Revision of the genus Tapholeon Wells, 1967 (Copepoda, Harpacticoida, Laophontidae)

Article *in* Journal of Natural History · December 2007

DOI: 10.1080/00222930701695629

CITATION
1

READS
182

4 authors, including:

Hendrik Gheerardyn
Eurofins Aquasense
46 PUBLICATIONS **2,323** CITATIONS
SEE PROFILE

Frank Fiers
Royal Belgian Institute of Natural Sciences
80 PUBLICATIONS **1,443** CITATIONS
SEE PROFILE

Marleen De Troch
Ghent University
275 PUBLICATIONS **3,623** CITATIONS
SEE PROFILE

Journal of Natural History, 2007; 41(37–40): 2479–2510

Taylor & Francis
Taylor & Francis Group

Revision of the genus *Tapholeon* Wells, 1967 (Copepoda, Harpacticoida, Laophontidae)

HENDRIK GHEERARDYN[1], FRANK FIERS[2], MAGDA VINCX[1] & MARLEEN DE TROCH[1]

[1]*Marine Biology Section, Biology Department, Ghent University, Ghent, Belgium, and* [2]*Royal Belgian Institute of Natural Sciences, Section of Recent Invertebrates, Brussels, Belgium*

(*Accepted 22 November 2006)*

Abstract
To date, only two species are known in the laophontid genus *Tapholeon* Wells, 1967 (Copepoda, Harpacticoida). In the present contribution, a redescription of the type species *T. ornatus* Wells, 1967, based on the type material, is provided. Furthermore, two new species are described from the coast of Kenya, *T. inconspicuus* sp. nov. and *T. tenuis* sp. nov. Two species, formerly attributed to *Asellopsis* Brady and Robertson, 1873 (namely *A. arenicola* Chappuis, 1954 and *A. chappuisius* Krishnaswamy, 1957), are allocated to *Tapholeon* based on the absence of sexual dimorphism in the swimming legs P2–P4. The former of the two species is redescribed based on additional material from the Comoros. An updated generic diagnosis and a key to the six species of *Tapholeon* are included.

Keywords: *Laophontidae, new species, redescription, Tapholeon.*

Introduction

The present paper is part of an extensive study of the copepod fauna associated with the coral degradation zone along the eastern coasts of Kenya and Zanzibar (Tanzania). In the lagoon, between the reef and the beach, different substrates, ranging from coral sand, fine coral gravel and coral rubble to large coral fragments, were sampled. To date, the qualitative samples from the Kenyan coast yielded 44 species of the family Laophontidae T. Scott, 1905, including 28 which are new to science (four species have been described so far; Gheerardyn et al. 2006a, 2006b). Two new Kenyan species are described here and recognized within the genus *Tapholeon* Wells, 1967. Hitherto, this genus consisted of only two species, *T. ornatus* Wells, 1967 and *T. uniarticulatus* Wells, 1967, both described from Inhaca Island (Mozambique). Wells (1967) established this genus mainly based on the complete absence of sexual dimorphism in the swimming legs P2–P4. Here we provide a redescription of the type species *T. ornatus*, based on the re-examination of the type material. Furthermore, two species, formerly attributed to *Asellopsis* Brady and Robertson,

Correspondence: Hendrik Gheerardyn, Marine Biology Section, Biology Department, Ghent University, Campus Sterre—Building S8, Krijgslaan 281, B-9000 Ghent, Belgium. Email: hendrik.gheerardyn@ugent.be

ISSN 0022-2933 print/ISSN 1464-5262 online
DOI: 10.1080/00222930701695629

1873 (namely *A. arenicola* Chappuis, 1954 and *A. chappuisius* Krishnaswamy, 1957), are allocated to *Tapholeon*. Based on additional material from the Comoros, the former of these two species is redescribed.

Material and methods

Along the eastern coast of Kenya, meiofauna samples were collected in 2002 from various dead coral substrates (ranging from coral sand, fine coral gravel and coral rubble to large coral fragments). Prior to fixation, epifauna from coral fragments and coral rubble were rinsed off with filtered seawater over a 1 mm and a 32 µm sieve. Samples from coral gravel were obtained by decanting the coral gravel (10 times) over a 32 µm sieve. Buffered formaldehyde was added to a final concentration of 4%. In the laboratory, samples were centrifuged three times with Ludox HS40 (specific density 1.18) and finally stained with Rose Bengal.

On Grande Comore, several samples of sediments were collected in 1981 following a slightly different procedure. To the sampled substrates, buffered formaldehyde was added immediately to a final concentration of 4%. In the laboratory, samples were rinsed with a jet of freshwater over a 5 mm and a 45 µm sieve, and centrifuged three times with Ludox HS40 (specific density 1.18).

Harpacticoid copepods were counted using a Wild M5 binocular, and were sorted out and stored in 75% ethanol. Observations and drawings were made from whole and dissected specimens mounted in lactophenol, using a light microscope (Leica DM LS) equipped with a drawing tube. Preparations were sealed with insulating varnish. In toto specimens were stored in 75% ethanol. The type specimens of *Tapholeon inconspicuus* Gheerardyn and Fiers sp. nov. and *T. tenuis* Gheerardyn and Fiers sp. nov. are deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (KBIN; Brussels; labelled COP). Specimens of the type series of *T. ornatus* Wells, 1967 and *T. uniarticulatus* Wells, 1967 were loaned from the Natural History Museum, London.

The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1–P6, first to sixth thoracopod; exp(enp)-1(2,3) to denote the proximal (middle, distal) segment of a ramus.

Systematic account

Family LAOPHONTIDAE T. Scott, 1905
Subfamily LAOPHONTINAE T. Scott, 1905 *sensu* Huys and Lee, 2000
Genus *Tapholeon* Wells, 1967

Updated diagnosis

Laophontidae: habitus slender and elongate, slightly depressed dorso-ventrally; with distinct convex curvature in lateral aspect; without demarcation between prosome and urosome. Cephalothorax slightly longer than wide, with parallel margins. Urosome only slightly tapering posteriorly. Anal operculum convex with serrate margin, not distinctly protruding. Caudal rami dorso-ventrally flattened. Dorsal surface depressed beyond implantation of seta VII. Seta IV and V rather short.

Sexual dimorphism in body size, antennule, P5, P6, genital segmentation, and ornamentation of ventral surface of urosome.

Rostrum prominent, fused to cephalothorax. Female antennule five- or six-segmented. Male antennule sub-chirocer. Second segment (both sexes) bearing small blunt process and strong, armed spine along posterior margin. Ultimate segment of female antennule bearing (at least) two stout setae. Antenna with reduced abexopodal seta on allobasis. Antennary exopod well developed; bearing four setae (one of which dwarfed). Mandibular palp uniramous, bearing one, one, three setae, representing basis, exopod, and endopod, respectively. Maxillule with two elements on coxal endite; basal endite with two setae and one curved spine; endopod represented by three setae; exopod with two setae. Maxillary syncoxa with three endites; praecoxal endite small, with one seta; both coxal endites with three elements; allobasis drawn out into claw, with two accessory elements; endopod represented by two setae. Maxilliped subchelate; syncoxa with one seta; endopod claw-shaped with one short seta at base. Exopod P1 one- or two-segmented. Swimming legs P2–P4 with two-segmented endopods and three-segmented exopods. Swimming leg setal formulae in Table I. Without sexual dimorphism in P2–P4. P5 with separate exopod and baseoendopod. Female P5 with endopodal lobe reaching at least to middle of exopod, bearing one apical and three lateral setae; exopod ovate to rhomboid, bearing five setae. Male P5 baseoendopod obsolete, without endopodal seta; exopod small, bearing three or four setae. P6 vestiges bearing one seta in female; vestiges asymmetrical in male, with each outer distal corner produced into cylindrical process bearing two setae.

Type species

Tapholeon ornatus Wells, 1967.

Other species

T. arenicolus (Chappuis, 1954) comb. nov.; *T. chappuisius* (Krishnaswamy, 1957) comb. nov.; *T. inconspicuus* Gheerardyn and Fiers sp. nov.; *T. tenuis* Gheerardyn and Fiers sp. nov.; *T. uniarticulatus* Wells, 1967.

