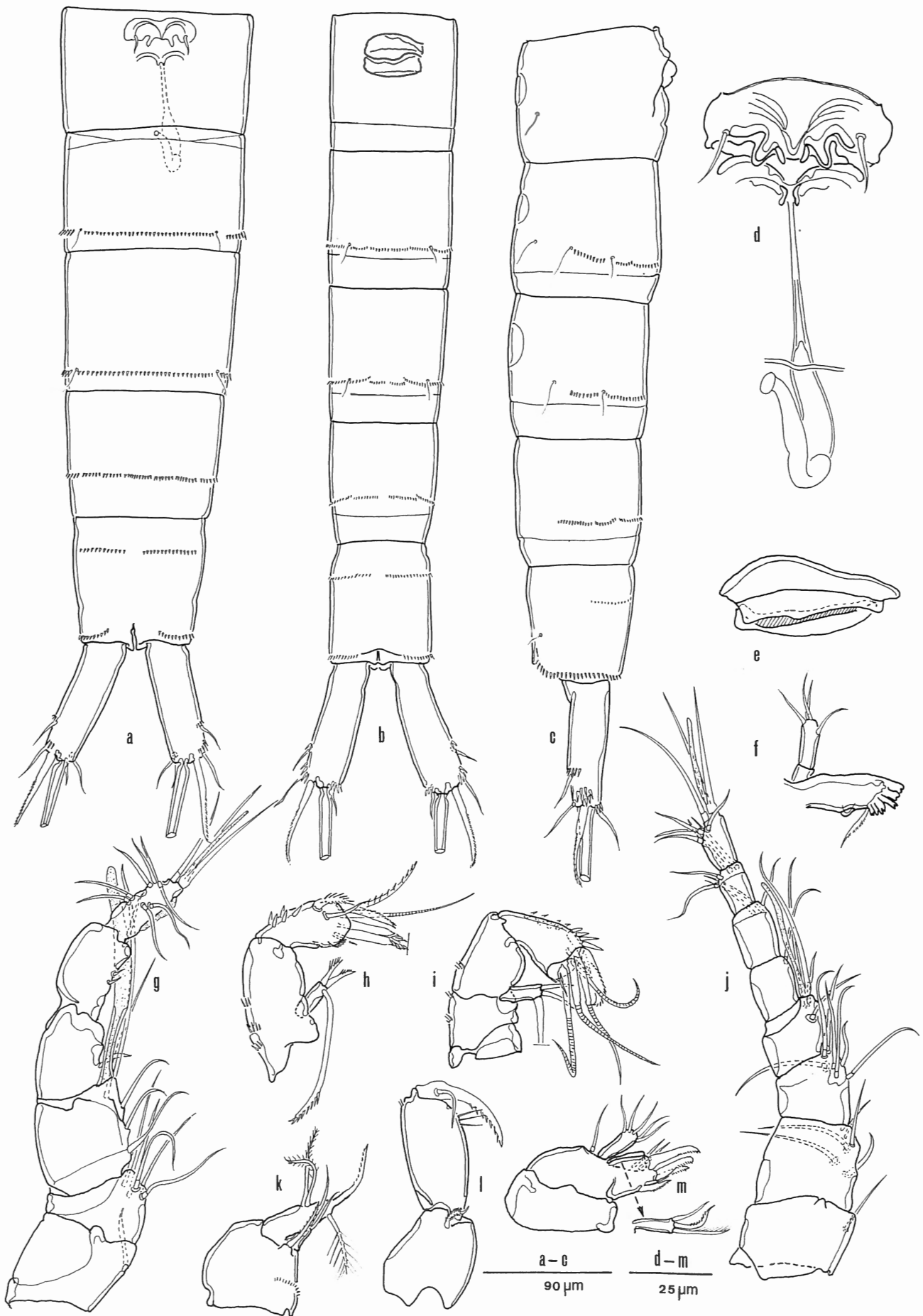
The general appearance, the long furcal rami, bearing six setae, the absence of inner setae on the exopodal segments of the P₁, the chaetotaxy of the male P₅ and the long U-shaped receptaculum seminis illustrate the phylogenetic proximity of *Abscondicola* n. gen. with *Antillesia*. The former differs from its sistergroup by the reduced armature of the exopodal segments in P₁-P₅ and the chaetotaxy of the P₅ in male and female.

The reduced condition of the chaetotaxy of all natatory legs in *Abscondicola* n. gen. is an advanced and unique feature which justifies the erection of the genus to accommodate *A. humesi* n. sp.

Other differences which may prove to be important in the generic diagnosis of *Abscondicola* n. gen. are the proportional lengths of the rami of the P₁, the modified inner seta on the exopodite P₄ and the shape of the egg sac. In *Abscondicola* n. gen. the proximal endopodal segment of P₁ reaches just beyond the second exopodal segment. In the two other genera of this family, the first endopodal segment is distinctly longer than the exopodite.

Abscondicola n. gen. also differs from all other genera in the special ornamentation of the seta on the proximal exopodal segment of P₄. *Cantrincola* and *Antillesia* bear a normally feathered seta on this segment. In *Abscondicola*, however, this peculiar seta is rigid and typically pectinate near the tip.

Fig. 14. - *Abscondicola humesi* n. gen., n. sp. : a. Female abdomen in ventral view; b. Male abdomen in ventral view; c. Male abdomen in lateral view; d. Female genital field; e. Male P; f. Mandible; g. Antennule of the male; h. Antenna, inner view; i. Antenna, outer view; j. Antennule of the female; k. Maxilla; l. Maxilliped; m. Maxillule.



At last, the shape of the egg sac clearly distinguishes *Abscondicola* n. gen. from its congeners. Egg sacs in *Antillesia* and *Cancrincola* were formed with two or three parallel strings of eggs. Consequently, in these genera the egg sac is long ovate or pearshaped. Females of *Abscondicola* n. gen., on the other hand form a single string of eggs attached on the anterior half of the genital field, reaching the anal segment with the proximal end. The sac never contains more than six eggs whereas sacs in *Cancrincola* and *Antillesia* comprise eight to twelve eggs.

***Abscondicola humesi* n. sp.**

Figs. 13 - 18

Type-series :

Holotype, dissected female, mounted on three slides (Cop 2902a, b, c); allotype, dissected male, mounted on three slides (Cop 2901a, b, c); dissected paratypes : adult female (Cop 2903a, b, c), adult male (Cop 2904a, b), 2 Cop II (Cop 2893 and Cop 2894), 1 Cop III (Cop 2895), 1 female Cop IV (Cop 2897), 1 male Cop (Cop 2896), 1 female Cop V (Cop 2900) and 1 male Cop V (Cop 2899); preserved paratypes (Cop 2906) : 16 adult females (2 ovigerous), 37 males, 7 Cop V, 11 Cop IV, 8 Cop III and 1 Cop II.

Type-locality :

Papua New Guinea, Madang Province, Laing Island. From the gill chambers of a female *Cardisoma hirtipes* DANA, 1852 (Decapoda). Collected along the western shore of the island near the jetty. Leg. F. FIERS & J. VAN GOETHEM, 18 November 1986 (field no. 86-82, IG. 27237).

Etymology :

The species is named after A.G. HUMES (University of Boston, Woods Hole).

Additional material :

- On *Cardisoma hirtipes* DANA, 1852 [female, carapax width : 65 mm, from the type-locality] : 9 females (6 ovig. and 5 males (preserved, Cop 2907)); [female, carapax width : 64 mm, from the type-locality] : 15 females (7 ovig.), 5 males, 1 female Cop V, 2 female Cop IV, 1 Cop III and 1 Cop II (preserved, Cop 2906).
- On *Cardisoma hirtipes* DANA, 1852 [male, carapax width : 89 mm] from Laing Island, north eastern side beyond the guest houses; Leg. F. FIERS & J. VAN GOETHEM, 15 November 1986 (field no. 86-79, IG. 27237) : preserved specimens (COP 2955) : 208 females (156 ovigerous), 66 males, 4 Cop III, 14 Cop II, 57 Cop I.
- On *Cardisoma hirtipes* DANA, 1852 [male, carapax width : 87 mm] from Laing Island (Madang province), Papua New Guinea, leg. J. BOUILLON, spring 1976, IG. 25484; 64 females (12 ovigerous but numerous egg strings observed in the residue), 12 males, 1 Cop III, all preserved (COP 2953) and 1 female *Leptocaris mucronatus* FIERS, preserved (COP 2954).

- On *Cardisoma rotundum* (QUOY & GAIMARD, 1824) [male, carapax width : 59 mm]; Laing Island, leg. MASSIN & LIEVROUW, 11 October 1983, IG. 26700 : 19 females (7 ovigerous), 19 males; 20 Cop V; 33 Cop IV, 3 Cop III, 1 Cop II, 1 Cop I (diss. Cop 2909a, b, Fig. 4a-k, preserved spec. Cop 2910).
- On *Cardisoma hirtipes* DANA, 1852 [damaged male, carapax width : 59 mm] from Manokwari Irian Jaya), det. I. GORDON, 25 March 1929, IG. 9223. Preserved, Cop 2936 : 5 females, 1 male, 1 Cop V and 1 cop II.

Figures :

Holotype : Fig. 14a, d, f, j, k, l, m, Fig. 15b, c, e, f, g; female paratype : Fig. 13a, b, c, Fig. 14h, i; allotype : Fig. 14d, Fig. 15b, c, e, g, Fig. 15a, d.

Description :

Female : habitus (Fig. 13a, b) : body vermiform, slightly tapering posteriorly; cephalothorax / body length ratio : 1/6; lateral margins of the cephalothorax bending in the anterior third; length, including rostrum and furcal rami, 930 μ m (holotype, 900 - 985 paratypes); rostrum minute and smooth except for two sensillae; anal operculum small, convex and naked; genital segments individualized; receptaculum seminis long with a U-shaped posterior part (Fig. 14d); anterior part less thick than posterior region; vulva small, difficult to see because of the thin walls; external complex rather large, bearing two setae and two sclerified lips.

Furcal rami three times as long as wide, having parallel margins and bearing six setae; dorsal seta implanted on two basal elements and situated near the inner distal edge of the ramus; lateral setae implanted in the distal third; outer apical seta strong, armed along the outer margin and implanted some distance from the principal seta; inner apical seta small and smooth; principal seta bulbous near the implantation and furnished with minute spinules in the second half.

Integumental organs : sensillae on the epimerae long and fragile; cephalothorax, thoracic and abdominal segments each with a minute median dorsal pore; inner tissue around the pore orifice differentiated forming an (difficult to observe) ovate area; prae-anal segment without dorsal pore and sensillae; anal segment with two sensillae.

Integumental structures : cephalothorax with two sclerified strips on the anterior dorsal surface; integument of the segments smooth; abdominal segments furnished with a spinulose row along the ventral posterior margin; anal segment with spinules near the implantation of the furcal rami and in the anterior half of the ventral surface; furcal rami with spinules near the implantation of the outer lateral setae.

Egg sacs : a single string with six eggs, reaching from the anterior part of the genital field to the anal segment.

Antennule (Fig. 14j) eight-segmented; surface of segments smooth; aesthetascs on the distal margins of segments four and eight; aesthetascs of a simple tubular shape; several setae articulating on a small basal part; all setae smooth. Antenna (Fig. 14h, i) with a semi-allobasis : inner surface