Table I. Species of *Tapholeon* Wells, 1967: number of exopodal segments in P1 and swimming leg setal formulae of P2–P4.

	P1	P2		P3		P4	
	exp	exp	enp	exp	enp	exp	enp
Tapholeon inconspicuus	1	0.1.123	0.120	0.1.223	0.221	0.1.223	0.121
Tapholeon tenuis	2	0.1.123	0.220	0.1.223	0.220	0.1.223	0.120
Tapholeon ornatus	2	0.1.123	0.120	0.1.223	0.220	0.0.223	0.120
Tapholeon arenicolus	2	0.1.123	0.020	0.1.223	0.120	0.0.223	0.120
Tapholeon uniarticulatus	1	0.1.122	0.120	0.1.222	0.121	0.1.222	0.121
Tapholeon chappuisius	2	0.1.122	0.020	0.1.222	0.020	0.1.222	0.020

exp, exopod; enp, endopod.

Tapholeon ornatus Wells, 1967
(Figures 1–4)

Type locality

Mozambique, Inhaca Island: Ilha dos Portuguesos, Barriera Vermelha beach (clean sand) and Saco da Inhaca (detritus sand) (Wells 1967).

Type material

Type specimens are deposited in the British Museum of Natural History, London (Wells 1967).

Material examined

Type material. One female holotype dissected on one slide (NHM 1967.8.4.106), one male paratype in one slide (NHM 1967.8.4.107), one female paratype in one slide (NHM 1967.8.4.108), one male and three female paratypes in 70% alcohol (NHM 1967.8.4.109), one female paratype dissected on five slides (NHM 2006.1492), one female paratype dissected on four slides (NHM 2006.1493), and one male paratype in one slide (NHM 2006.1494); all from the type locality.

Additional material. One female dissected on one slide (COP 1991), nine females and 13 males in 70% alcohol (COP 1990); all from Comoros, southeast coast of Grande Comore, Ouroveni (11°54′S, 43°29′E), small protected creek with mangrove, fine sand sample; collected 3 August 1984 by Groupe Plongée de l'Expedition Karthala.

Redescription of female

Total body length 448–514 μm (n=4; average=484 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 103 μm. Measurements by Wells (1967): average length 443 μm (range 364–507 μm) (measured from base of rostrum to distal edge of last somite, thus excluding caudal rami).

Rostrum (Figure 2A) well-developed, broad at base; fused to cephalothorax; with pair of sensilla anteriorly.

Habitus (Figure 1A, B) elongate and slender, slightly dorso-ventrally depressed; with distinct convex curvature in lateral aspect; without demarcation between prosome and urosome. Cephalothorax slightly longer than wide, with parallel margins. Free prosomites and following urosomite equally wide; genital double-somite and following urosomite slightly extended laterally, resulting in posteriorly directed lateral process; urosome scarcely tapering posteriorly. Second and third urosomite fused to form genital double-somite. Genital double-somite with transverse surface ridge dorsally and laterally, indicating original segmentation; fused ventrally. Anal operculum convex with slightly serrate margin, not distinctly protruding.

Integument of cephalothorax with pattern of slight depressions; regularly ornamented with small sensilla. Pleurotergites of prosomites and urosomites and dorsal surface of anal somite densely clothed irregularly with small denticles, some of which organized in transversal rows. Posterodorsal margin of cephalothorax smooth, of all free somites serrate. Posterodorsal margins of cephalothorax and free somites clothed with slender hairs, all bearing number of sensilla (not in penultimate urosomite).

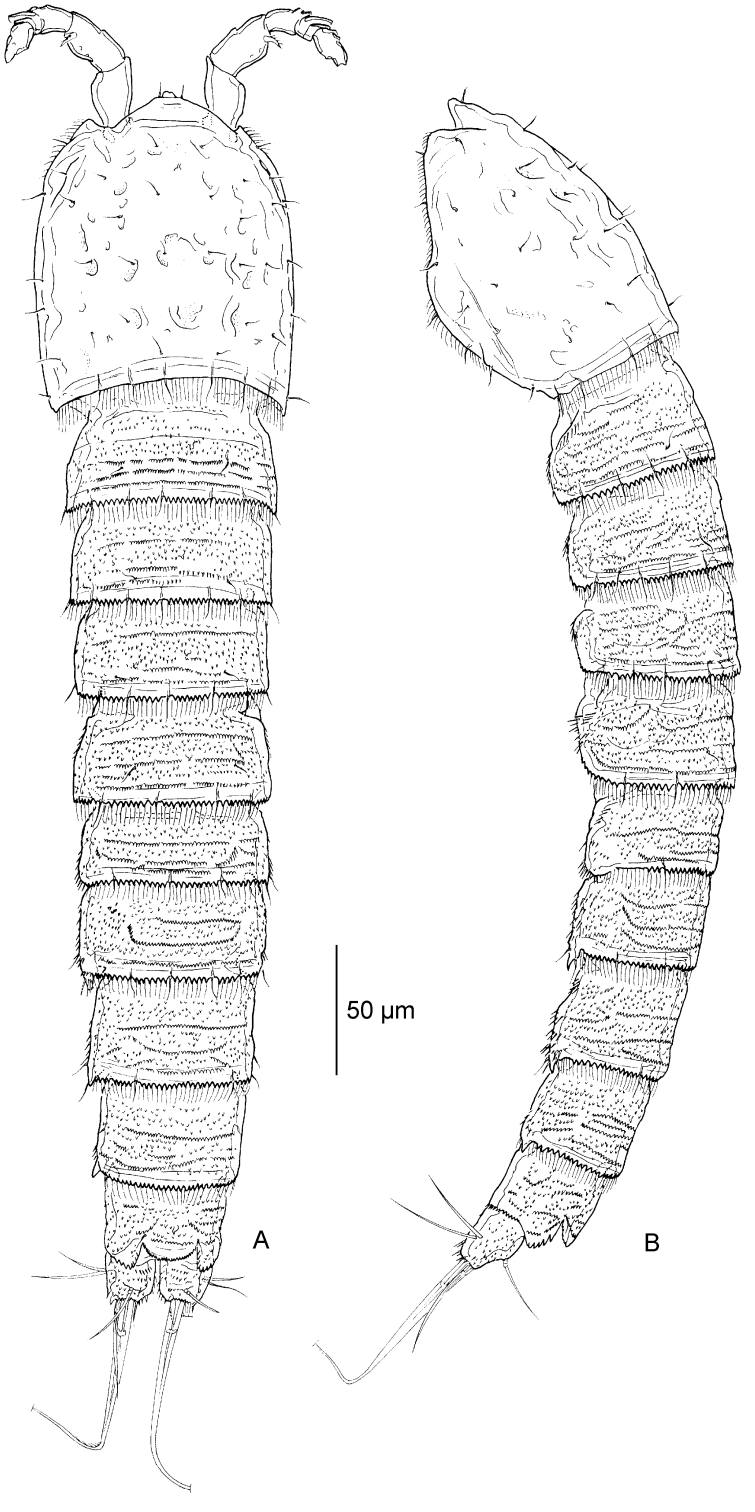

Figure 1. *Tapholeon ornatus* Wells, 1967. (A) Female habitus, dorsal; (B) female habitus, lateral. Scale bar in µm.