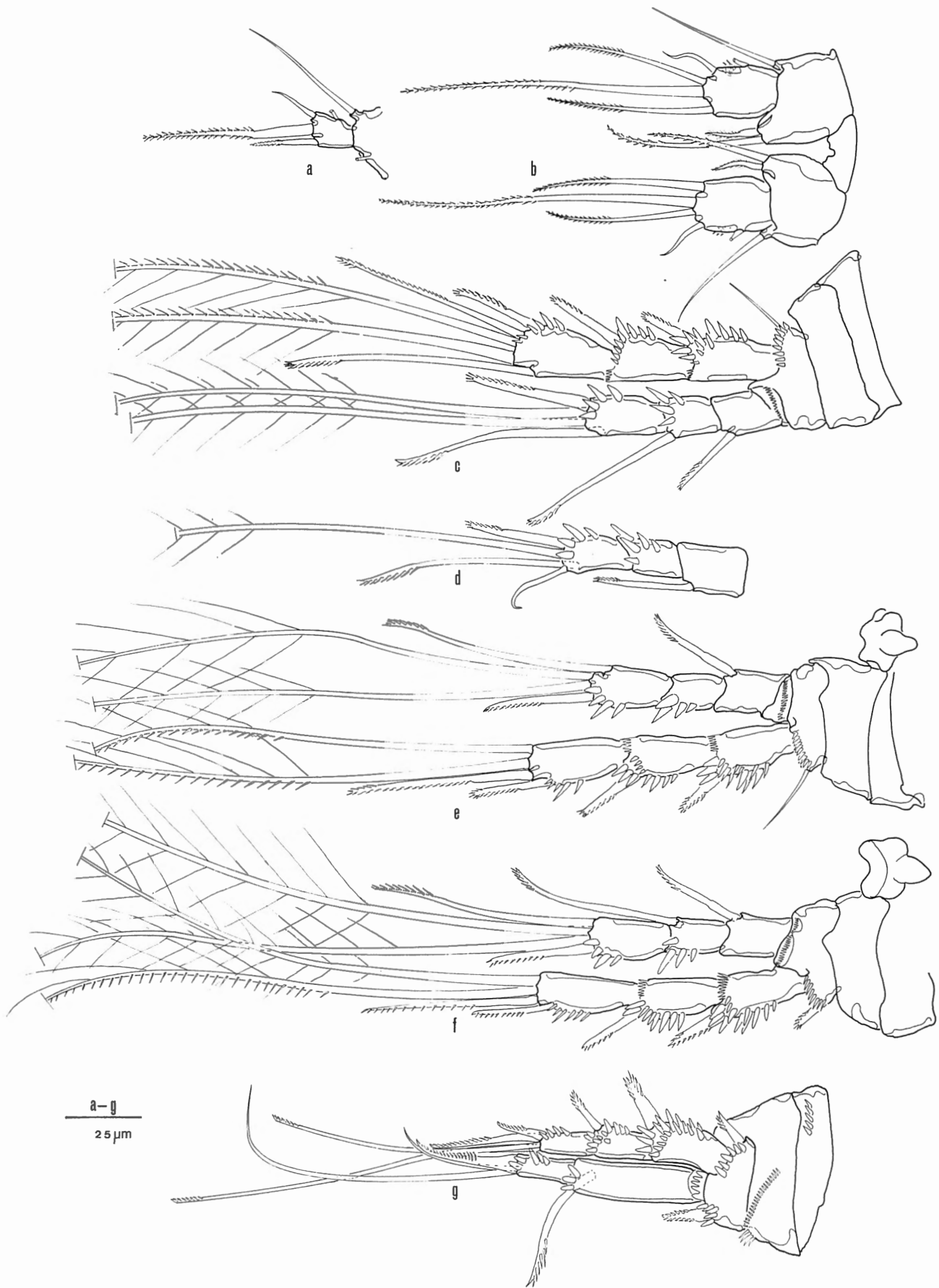


Fig. 15. - *Abscondicola humesi* n. gen., n. sp.: a. Male P_5 ; b. Female P_5 ; c. Female P_4 ; d. Male endopodite P ; e. Female P_3 ; f. Female P_2 ; g. Female P_1 .

of coxa and basis fused together, outer surface separated near the articulation of the exopodite; anterior margin of coxa and basis with some small spinules; exopodite one-segmented, about twice as long as wide, bearing two short apical setae and a long lateral pectinate one; endopodal segment bearing laterally one armed spine and a smooth seta, and apically, one armed spine and five setae; lateral margins furnished with strong spinules.

Mandible (Fig. 14f) rather small and not strongly sclerified; biting edge with six multi-dented teeth and a spinulose seta; coxa-basis and endopodite cylindrical, twice as long as wide; basis without setae, endopodite bearing four slender ones.

Maxillule (Fig. 14m): arthrite with four armed spines and two slender setae; coxa and basis with respectively three and five setae; exopodite minute, bearing a single seta; endopodite absent.

Maxilla (Fig. 14k): syn-coxa with a row of minute spinules on the surface and two endites; proximal endite small, bearing one seta; distal endite cylindrical and having two apical setae; basis prolonged to a spiniform long structure, bearing a single seta near the proximal part of the extension; endopodite obsolete, represented by two setae.

Maxilliped (Fig. 14l) prehensile; basis with a seta; first endopodal segment with three fragile hairs on the inner margin; claw armed and bearing one seta, implanted near the articulation with the supporting segment.

P₁ (Fig. 15g): prae-coxa, coxa and basis with rows of spinules; articulation between basis and endopodite covered with an incised fringe; outer and inner spine of the basis spinulose; exopodite three-segmented with strong spinules along the anteriorly directed outer and apical margins of the segments; endopodite two-segmented and reaching just beyond the exopodite; first endopodal segment 3.5 times as long as wide, bearing a long strong seta, armed distally along one side; second endopodal segment with a rigid claw, a short and a long smooth seta.

P₂-P₄ (Fig. 15f, e, c, respectively); prae-coxae and coxae smooth; basis with a spiniform row near the outer spine and an indented fringe near the articulation with the endopodite; basis of P₂ with an outer spine, basis of P₃ and P₄ with an outer smooth seta; rami three-segmented; chaetotaxy in table I; inner setae on the endopodal segments and inner seta of the third exopodal segment P₄ rather robust and only armed apically along one side; endopodite P₂ reaching towards the middle of the third exopodal segment while the endopodites of P₃ and P₄ only reach beyond the articulation between segments two and three.

P₅ (Fig. 15b): baseoendopodites of both legs connected with a coupler; endopodal lobe small bearing two apical setae; exopodite nearly 1.5 times as long as wide, bearing four setae, implanted along the distal margin; outer exopodal margin furnished with a few spinules and having a distinct pore orifice.

Male: habitus (Fig. 13d): largest width near the posterior margin of the cephalothorax ($\pm 125 \mu\text{m}$); body, beyond cephalothorax, more tapered than in the female; length, including rostrum and furcal rami, 890 μm (allotype, paratypes: 838-895, n=10); integumental structures of the abdominal segments as in the female (Fig. 14b, c).

Antennule (Fig. 14g): sub-chirocer and six-segmented; aesthetasc on segment three and six; inner margin of ultimate segment covered with a cushion-like structure.

Mouthparts as in the female.

P₁ without any trace of sexual dimorphism; P₂, P₄ and exopodite P₃ as in the female; endopodite P₃ (Fig. 15d) with a smooth and curved inner apical seta on the third segment; other appendages and structures of P₃ as in the female.

P₅ (Fig. 15a): baseoendopodite not articulating with the supporting segment, without endopodal setae but with a pore orifice; exopodite with slightly convergent margins, bearing three setae, implanted on the distal margin.

P₆ (Fig. 14e) present as an asymmetrically median structure on the ventral surface of the sixth somite; consists of a large transversal slit closed with a curved plate; the whole structure is strongly sclerified and forms a distinct elevation on the ventral surface of the segment (see Fig. 14c).

Variability:

Besides the normal variation in body length, differences were only observed in the proportional lengths of the baseoendopodal setae of the female P₅. The female holotype shows considerable differences between the left and right innermost seta. In other females, these setae are of equal length.

The sole copepodid I found in the samples (see below) lacks the outer spines of the exopodite on one side (Fig. 16j). The opposite leg bears the (presumably) normal chaetotaxy (Fig. 16i, table IV).

COPEPODID DEVELOPMENT

Copepodid I (from the decapod C. rotundum)

Habitus (Fig. 16a, b): body with four segments; length, including rostrum and furcal rami, 160 μm ; anal segment with a transverse row of spinules in the posterior third of the ventral surface and constricted laterally near the onset of the comb (Fig. 16c); furcal rami twice as long as wide, bearing two dorsal setae, two lateral and two apical ones; lateral setae with bulbous proximal part; apical ones fused and armed along the stem; inner dorsal seta articulating on two basal parts; spinules present near the implantation of the setae.

Antennule (Fig. 16f) five-segmented, bearing an aesthetasc on the second and fifth segments.

Fig. 16. - *Abscondicola humesi* n. gen., n. sp., copepodid I: a. Habitus in dorsal view; b. Habitus in lateral view; c. Third, fourth and anal somite in ventral view; d. Endopodal segment of the mandible; e. Maxilliped; f. Antennule; g. Antenna, allobasis, outer view; h. Antenna, inner view; i. Exopodite P₁ with normal chaetotaxy; j. P₁, exopodite with abnormal chaetotaxy; k. P₂.



Table IV :

Chaetotaxy of the copepodids of *Abscondicola humesi* n. gen., n. sp. (notation of setal formula as in HUMES and HO, 1969).