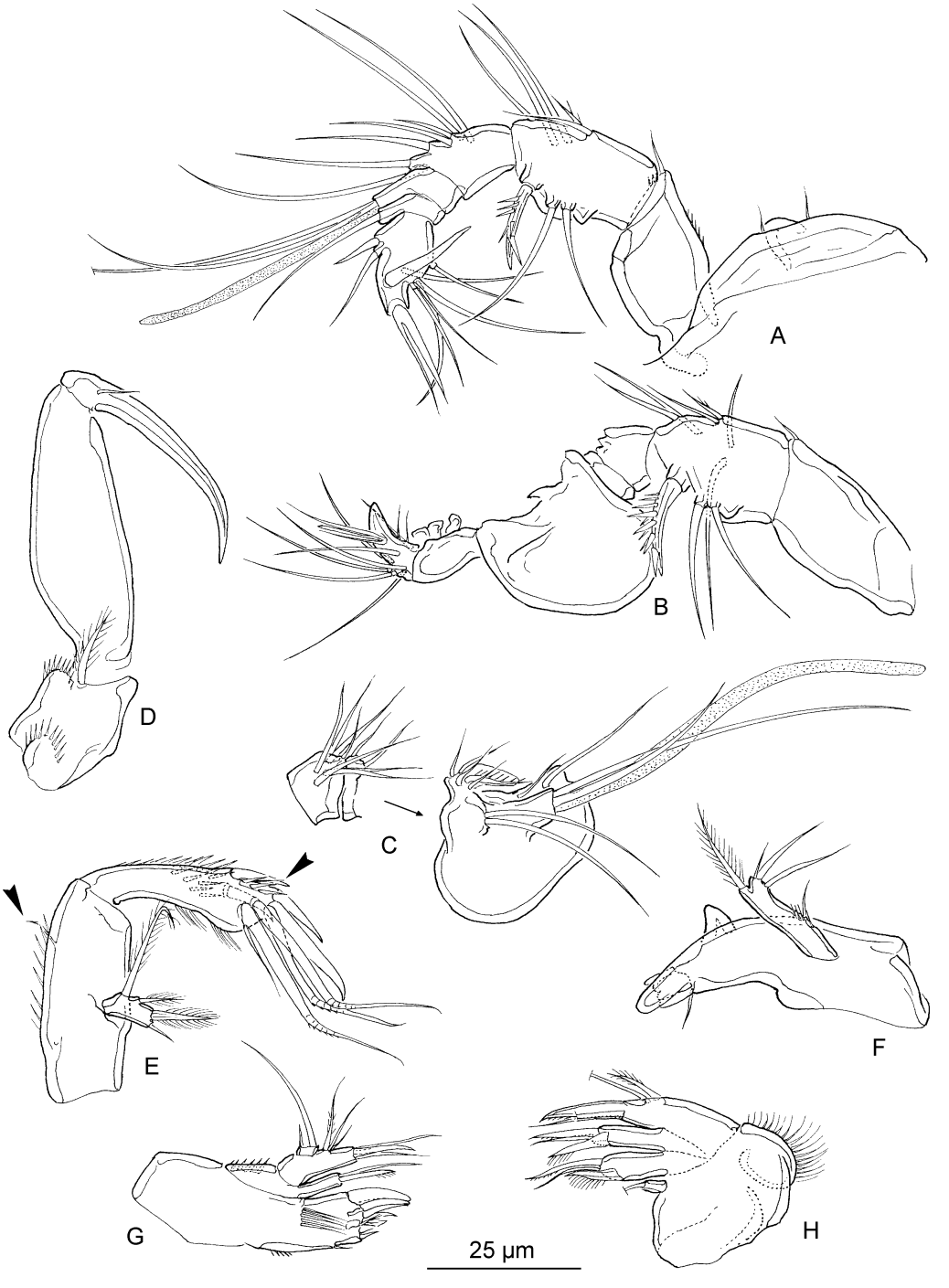

Figure 2. *Tapholeon ornatus* Wells, 1967. (A) Female antennule and rostrum, dorsal; (B) male antennule (armature of segments III, IV, and V omitted), dorsal; (C) male antennule (segments III, IV, and V), ventral; (D) female maxilliped; (E) female antenna (abexopodal seta and small subapical seta on enp arrowed); (F) female mandible; (G) female maxillule; (H) female maxilla. Scale bar in µm.

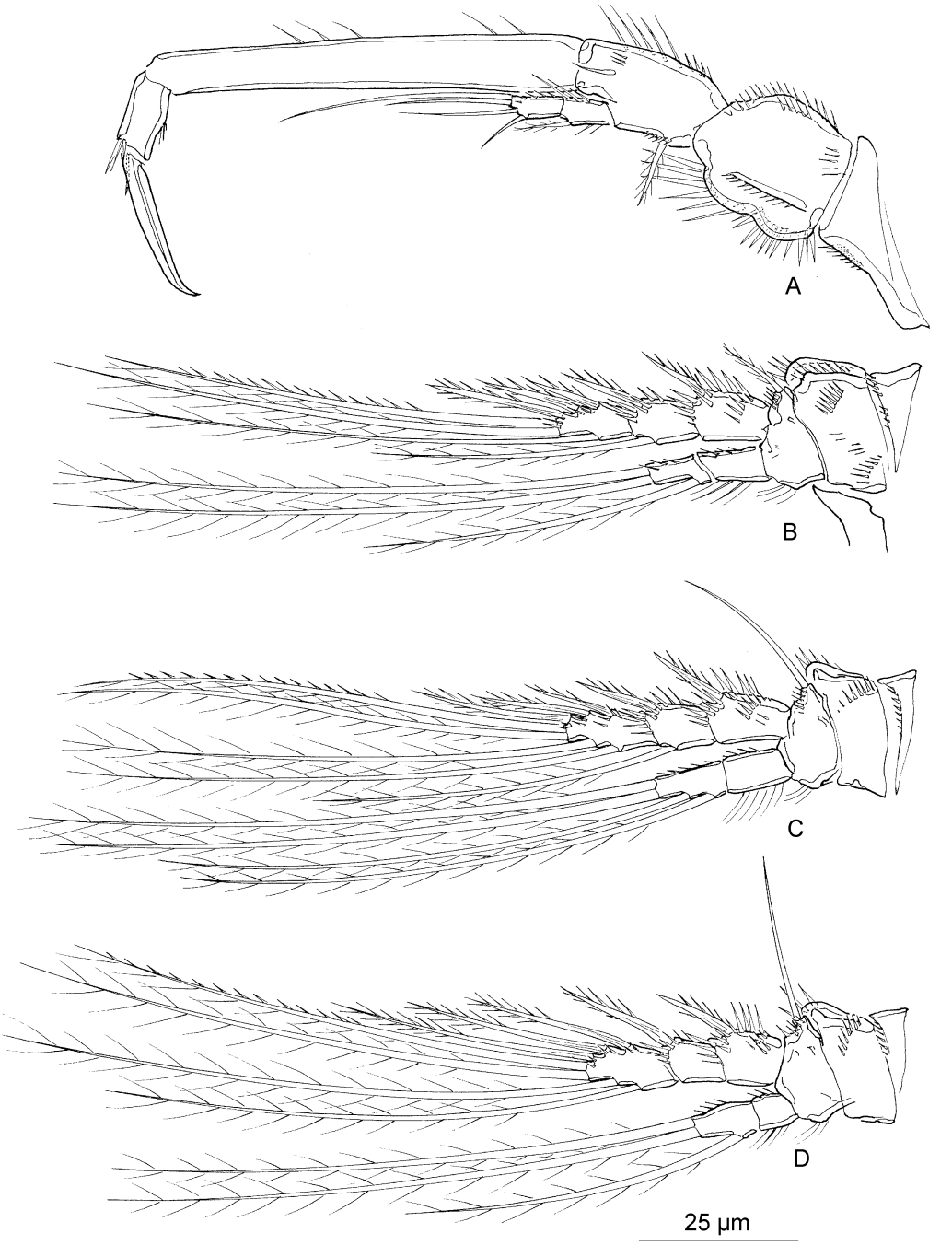

Figure 3. *Tapholeon ornatus* Wells, 1967. (A) Female P1, anterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior. Scale bar in µm.