	Cop I	Cop II	Cop III	Cop IV	Cop V
P ₁ exo	0,2,IV	0,I-0,2,III	=	=	0,I-0,I-0,2,II
end	0,2I,0	1,0-0,2I,0	=	=	1,0-0,2I,0
P ₂ exo	0,2,III	0,I-0,2,II	=	0,I-0,2,III	0,I-0,I-0,2,II
end	0,2,I	1,0-1,2,I	=	1,0-2,2,I	1,0-1,0-1,2,I
P ₃ exo	3	0,2,III	0,I-0,2,II	0,I-0,2,III	0,I-0,I-0,2,II
end		0,2,I	1,0-1,2,I	1,0-1,2,I	1,0-0,0-1,2,I
P ₄ exo		3	0,2,III	0,I-1,2,III	0,I-0,I-1,2,II
end			0,2,I	1,0-1,2,I	1,0-1,0-1,2,I
P ₅ exo			—/—	4/3 *	4/3
bas				2/0	3/0
P ₆				—/—	3/—

* Female/male chaetotaxy; —means leg not present.

Antenna (Fig. 16g, h) : prae-coxa present; allobasis with one-segmented exopodite; the latter bearing three setae; endopodal segment with adult chaetotaxy.

Mandible (Fig. 16d) : gnathobasis and first segment (basal) of the palp as in the adult; endopodal segment with one lateral and four apical setae.

Maxillule and maxilla as in the adult.

Maxilliped (Fig. 16e) : basis with a single seta and devoid of integumental structures; endopodal segment with smooth surfaces; endopodal claw with a thick proximal part, bearing a long smooth seta and a hook-shaped distal half, furnished with teeth.

P₁ (Fig. 16j) : intercoxal plate, prae-coxa, coxa and basis present; inner spine of the basis absent, outer one present; endopodite and exopodite one-segmented; chaetotaxy in table IV; integumental structures of both rami as in the adult.

P₂ (Fig. 16k) : protopodite components present; endopodite and exopodite one-segmented; table IV for chaetotaxy.

P₃ (Fig. 16c) : represented as two small elevations along the posteroventral margin of the third somite; each leg with three minute setae.

Copepodid II

Habitus (Fig. 17a) cylindrical with six segments; length, including rostrum and furcal rami, 335-385 µm; anal segment slightly tapering and about 1.5 times as long as wide; integument of the cephalothorax and thoracic segments smooth; anal segment with a transverse row of spinules on the ventral surface and a few spinules near the proximal lateral edges.

Furcal rami about 2.7 times as long as wide; shape and ornamentation as in the adult.

Antennule (Fig. 17i) six-segmented; aesthetascs on second and sixth segments; antenna as in the adult but exopodite with a short setulose seta instead of a long one (Fig. 16k); mandible, maxillule, maxilla and maxilliped as in the adult.

P₁ (Fig. 17b) : prae-coxa, coxa, basis and intercoxal plate present; integumental structures and spines as in the adult; exopodite and endopodite two-segmented; inner seta on proximal endopodal segment small; chaetotaxy in table IV.

P₂ (Fig. 17c) : parts of the protopodite present; exopodite and endopodite two-segmented; inner setae of endopodal segments small and feathered along the stem; chaetotaxy in table IV.

P₃ (Fig. 17d) : protopodite as in P₂; endopodite and exopodite one-segmented; endopodite with three appendages only; chaetotaxy in table IV.

P₄ (Fig. 17e) : both legs represented as a curved lobe, bearing three minute setae apically.

Copepodid III

Habitus as in Cop II but with seven segments; length, 415-450 µm; furcal rami three times as long as wide; anal segment as in Cop II.

Antennule (Fig. 17j) six-segmented; differs from the preceding stage in number of setae and in the proportional lengths of the second segment; mouthparts and P₁ as in Cop II.

P₂ (Fig. 17f) as in the preceding copepodid; P₃ (Fig. 17h) with two-segmented rami, chaetotaxy in table IV.

P₄ (Fig. 17g) parts of the protopodite present and ornamented as in the adult; rami one-segmented; chaetotaxy in table IV.

P₅ not present.

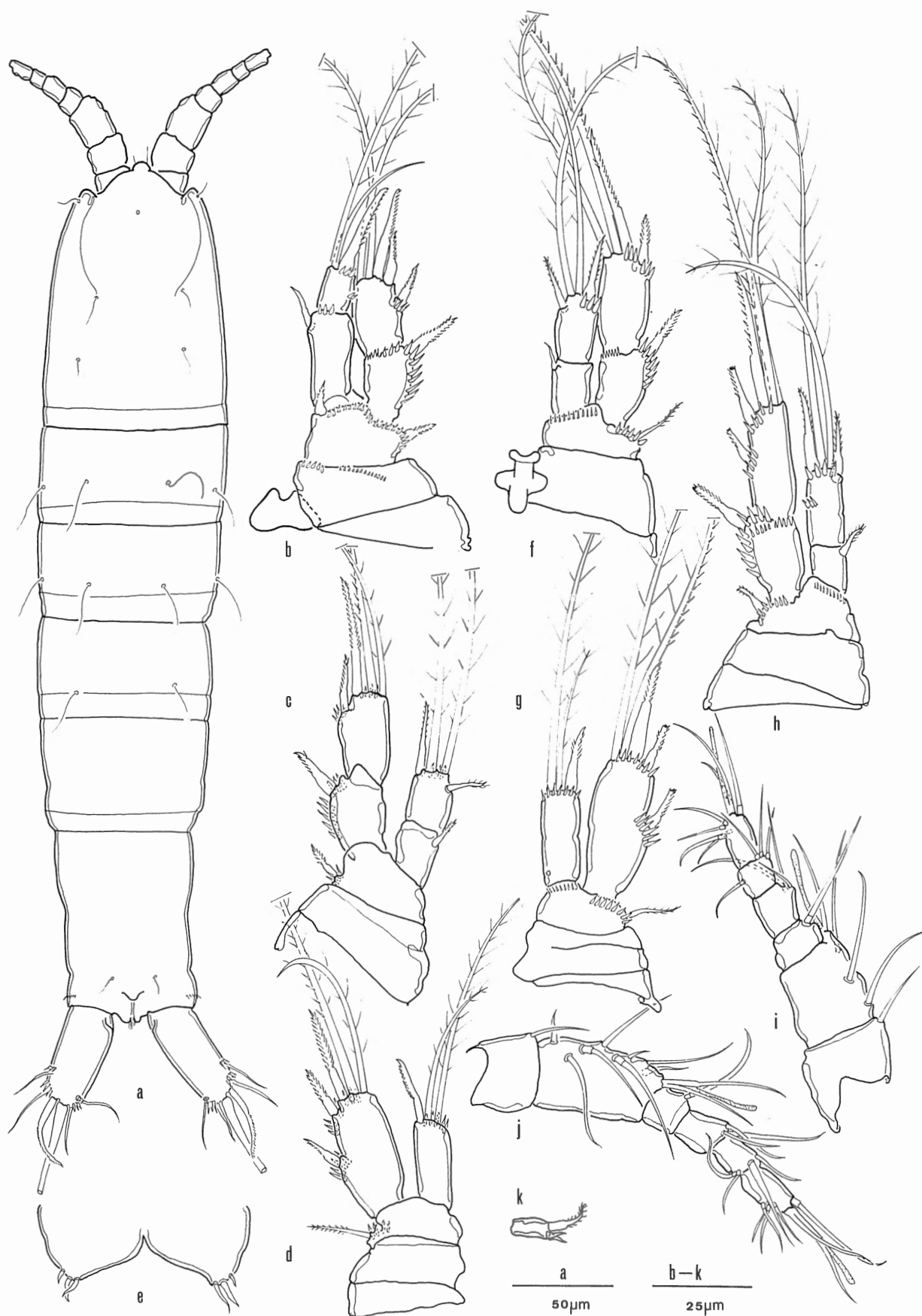
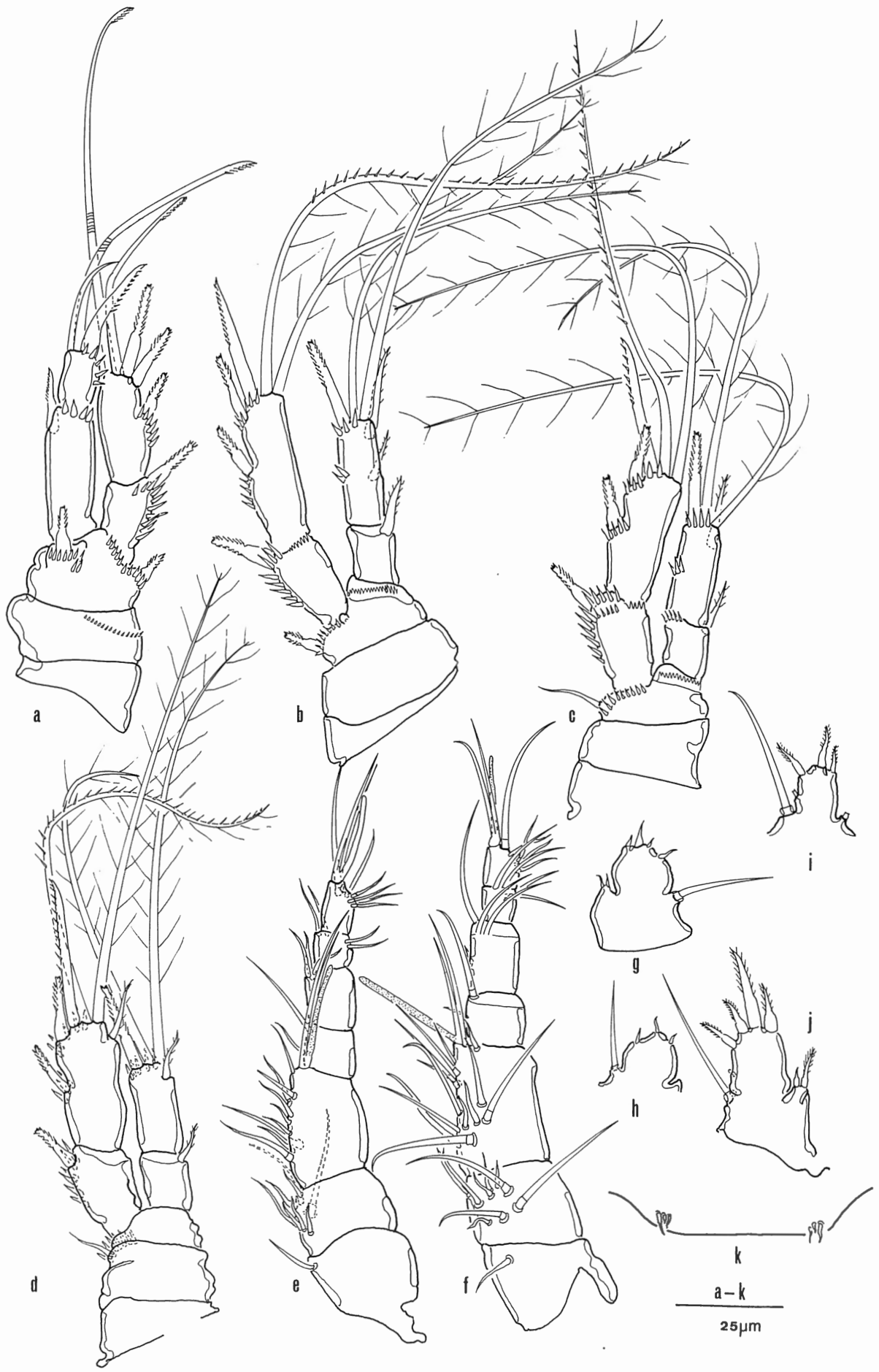


Fig. 17. - *Abscondicola humesi* n. gen., n. sp.: a. Cop II, habitus; b. P₁, Cop II; c. P₂, Cop II; d. P₃, Cop II; e. P₄, Cop II; f. P₂, Cop III; g. P₄, Cop III; h. P₃, Cop III; i. Antennule, Cop II; j. Antennule, Cop III; k. Exopodite antenna, Cop V.



Copepodid IV : female

Body with eight segments; penultimate somite (first abdominal segment) with a small row of minute spinules in the posterior third of the lateral margin; length, 635-650 μm ; anal segment and furcal rami as in the preceding copepodid.

Antennule eight-segmented with adult chaetotaxy and proportional lengths; mouthparts as in the former copepodids. P₁-P₄ (Fig. 18a-d) with two-segmented rami; chaetotaxy in table IV; ornamentation of the protopodite components as in adult; inner setae of the endopodite small, rather thick and feathered.

P₅ (Fig. 18g) : represented as a single segment with a small baseoendopodal and a large circular exopodal lobe; baseoendopodite with two apical setae, exopodite bearing four setae; except for the seta of the basis, setae of the P₅ minute.

P₆ not present.

Copepodid IV : male

Differs from the female Cop IV in the antennule, P₅ and the body length (625-630 μm).

Antennule (Fig. 18e) seven-segmented bearing an aesthe-tasc on third and seventh segments; number and lengths of setae different than in the female antennule.

P₅ (Fig. 18h) : basal part nearly obsolete; baseoendopodal lobe minute, without setae; exopodite circular as in the female but with three small setae only.

P₆ not present.

Copepodid V : female

Habitus : body with nine segments; small rows of spinules on the lateral sides of first and second abdominal segments (seventh and eighth segments); length, 760-785 μm .

Antennule and mouthparts as in the adult except for the much smaller exopodal seta of the antenna (Fig. 17k).

P₁-P₄ as in the adult, with three-segmented rami and an adult chaetotaxy; inner setae of the endopodites still short and feathered along both sides.

P₅ (Fig. 18j) : same shape as in Cop IV but with longer setae and a nearly rectangular exopodal lobe; exopodal pore present.

P₆ (Fig. 18k) : represented by three minute setae, implanted along the posterior ventral margin of the sixth somite.