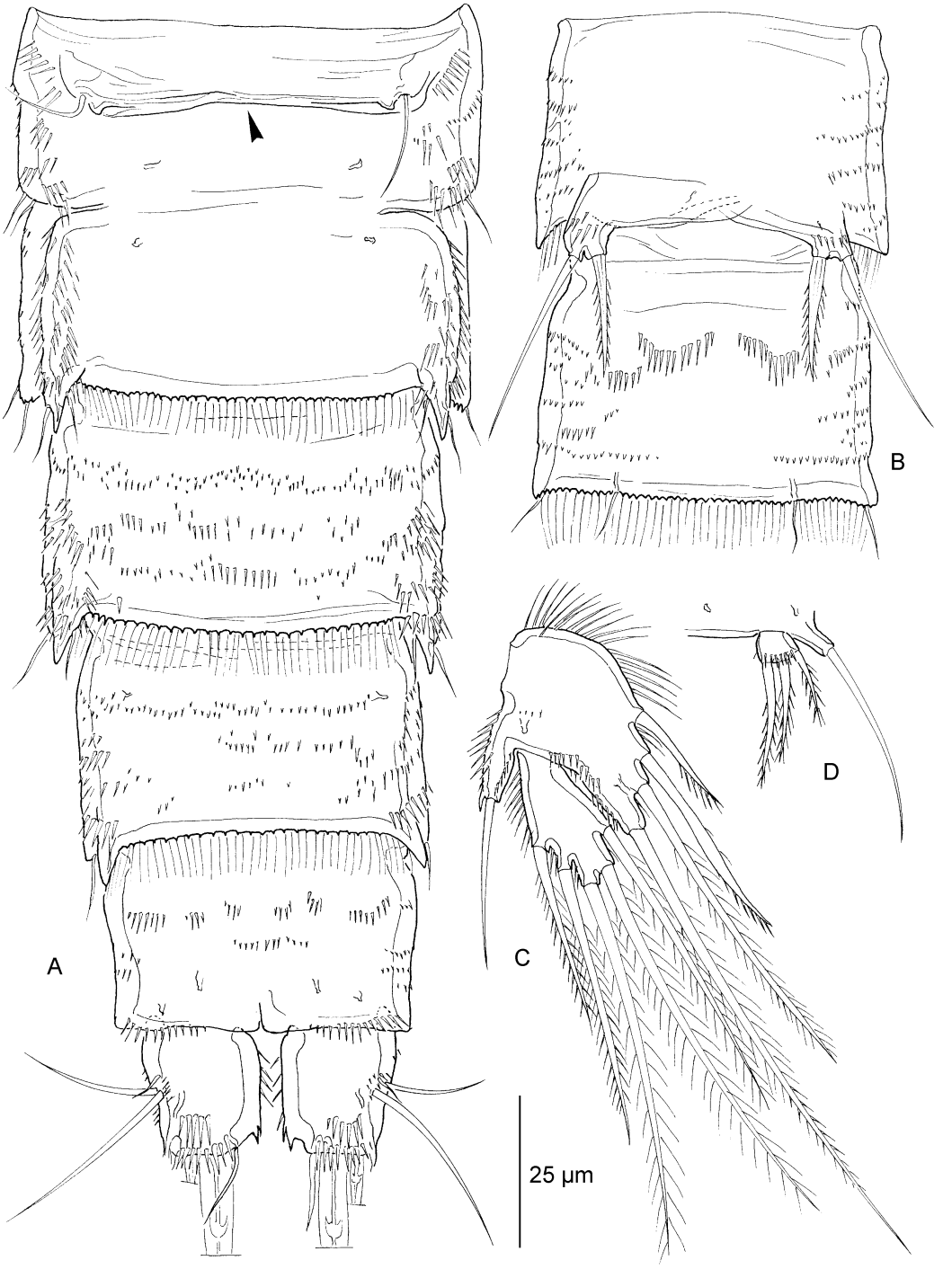

Figure 4. *Tapholeon ornatus* Wells, 1967. (A) Female urosome (copulatory pore arrowed), ventral; (B) male second and third urosomite, ventral; (C) female P5, anterior; (D) male P5, anterior. Scale bar in µm.

Ventral surface (Figure 4A) of genital double-somite smooth. Copulatory pore minute, situated in middle of anterior somite. Ventral surface of following somites clothed with transversely arranged small denticles and spinules. Genital double-somite and following two urosomites laterally with spinules. Ventral surface of caudal rami smooth, with few small spinules laterally and two spinular rows apically. Posteroventral margins of genital double-somite and of following two urosomites slightly serrate, bearing row of slender spinules.

Caudal rami (Figure 5G) slightly flattened; as long as broad. Dorsal surface depressed beyond implantation of seta VII. Dorsal surface covered with small denticles; inner margin bearing transversal rows of spinules along proximal half, with transversal row of strong denticles medially from seta VII. Seta I, II, and III inserted near middle of outer margin; seta VII near middle of ramus. Seta IV and V not fused, both unipinnate; all other setae naked. Seta I rudimentary.

Antennule (Figure 2A) six-segmented; suture between fourth and fifth segment faint. First segment with small spinules along anterior margin. Second segment bearing small blunt process along posterior margin. Majority of setae long and slender; second segment with strong, armed spine along outer margin; ultimate segment bearing two stout setae, one fused basally to slender seta. Armature formula: 1-[1], 2-[8], 3-[7], 4-[1+(1+ae)], 5-[1], 6-[11]. Apical aesthetasc could not be discerned.

Antenna (Figure 2E): allobasis with spinular row along abexopodal side; with one minute abexopodal seta. Exp unisegmented and small, bearing one long plumose seta, two short bipinnate setae, and one small naked seta. Enp with spinular rows and two subapical frills; with following armature: subapically, two spines and one small seta; apically, two strong spines, three geniculate, pinnate setae, and one slender seta.

Mandible (Figure 2F): gnathobase formed by several blunt teeth and one seta. Palp uniramous; endopod and exopod represented by three and one smooth seta(e), respectively. Basal seta plumose.

Maxillule (Figure 2G): praecoxa with arthrite bearing spinular row on posterior surface, medial margin furnished with eight setae/spines. Coxal endite with one seta and one pinnate spine. Basal endite with two naked setae and one curved spine. Endopod obsolete, represented by three setae. Exopod one-segmented with two apical setae.

Maxilla (Figure 2H): syncoxa with three endites; with row of spinules along outer margin. Praecoxal endite small, with one seta. Both coxal endites with one strong, pinnate spine, one slender, naked and one slender, pinnate seta. Allobasis drawn out into slightly curved, distally pinnate claw; bearing two slender setae. Endopod obsolete, represented by two setae.

Maxilliped (Figure 2D): syncoxa with one pinnate seta and two rows of spinules. Endopod claw-shaped, naked; with short naked seta at base.

P1 (Figure 3A): coxa with several spinular rows as figured. Basis with one pinnate seta along outer margin; medial seta arising on anterior surface; long spinules along inner and few, small spinules along outer margin and on anterior surface. Exopod two-segmented; exp-2 bearing four setae. Enp-1 4.5 times as long as exp; with few spinules along inner margin. Enp-2 with spinules along outer margin and distal inner corner; with one smooth claw and one minute, naked accessory seta.

P2–P4 (Figure 3B, C, D): setal formula in Table I. Exopods three-segmented and endopods two-segmented. Praecoxae triangular with distal row of small spinules. Coxae with rows of spinules along outer margin. Bases with spinular row near insertion place of pinnate (P2) or naked (P3–P4) basal seta. Segments of endopods and exopods with pattern of spinules as figured.

P5 (Figure 4C) with separate exopod and baseoendopod. Margins of rami furnished with spinules, surfaces smooth. Baseoendopod reaching to distal fourth of exopod. Basal seta arising from cylindrical setophore, with tube pore proximally and small, spinous process along outer distal margin. Proximal spines of endopodal lobe unipinnate; sub-apical and apical seta plumose. Exopod rhomboid; two times as long as wide; bearing five plumose setae.

P6 vestige (Figure 4A) bearing one seta.

Redescription of male

Total body length 448–480 μm ($n=2$; average=464 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 84 μm. Measurements by Wells (1967): average length 389 μm (range 351–468 μm) (measured from base of rostrum to distal edge of last somite, thus excluding caudal rami).

Habitus as in female; except for fully separated second and third urosomites and lack of lateral extensions in second to fifth urosomites (Figure 4B). Ventral surface of third urosomite with several rows of spinules and small denticles.

Antennule (Figure 2B, C) seven-segmented; sub-chirocer. Shape of first and second segment as in female. Setae on ultimate segment all slender, i.e. without any stout setae as in female. Armature formula: 1-[1], 2-[9], 3-[7], 4-[2], 5-[11+(1+ae)], 6-[0], 7-[9+acrothek]. Apical acrothek consisting of small aesthetasc fused basally to two setae.

Antenna, mouthparts, and P1–P4 as in female.

P5 (Figure 4D): endopodal lobe of P5 obsolete; with tube pore and without seta. Basal seta on setophore, with tube pore proximally. Exopod small; slightly wider than long; bearing three plumose setae. Anterior surface with spinules.