Copepodid V : male

Habitus as in the female; length, 760-795; mouthparts and legs as in the female; endopodite P₃ without dimorphic features.

Antennule (Fig. 18f) seven-segmented as in Cop IV but slightly longer and with a larger number of setae on the segments.

P₅ (Fig. 18i) as in the preceding stage but with longer setae and a more rectangular exopodal lobe; exopodal and baseoendopodal pore clearly distinguishable.

P₆ not present.

ECOLOGICAL CONSIDERATIONS

Laing Island, a small island along the northern coast of Papua New Guinea (see FIERs, 1982 : Fig. 1), is inhabited by four different species of decapods of the family Gecarcinidae. *Cardisoma carnifex* (HERBST, 1796), *Cardisoma hirtipes* DANA, 1851 and *Gecarcoidea lalandii* H. MILNE-EDWARDS, 1837 are the most abundant species while *C. rotundum* (QUOY & GAIMARD, 1824) is rare and has been reported only twice (OVAERE, pers. comm.).

During a short stay at the station in 1986, the distribution of these four species was roughly mapped. It appeared that *C. carnifex* and *G. lalandii* occupy the highest elevations corresponding to the central parts of the island. The two other decapod species prefer the areas situated nearer to the shores but are (at least *C. hirtipes*) very abundant in the swampy northern and southern areas.

Burrows of *C. carnifex* and *G. lalandii* differ markedly from those of the two other species. The former dig sloping but almost straight burrows until they reach the groundwater table. The bottom of the hole is wet and contains only a few centimeters of water at the most. In contrast, *C. hirtipes* and *C. rotundum* dig more curved tunnels. Because of their position along the shores and in the swampy areas of the island, these burrows contain much more water and the walls are extremely waterlogged.

It is generally known that a coral island acts as a sponge so that during high tide many burrows near the shore become filled up with water. Measurements showed that the infiltration of seawater keeps the salinity of the water in the burrows between 16 and 28 ‰. In the centrally situated burrows, occupied by *C. carnifex* and *G. lalandii*, tides have much less impact and salinity is considerably lower (3 - 10 ‰).

Abscondicola humesi n. gen., n. sp. has never been found in the gill chambers of *Cardisoma carnifex* or *Gecarcoidea lalandii* although several specimens were examined. However, the harpacticoid heavily infested all specimens in collection of *C. hirtipes* and *C. rotundum*. It is assumed that the different ecologies of the two decapod groups determines the presence or absence of *Abscondicola humesi*.

Important in this context is the observation that nauplii of the copepod are extremely rare in the gill chambers. Although all copepodid stages and many gravid females

were present only two nauplii were found in all the residues. Thus, it seems thus possible that the eggs of the copepod associate hatch outside the gill chambers. If so, the environmental parameters need to remain between certain limits for the nauplii to develop. The absence of *Abscondicola humesi* in *Cardisoma carnifex* and *Gecarcoida lalandii* may be related to their occurrence in the highest parts of the island where the environmental conditions are unsuitable for the development of the nauplii.

ZOOGEOGRAPHY

Until now, Cancrincolidae n. fam. were known from the shores of the central Atlantic only. The distribution pattern of the five previously known species is intriguing because of their co-occurrence and trans-atlantic distribution. The above-described species, *Abscondicola humesi* n. gen., n. sp. is the first representative of this family in the Pacific Ocean and some assumptions about zoogeography of the family may be put forward.

Considering the extent of the Pacific Ocean, the northern coast of Papua New Guinea — type-region of *Abscondicola humesi* — is rather marginal. We expect however, that this species occupies a much larger area. As documented by TÜRKAY (1974) the decapods *Cardisoma hirtipes* and *C. rotundum* are widely distributed throughout the west Pacific region. To the west, in the Indian Ocean, their occurrence is more restricted. *C. hirtipes* has been reported from the Gulf of Bengal and from some localities in western Indonesia. *C. rotundum* shows a more south-western distribution in the Indian Ocean. It is quite possible that their associated copepod, *Abscondicola humesi* shows the same range.

The eastern range limit of *Cardisoma hirtipes* and *C. rotundum* coincides with the East Pacific Barrier (BRIGGS, 1974). Along the South and Central American coasts a related decapod species, *Cardisoma crassum* SMITH, 1870, occurs but none of the host crabs of *Abscondicola humesi* have ever been reported from this region (TÜRKAY, 1970). Although it is conceivable that cancrinicolid species form associations with this crab too, neither specimens of *Cardisoma crassum* nor reports of associated harpacticoids are available at the moment.

The monotypic genus *Antillesia* is widely distributed in the Caribbean province where it lives with *Cardisoma guanhumii*. Notwithstanding the fact that the same decapod species is infested by *Cancrincola jamaicensis*, HUMES (1958) never mentioned that he found *Antillesia cardisoma* and *Cancrincola jamaicensis* together in the same host. It seems reasonable to assume that particular environmental conditions in which *Cardisoma guanhumii* lives — such as were discussed for *Abscondicola humesi* — determine which one of the harpacticoid species is present.

Antillesia is undoubtedly more closely related to *Abscondicola* than to the Atlantic genus *Cancrincola*. They share many features not present in the genus *Cancrincola* and are sister-taxa.

The phylogenetic relationship between *Antillesia* and *Abscondicola* and the distribution pattern of the former in

the Caribbean shows a remarkable resemblance with the eastern Pacific-Caribbean track as shown by ROSEN (1976) for a great diversity of taxa. Apparently, *Antillesia cardisoma* or a sister species occur in the gill chambers of east Pacific Gecarcinidae while the presence of *Antillesia* in the Caribbean results from dispersal events in the past.

Besides *Antillesia*, the four other Atlantic species of the Cancrincolidae exhibit a bizarre distribution pattern. Two species, *Cancrincola jamaicensis* and *C. longiseta*, have a trans-Atlantic range while *C. plumipes* and *C. abbreviata* show a more restricted distribution. *C. plumipes* has been reported from the southeastern coasts of the U.S.A. but *C. abbreviata* occurs along the West African coast only.

It is clear that *Cancrincola longiseta* represents the most primitive branch in the genus *Cancrincola*. Moreover, *Cancrincola longiseta* seems to be more closely related to *C. plumipes* and *C. abbreviata* than to *C. jamaicensis*. These three species share a short inner seta on the first endopodal segment of the P₁ and occur exclusively in crabs of the family Sesarmidae. This particular species group is the most primitive branch in the genus and was presumably the first representative in the Atlantic Ocean. Because they are associated exclusively with sesarmid crabs, the gill chambers of the Atlantic Gecarcinidae were an unoccupied microhabitat at that time. The development of abilities to infest gecarcinid crabs meant a major breakthrough for the Atlantic Cancrincolidae and probably explains the wide distribution of *C. jamaicensis*. The extended range of this species into the Caribbean can be seen as a faunal element of the Eastern Atlantic (West African) - Caribbean track (ROSEN, 1976).