P6 vestiges (Figure 4B) asymmetrical. One vestige functional; one vestige fused to somite. Both produced into cylindrical process bearing one pinnate, strong inner and one naked outer seta.

Amendments

The most important amendment undoubtedly is the presence of two inner setae on exp-3 of P4, instead of one seta as mentioned by Wells (1967). The preparations of the holotype only contained the left P4 (also drawn by Wells), which clearly shows two inner setae on exp-3. Furthermore, a small abexopodal seta is present on the allobasis of the antenna. Drawings were made, based on one female (NHM 2006.1492) and one male paratype (NHM 2006.1494). All characteristics were carefully verified on the female holotype (NHM 1967.8.4.106) and the male paratype (NHM 1967.8.4.107).

Variability

The specimens from the Comoro Islands agree in all aspects with the type specimens from Mozambique.

Differential diagnosis

Species discrimination within *Tapholeon* is mainly based on the chaetotaxy of the swimming legs. *Tapholeon ornatus* bears three outer spines on the ultimate segments of the exopods of

P2–P4, lacks an inner seta on exp-2 of P4, and bears three, four and three setae on the second endopodal segments of P2–P4, respectively. Also, the pleurotergites of the body somites of this species are densely clothed with small denticles, some of which are organized in transversal rows.

Distribution

Inhaca Island, Mozambique (Wells 1967); Grande Comore, Comoro Islands (present study).

Tapholeon arenicolus (Chappuis, 1954) comb. nov.
(Figures 5, 6)

Synonym. Asellopsis arenicola Chappuis, 1954.

Type locality

Comoro Islands, Grande Comore (beach of Mitsamiouli), very fine coral sand, and gravel with coral rubble and shell debris (Chappuis 1954).

Type material

Unknown.

Additional material

Comoros, southeastern coast of Grande Comore, Ouroveni (11°54′S, 43°29′E), small protected creek with mangrove, sample of fine sand, two dissected females (COP 1984, COP 1985), one dissected male (COP 1986), and more than 50 specimens preserved in alcohol (COP 1987); collected 3 August 1984 by Groupe Plongée de l'Expedition Karthala.

Redescription of female

Total body length 354–398 μm (n=10; average=373 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 97 μm. Measurements by Chappuis (1954): 0.4 mm without caudal setae.

Rostrum triangular and prominent; fused to cephalothorax.

Habitus (Figure 5A): body elongate and slender; urosome weakly tapering towards anal somite. Genital double-somite and following urosomite slightly extended laterally. Integument of cephalothorax and pleurotergites with irregular pattern of small denticles. Posterodorsal margin of cephalothorax smooth, of free prosomites smooth along median part but serrate laterally, of all urosomites serrate. Posterodorsal margins of all free somites (except second urosomite) clothed with slender hairs. Anal operculum convex with slightly serrate margin, not protruding.

Ventral surface of genital double-somite and following urosomites smooth. Posteroventral margins of genital double-somite and of next two urosomites with long, slender hairs.

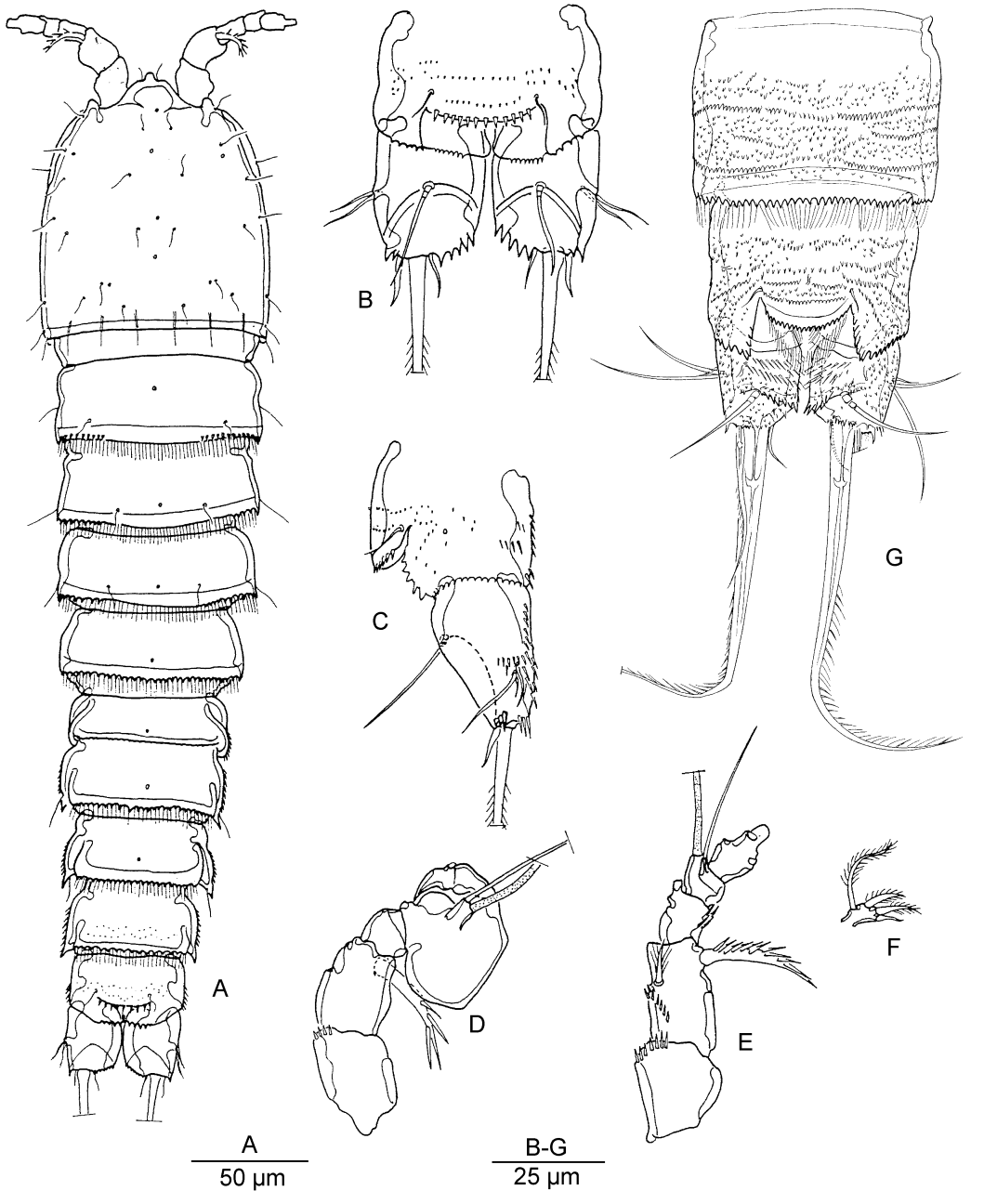

Figure 5. (A–F) *Tapholeon arenicolus* (Chappuis, 1954) comb. nov.: (A) female habitus, dorsal; (B) female caudal rami, dorsal; (C) female caudal rami, lateral; (D) male antennule (armature omitted), ventral; (E) female antennule (armature omitted), ventral; (F) female antennary exopod. (G) *Tapholeon ornatus* Wells, 1967: female anal somite and caudal rami, dorsal. Scale bars in µm.

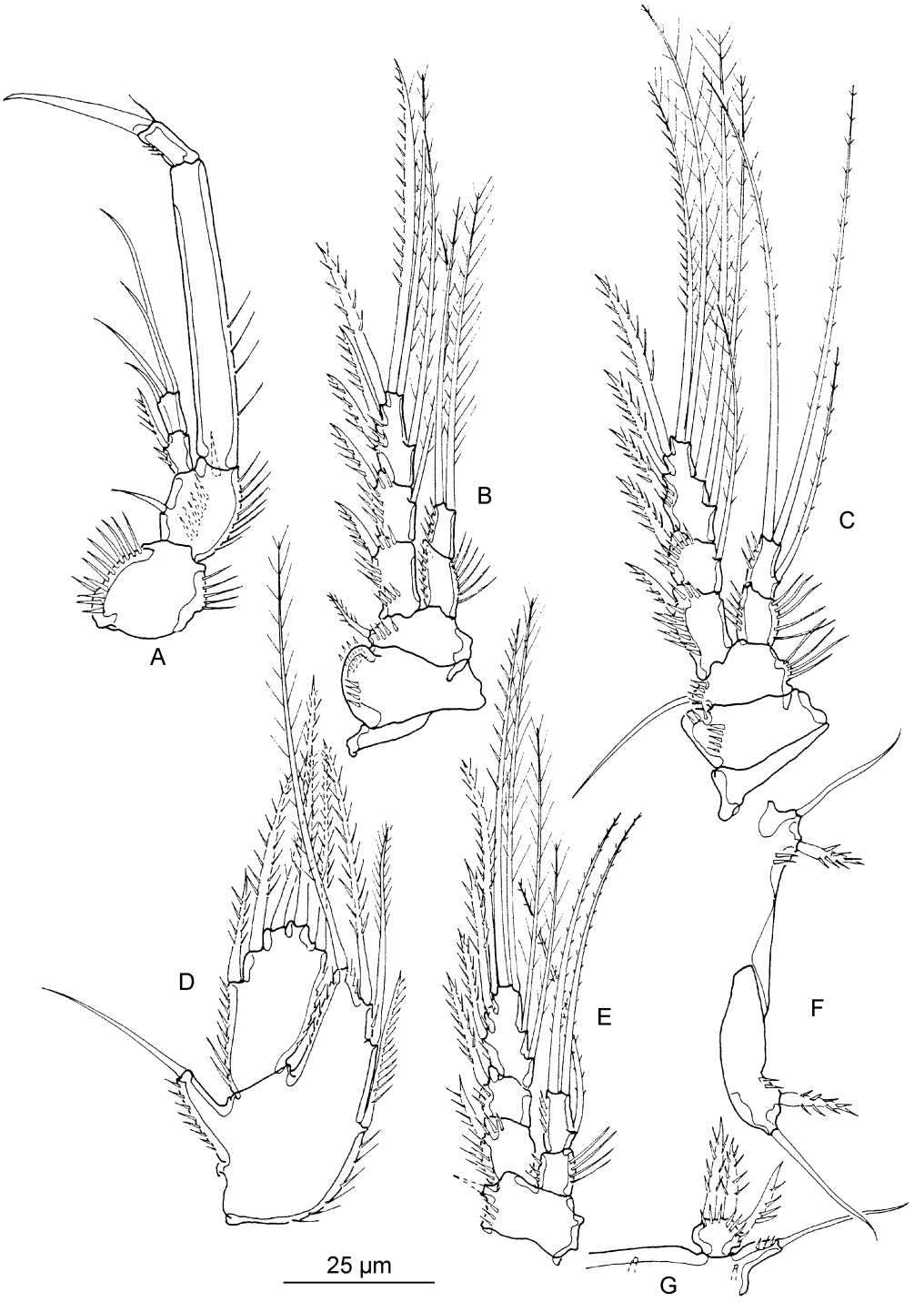

Figure 6. *Tapholeon arenicolus* (Chappuis, 1954) comb. nov. (A) Female P1, posterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P5, anterior; (E) female P4, posterior; (F) male P6, anterior; (G) male P5, anterior. Scale bar in µm.

Caudal rami (Figure 5B, C) flattened; as long as wide, with subquadrate appearance in dorsal view; tapering strongly towards apical margin in lateral view. Surface strongly concave beyond implantation of dorsal seta. Distal inner corner rounded, strongly serrate. Lateral margin spinulose. Seta IV short; seta V about two times length of caudal ramus and pinnate; all other setae naked. Seta VII inserted near middle of ramus.

Antennule (Figure 5E) six-segmented. First, second, and third segment each with row of spinules. Second segment with strong, armed spine along outer margin. Ultimate segment with rounded tip. Armature formula as in type species.

Antenna (Figure 5F) and mouthparts as in type species.

P1 (Figure 6A) with pattern of spinules as figured. Exopod two-segmented; exp-2 bearing four setae. Enp-1 four times as long as exp.

P2–P4 (Figure 6B–D) with three-segmented exopods and two-segmented endopods, with pattern of spinules as figured. Setal formula in Table I.

P5 (Figure 6D) with separate exopod and baseoendopod. Margins of rami furnished with spinules, surface smooth. Baseoendopod reaching beyond middle of exopod; bearing one apical and three lateral setae. Exopod ovate; two times as long as wide; bearing five setae.

P6 vestige bearing one seta.

Redescription of male

Total body length 346–384 μm ($n=10$; average=362 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 88 μm. Habitus as in female; except for fully separated second and third urosomites and lack of lateral extensions in second to fourth urosomites. Ventral surface of third urosomite with transversal row of large spinules.

Antennule (Figure 5D) sub-chirocer. Shape of first and second segment as in female. Armature formula as in type species.

Antenna, mouthparts, and P1–P4 as in female.

P5 (Figure 6G): endopodal lobe obsolete; without seta. Exopod small; bearing three strongly armed setae.

P6 vestiges (Figure 6F) asymmetrical; each bearing a plumose inner and a naked outer seta.

Remarks

Chappuis (1954) assigned this species to the genus *Asellopsis* Brady and Robertson, 1873 because of the remarkably flattened (asellopsiform) caudal rami. Also, at the time of description the genus *Tapholeon* had not been established. However, Chappuis (1954) made no reference to a three-segmented endopod P3 in the male, but only mentioned a slightly shorter inner seta on the second endopodal segment of this leg. In the present material, neither a three-segmented male endopod nor a differentiated seta was found. Therefore, *A. arenicola* should be excluded from the genus *Asellopsis*, which typically displays pronounced sexual dimorphism in the third leg. Fortunately, Chappuis (1954) illustrates the peculiar seta on the second antennular segment. The thickened antennular seta, the lack of sexually dimorphic structures in the legs, and the strongly reduced shape of the P5 in the male clearly indicate that *A. arenicola* must be transferred to the genus *Tapholeon*. Other differences with the original decription are: P1 exopod with four setae on the second segment, instead of three as shown by Chappuis (1954); the much longer setae

(reaching far beyond the exopod) of the endopods of P2–P4; the presence of an inner seta on exp-2 of P3 and the plumose setae on the rami of the P5.

Differential diagnosis

The present species bears three outer spines on the ultimate segments of the exopods of P2–P4, lacks an inner seta on exp-2 of P4, and bears two, three and three setae on the second endopodal segments of P2–P4, respectively.

Distribution

Grande Comore, Comoros (Chappuis 1954; present report).

Tapholeon chappuisius (Krishnaswamy, 1957) comb. nov.
Synonym. Asellopsis chappuisius Krishnaswamy, 1957.

Type locality

India, Madras: Mandapam, sandy beach (Krishnaswamy 1957).

Type material

Unknown.

Diagnosis

Body strongly tapering towards caudal rami. Caudal rami slightly longer than wide. Antennule five-segmented. Antennary exopod well developed bearing three (?) setae. P1 with two-segmented exopod; exp-2 bearing three (?) setae. Exp-2 of P2–P4 with inner seta. Exp-3 of P2 with one inner seta and two outer spines; exp-3 of P3 and P4 each with two inner setae and two outer spines. Enp-2 of P2–P4 with only two apical setae each. Female P5 with four baseoendopodal and five exopodal setae. Baseoendopod reaching almost to distal margin of exopod. Exopod ovate, about two times as long as wide. Male swimming legs P1–P4 as in female. Endopodal lobe of male P5 without seta. Exopod small; bearing four setae.

Length of female: 1.2 mm (Krishnaswamy 1957), 0.56 mm (Rao and Ganapati 1969). Length of male: 0.9–1 mm (Krishnaswamy 1957).

Remarks

For the same reason as mentioned for *T. arenicolus* (Chappuis, 1954) comb. nov., Krishnaswamy (1957) assigned this species to the genus *Asellopsis* Brady and Robertson, 1873. However, *A. chappuisius* must be allocated to the genus *Tapholeon* because of the lack of sexual dimorphic structures in the swimming legs. The presence of an armed, strong spine on the second segment of A1 might have been overlooked. The lack of type material however prevented verifying this.