In his vicariance model of the Caribbean biogeography, ROSEN (1976) argued that the fauna of the Eastern Pacific-Caribbean track represents the youngest faunal element in the Caribbean region. Thus, if *Antillesia* originated in the (Indo-) Pacific Ocean, as presumed above, it dispersed in the Caribbean after *Cancrincola jamaicensis* established its relationships with *Cardisoma guanhumii*.

If these assessments approach the real history of the Cancrincolidae, we have to admit that development of abilities to infest Gecarcinidae happened twice within the Cancrincolidae: once in the (indo-) pacific genera — i.a. *Abscondicola* and *Antillesia* — and once within the Atlantic genus *Cancrincola*.

However, if we consider *Cancrincola jamaicensis* as an intermediate branch between the primitive Cancrincolidae and *Antillesia-Abscondicola*, it has to be assumed that the possibility to infest gecarcinid decapods arose only once. This hypothesis is, phylogenetically, the most parsimonious alternative but seems to be in conflict with recent observations. Indeed, as demonstrated for several other harpacticoid groups like Darcythompsoniidae, certain Laophontidae, Cyliindropsyllidae, Ectinosomatidae etc., the strong Amphi-American affinities are obvious (MIELKE, 1981; 1982a; 1982b; FIERS, 1986a; 1986b). Therefore, in the present analyses, the less parsimonious hypothesis in which the association with gecarcinid crabs is assumed to have originated twice, is favoured instead of the most parsimonious alternative.

COMPARISON OF THE DEVELOPMENTAL SEQUENCES

The present comparison of the copepodid development is based on observations of the copepodids of four species out of six. The development of *Antillesia cardisomae* is only partially described while copepodids of *Cancrincola abbreviata* and *C. plumipes* were not available at all. Instead of repeatedly mentioning that the development of this three species is unknown, the following analyses considers that the developmental sequences of *C. plumipes* and *C. abbreviata* resemble the development of *C. jamaicensis* and that of *Antillesia cardisomae* approaches the development of *Abscondicola humesi*. However, only a few topics will be mentioned because of the incompleteness of the data set and forced assumptions would be to speculative. Whenever the missing stages will be described, important features from the juvenile morphology may complete the generic diagnosis of the three genera.

The first copepodids of the species of *Cancrincola* show an exopodite on the antenna which markedly differs from the adult exopodal ramus. The margins of this appendage in the first copepodid are strongly lobed with rigid sclerifications while it bears five setae instead of three as in the adult. In the second copepodid, the differences disappear and the general appearance of this ramus resembles closely the adult shape. It seems reasonable that the shape of the exopodite in the first copepodid results from an ancestral multi-segmented appendage. This ancestral feature is not present in *Abscondicola* (probably in *Antillesia* also). The first copepodid bears an exopodite on the antenna which is nearly identical with the adult ramus.

One of the main generic features of the genus *Abscondicola* is the presence of two outer spines on the third exopodal segments of the legs. All other species of the Cancrincolidae bear three outer spines on this segment (see Table I). Comparing the development of the chaetotaxy in *Abscondicola* with that of *Cancrincola* and *Antillesia*, it appears that the P_1 and P_2 in the second copepodid of the former exhibit a chaetotaxy resembling the two other genera. The number of setae of these legs in *Cancrincola* and *Antillesia* increases in the three successive stages following the second copepodid. In *Abscondicola* however, the setal number remains unchanged in the third and fourth stage.

The third exopodal spine appears normally in the fifth copepodid stage, in which the morphology of the legs is nearly identical with that of the adult. This development pattern is also shown by the cancrincolid genera *Cancrincola* (except for the segmentation in *C. jamaicensis*) and *Antillesia*. In *Abscondicola* the three-segmented rami appear in the same copepodid stage but the development of the third outer spine is omitted. Thus the onset of the chaetotaxy in the development of *Abscondicola* occurs in the same stages as the other genera but the development towards an adult setal formula appears to be delayed. According to the heterochronic nomenclature of Mc NAMARA (1986), the adult chaetotaxy of *Abscondicola* exhibits juvenile features (paedomorphosis) resulting from neotenic events in the development.

Other specific and generic features such as the two-segmented rami in the fifth copepodid of *C. jamaicensis*, the differences in the chaetotaxy of the species of *Cancrincola* and the shape of the P_5 in the genera, may be discussed in relation to heterochronic events. However, since the development of some species is not entirely known yet, conclusions about such processes may be to speculative. Harpacticoids in general develop the P_6 in the fourth copepodid. The leg appears as a small socle with three setae, resembling the first appearance of the other legs in all aspects. Normally both male and female copepodids have the P_6 in this stage. In *Abscondicola* and *Antillesia* however the P_6 appears first in the fifth female copepodid but does not develop in the males until the adult stage. In contrast with these two genera, the copepodids of *Cancrincola* species never exhibit a normal genital field in the females and a typical plate in the males. Comparing the general developmental pattern known from other harpacticoids, the onset of the P_6 in Cancrincolidae is post-displaced (McNAMARA, 1986).

In this context, it seems worthwhile to speculate on the origin of the separate genital and first abdominal segment of this family. Regarding the development of the body segmentation in harpacticoid copepods, the sixth leg bearing segment appears first in the third copepodid as the prae-anal segment. The fusion between the genital and the first abdominal segments to form the genital double segment is a typical adult feature and occurs never in the copepodids. We saw in the former paragraph that the P_6 , which undoubtedly represents a part of the genital field, is post-displaced and appears in the fifth copepodid or only in the adult. Remarkable is the fact that the natatory legs and the other appendages exhibit a normal developmental pattern. It seems that heterochronic events acted particularly on the anterior somites of the abdomen of this podoplean taxon. The separate genital and first abdominal segments are probably a result of post-displacement of the onset of the normal fusion of these segments, causing the total loss of this characteristic. Thus, what appeared to represent an ancestral trait, seems to be a highly advanced characteristic which differentiates the taxon from its relatives.

Phylogenetically, the post-displaced onset of the P_6 in *Cancrincola* represents a derived condition. Based on the conservative nature of the adult characteristics, the taxon *Cancrincola* is difficult to establish in a cladistic way. However, since the developmental sequence of P_6 markedly differs from the general developmental pattern and especially from the closely related genera in the family, one autapomorphy characterize the genus *Cancrincola* as a distinct taxon in the family Cancrincolidae.

Recently, FERRARI (1988) analysed the development pattern of the post-maxillipedal legs and clearly showed that similar adult segment numbers result from different developmental patterns. His analysis concerns only the number of segments of each leg in the successive juvenile stages and is based entirely on the descriptions appeared in literature. However, the data in literature are not always correct and have to be cited with caution. For example, the deve-

lopment sequence of a bud on the somites in the earliest stage of a leg is not easily visible and is probably often overlooked. On the other hand, references and descriptions of juveniles may be wrong. For example, the copepodid development of *Laophonte setosa* described by GOSWAMI (1977) deals not with this species and even not with a species of the family Laophontidae at all.