Several comments on the species description by Krishnaswamy (1957) are necessary. The antennule is described as being five-segmented. The faint suture, separating segment four and five (as seen in the type species), might have been missed and, therefore, the

antennule might be six-segmented. The drawing of the exopod of the antenna shows only three setae. In the species of the genus *Tapholeon*, one seta of the antennary exopod is very slender and small, and can easily be overlooked. A much more important problem arises in the enumeration of the legs. The figure of the P4 (Krishnaswamy 1957) undoubtedly illustrates the P2 of this species. P4 has two inner setae on the last exopodal segment in the majority of the species and never has an endopod reaching to the apical edge of the second exopodal segment. Consequently, the figure of P2 must be another leg and seems to represent P3 because: (1) the third exopodal segment bears two inner setae and (2) the endopod reaches to the middle of the second exopodal segment. The description of P2 has to be considered as the description of the P4. This amendment results in an entirely different setal formula as given in Table I.

Most curiously, Rao and Ganapati (1969) follow Krishnaswamy (1957) in their redescription of *T. chappuisius*. However, the drawings given by Rao and Ganapati (1969, Figure 16) appear to be duplicates from the original ones.

Differential diagnosis

T. chappuisius comb. nov. bears two outer spines on the ultimate segments of the exopods of P2–P4 and only bears two apical setae on the second endopodal segments of P2–P4.

Distribution

Madras (Krishnaswamy 1957) and Waltair (Rao and Ganapati 1969), both in the Bay of Bengal.

Tapholeon inconspicuus Gheerardyn and Fiers sp. nov.
(Figures 7–9)

Type locality

Western Indian Ocean, Kenyan coast, Wasini Island (4°40′S, 39°23′E), red (terrigenous?) sediment, water depth 3–4 m.

Material

From type locality: one female holotype dissected on four slides (COP 4734a–d); one male allotype dissected on three slides (COP 4735a–c); one male and one female paratype preserved in 70% alcohol (COP 4736); collected 28 February 2002 by M. Raes.

Etymology

The specific name *inconspicuus* (Latin meaning inconspicuous) refers to the low occurrence of this species in a sample with a high number of *Tapholeon tenuis* sp. nov.

Description of female

Total body length 389–415 μm ($n=2$; average=402 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 97 μm.

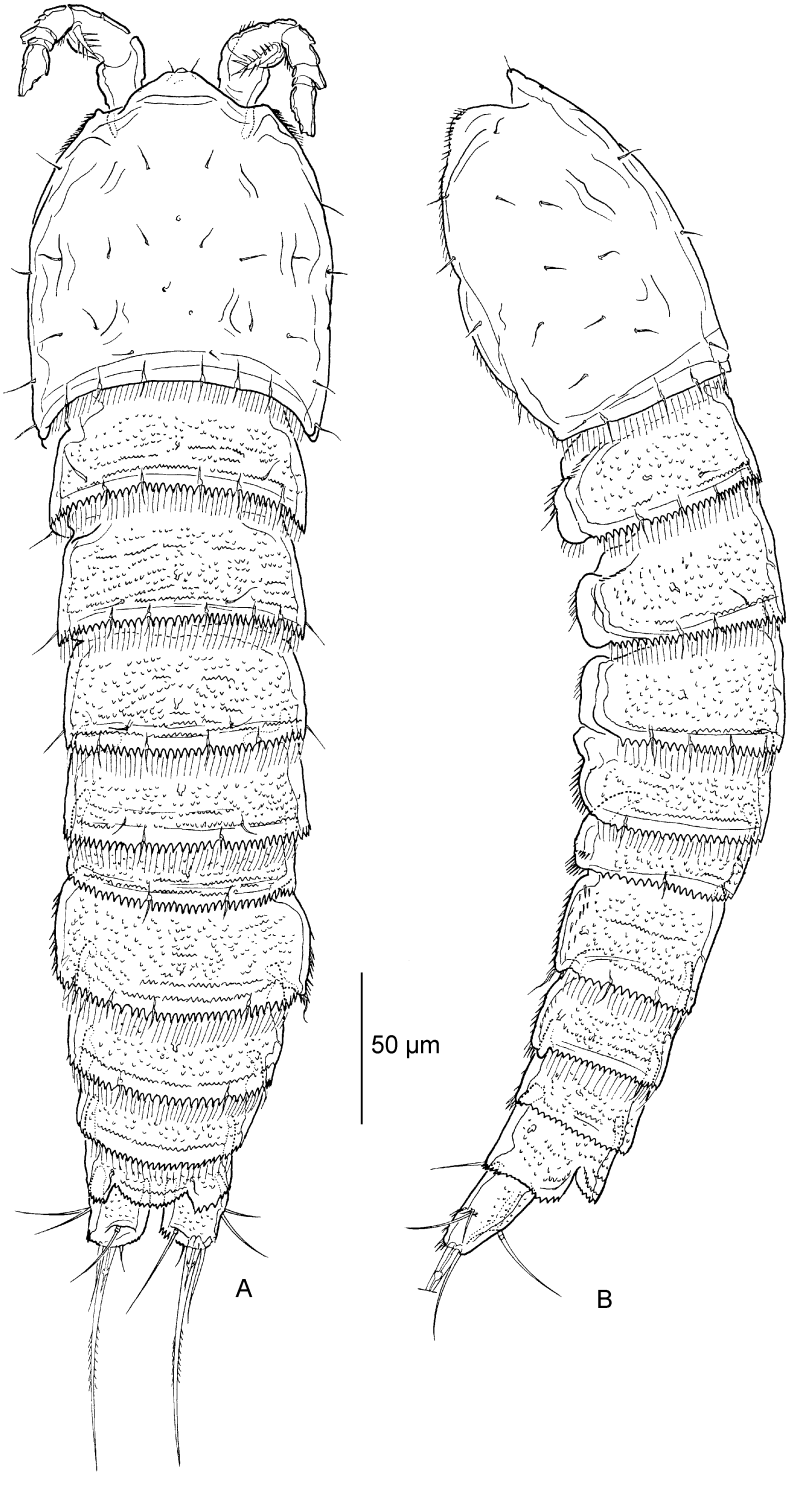

Figure 7. *Tapholeon inconspicuus* Gheerardyn and Fiers sp. nov. (A) Female habitus, dorsal; (B) female habitus, lateral. Scale bar in µm.