Personal observations on the development of several Laophontidae and harpacticoids in general, clearly revealed that numbers of segments in the successive copepodid stages still are not the way to define homologies. Only careful observations on the appearance of setae and comparison of them in closely related taxa may prove that segments are lost or integrated. If we see how drastic changes may occur in a small taxon, such as the here described Cancrincolidae, we have to be very careful with generalizations. However, personally I am convinced that FERRARI'S (1988) common pattern of the development for the legs, as represented in his Fig. 2 (p. 265), is of great

importance and an interesting blueprint to work with, but we are still a long way from the evolutionary interpretation of it in the phylogeny of copepods.

Acknowledgements

I am much indebted to Dr. J. VAN GOETHEM (K.B.I.N.) who gave me the opportunity to visit the station at Laing Island and for his help in gathering the crabs during several nightly raids.

Drs. A. OVAERE (K.B.I.N.) kindly identified the host crabs and provided me with interesting literature about these animals.

I gratefully acknowledge Prof. Dr. J.H. STOCK of the University of Amsterdam, who kindly put the copepods at my disposal, collected during the West Indian Expeditions by the following members of the University of Amsterdam: 1980 — L. BOTOSANEANU, J. NOTENBOOM; 1982 — L. BOTOSANEANU, N.W. BROODBAKKER, S.E.N. VAN LIESHOUT, J. NOTENBOOM. J.H. STOCK, M. STOCK, E.S.W. WEINGBERG, F. ZIJLSTRA.

I wish to thank also Dr. G. BOXSHALL (British Museum, Natural History) for his invaluable comments on the manuscript.

References

- BOXSHALL, G.A., FERRARI, F.D. & TIEMANN, H., 1984. The ancestral Copepod: towards a consensus of opinion at the First International Conference on Copepoda. *Crustaceana* suppl. 7: 68-84.
- BRIGGS, J.C., 1974. *Marine Zoogeography* i-xi, 1-475 (McGraw-Hill, New York).
- FIERS, F., 1982. New Canuellidae from the northern coast of Papua New Guinea (Copepoda, Harpacticoida). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, 54 (4): 1-32, Pl. 1-17.
- FIERS, F., 1986a. Harpacticoid Copepods from the West Indian Islands: Laophontidae (Copepoda, Harpacticoida). *Bijdragen tot de Dierkunde*, 56: 132-164.
- FIERS, F., 1986b. Harpacticoid Copepods from the West Indian Islands: Darcythompsoniidae (Copepoda, Harpacticoida). *Bijdragen tot de Dierkunde*, 56: 282-290.
- FERRARI, F.D., 1988. Developmental patterns in numbers of ramal segments of copepod post-maxillipedal legs. *Crustaceana*, 54: 256-293.
- GOSWAMI, S., 1977. Laboratory culture of a harpacticoid copepod *Laophonte setosa* (Boeck). In: Proceedings of a Symposium on Warmwater Zooplankton - *Special Publication of the National Institute of Oceanography, Goa*: 563-570.
- GOTTO, R.V., 1979. The Association of Copepods with Marine Invertebrates. *Advances in Marine Biology*, 16: 1-109.
- HUMES, A.G., 1941. A new harpacticoid copepod from Bornean crabs. *Journal of the Washington Academy of Sciences*, 37: 170-178.
- HUMES, A.G., 1956. *Pholetiscus rectisetus* n. sp. des cavités branchiales d'un crabe à Madagascar (Copepoda, Harpacticoida). *Mémoires de l'Institut Scientifiques de Madagascar*, ser. A, 11: 79-84.
- HUMES, A.G., 1957. The genus *Cancrincola* (Copepoda, Harpacticoida) on the west coast of Africa. *Bulletin de l'I.F.A.N.*, 19, ser. A, 1: 180-197, Pl. I-III.
- HUMES, A.G., 1958. *Antillesia cardisomae* n. gen., n. sp. (Copepoda, Harpacticoida) from the gill chambers of land crabs, with observations on the related genus *Cancrincola*. *Journal of the Washington Academy of Sciences*, 48: 77-89.
- HUMES, A.G. & Ho, Ju-Shey, 1969. The genus *Sunaristes* (Copepoda, Harpacticoida) associated with the hermit crabs of the western Indian Ocean. *Crustaceana*, 17: 113-130.
- LANG, K., 1936. Beiträge zur Kenntnis der Harpacticiden. 6. Bemerkungen über die Familie Ameiridae. *Zoologischer Anzeiger*, 114: 133-136.
- LANG, K., 1948. *Monographie der Harpacticoiden* Hakan Ohlsson, Lund, Vol. 1 & 2: p. 1-1682.
- LANG, K., 1965. Copepoda Harpacticoida from the Californian Pacific coast. *Kungliga Svenska Vetenskapsakademiens Handlingar*, ser. 4, 10: 1-566.
- MCMANARA, K.J., 1986. A guide to the nomenclature of heterochrony. *Journal of Paleontology*, 60: 4-13.
- MIELKE, W., 1981. Intersitielle Ectinosomatidae (Copepoda) von Panama. *Mikrofauna Meeresbodens*, 5: 1-45.
- MIELKE, W., 1982a. Interstitielle Fauna von Galapagos XXIX. Darcythompsoniidae, Cylindropsyllidae (Harpacticoida). *Mikrofauna Meeresbodens*, 85: 1-52.
- MIELKE, W., 1982b. Three Variable *Arenopontia* Species (Crustacea, Copepoda) from Panama. *Zoologica Scripta*, 11: 199-207.
- PEARSE, A.S., 1930. Parasites of Japanese Crustacea. *Annotationes Zoologicae Japonensis*, 13: 1-8.
- PEARSE, A.S., 1951. Parasitic Crustacea from Bimini, Bahamas. *Proceedings of the United States National Museum*, 1101: 341-372.
- PETKOVSKI, T.K., 1978. Zweiter Fund von *Cancrincola jamaicensis* C.B. Wilson (Copepoda, Harpacticoida, Ameiridae) auf Kuba. *Fragmenta Balcanica*, 10: 12 (232): 99-110.
- ROSEN, D.E., 1976. A Vicariance Model of Caribbean Biogeography. *Systematic Zoology*, 24: 431-464.

TÜRKAY, M., 1970. Die Gecarcinidae Amerikas. Mit einem Anhang über *Ucides* RATHBUN. *Senckenbergiana Biologica*, 51 : 333-354.

TÜRKAY, M., 1974. Die Gecarcinidae Asiens und Ozeaniens. *Senckenbergiana Biologica*, 55 : 223-259.

WAGENAAR HUMMERLINCK, P., 1979. De grotten van de Nederlandse Antillen - Caves of the Netherlands Antilles. *Publication of the Foundation for Scientific Research in Surinam and the Netherlands Antilles*, Natural History Series, 1 : 1-176.

WILSON, C.B., 1913. Crustacea parasites of West Indian Fishes and land crabs, with descriptions of new genera and species. *Proceedings of the United States National Museum*, 44 : 189-277.

WILSON, C.B., 1935. Parasitic Copepods from the Dry Tortugas. *Papers of the Tortugas laboratory*, 29 : 329-347.

Frank FIERS
Department of Invertebrates
Koninklijk Belgisch Instituut
voor Natuurwetenschappen
Vautierstraat 29
B-1040 Brussels