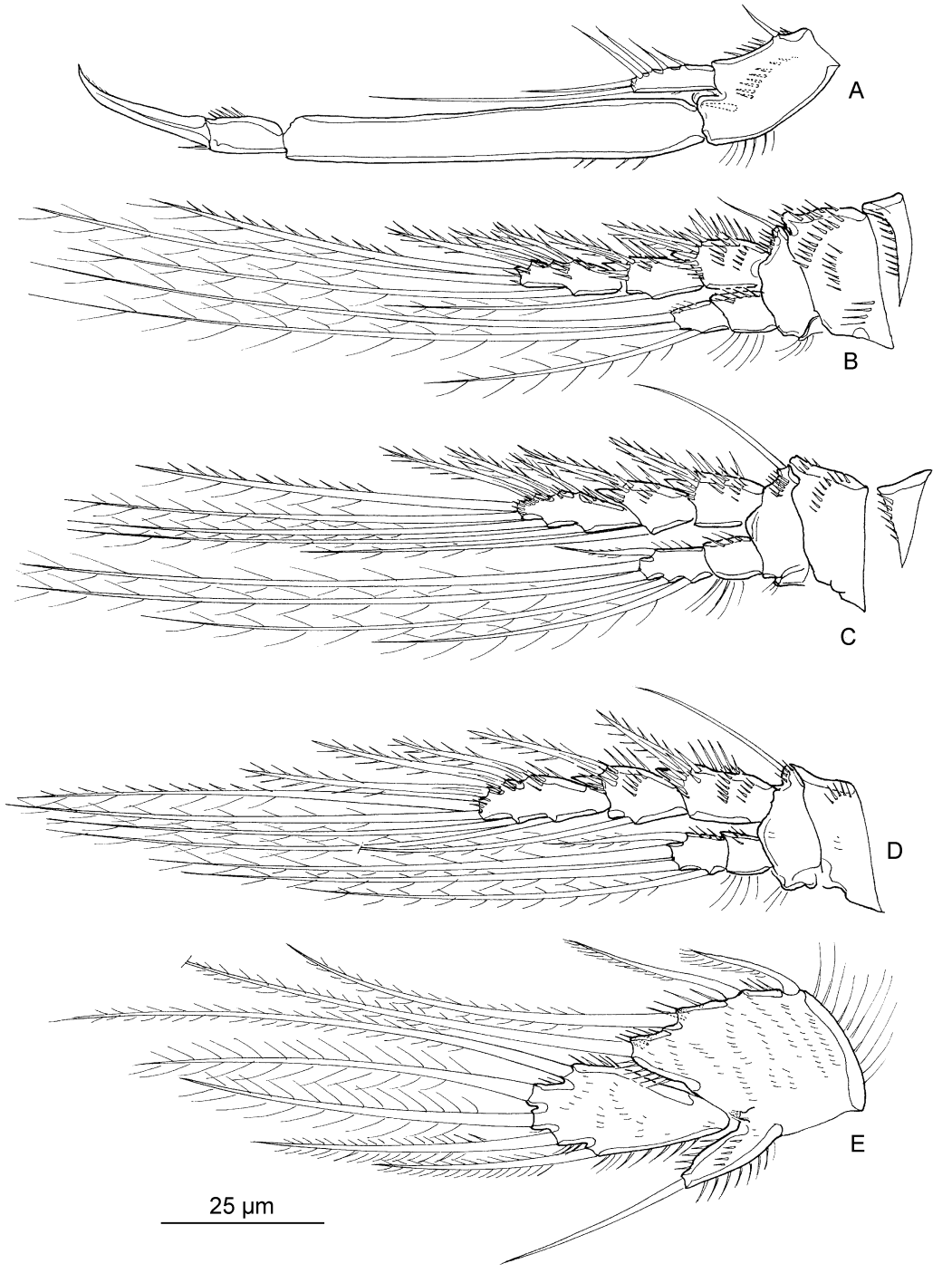

Figure 8. *Tapholeon inconspicuus* Gheerardyn and Fiers sp. nov. (A) Female P1, posterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior; (E) female P5, anterior. Scale bar in µm.

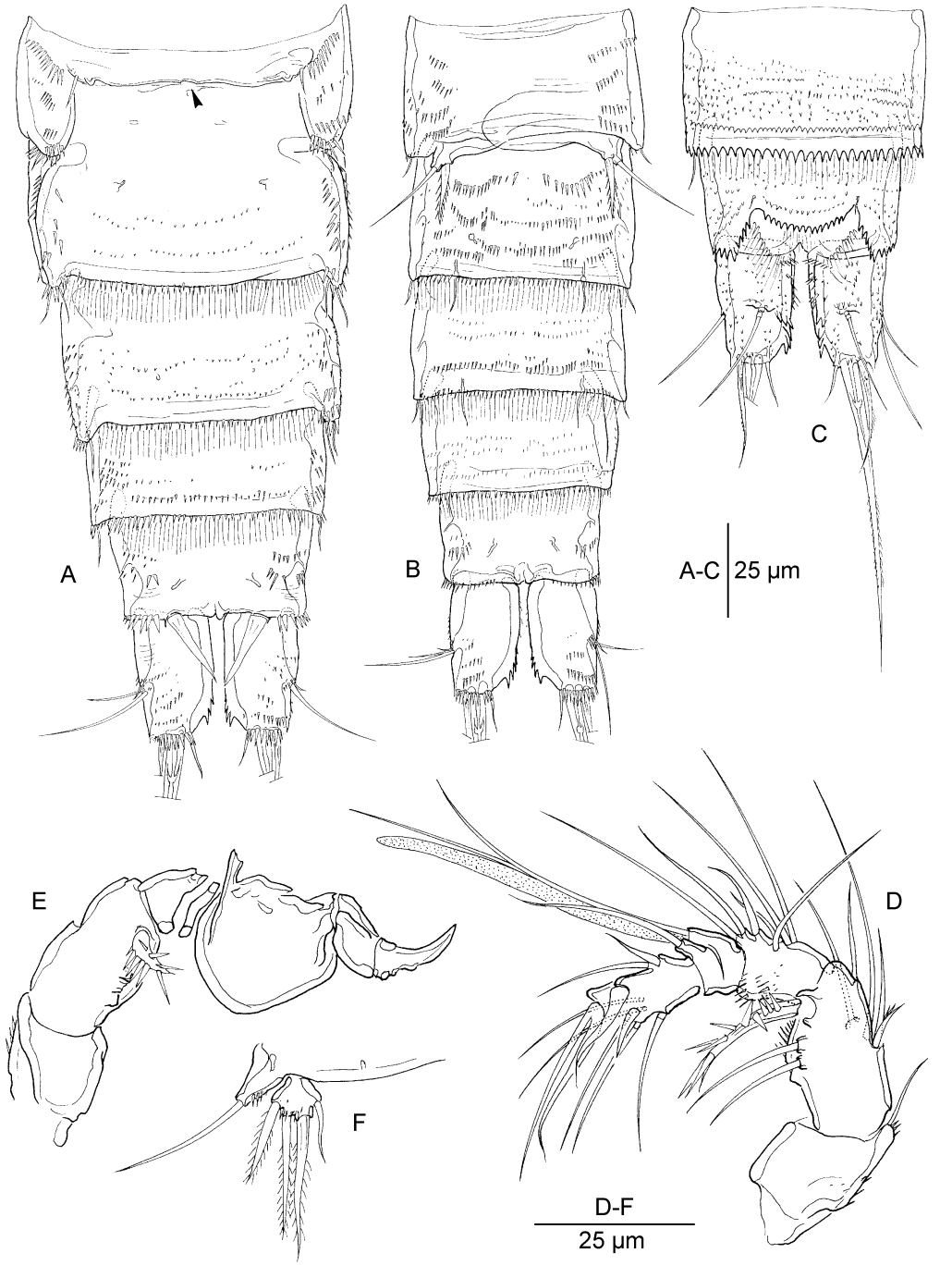

Figure 9. *Tapholeon inconspicuus* Gheerardyn and Fiers sp. nov. (A) Female urosome (copulatory pore arrowed), ventral; (B) male urosome, ventral; (C) female anal somite and caudal rami, dorsal; (D) female antennule, dorsal; (E) male antennule (armature omitted), dorsal; (F) male P5, anterior. Scale bars in µm.

Habitus (Figure 7A, B) elongate, somewhat more robust; slightly dorso-ventrally depressed; with distinct convex curvature in lateral aspect. Genital double-somite and following urosomite slightly extended laterally. Integument of cephalothorax smooth; regularly ornamented with small sensilla. Pleurotergites of prosomites and urosomites and dorsal surface of anal somite clothed with irregular pattern of small denticles, some of which arranged in transversal rows. Posterodorsal margin of cephalothorax smooth, of all free somites strongly serrate. Posterodorsal margins of cephalothorax and free somites (except second urosomite) with long slender hairs, all bearing number of sensilla (not in penultimate urosomite). Anal operculum convex with slightly serrate margin, not protruding.

Ventral surface (Figure 9A) of genital double-somite smooth in anterior half, bearing small spinules in posterior half. Copulatory pore minute, situated in middle of anterior somite. Ventral surface of following two urosomites with rows of small spinules. Genital double-somite and following two urosomites laterally with spinules. Anal somite ventrally smooth, laterally with few spinules. Ventral surface of caudal rami with few rows of small spinules. Posteroventral margins of genital double-somite and of following two urosomites bearing row of small spinules and clothed with long slender hairs. Posteroventral margin of anal somite with row of spinules; one pair of spinules very long (two-thirds length of caudal ramus) and flattened.

Caudal rami (Figure 9C) flattened; 1.5 times as long as wide; not touching each other along inner margin. Dorsal surface covered with small denticles; inner margin with small spinules along proximal half. Distal half of inner margin strongly serrate. Seta I, II, and III inserted just beyond middle of outer margin, seta VII near middle of ramus. Seta IV and V not fused, both pinnate; all other setae naked. Seta I rudimentary.

Antennule (Figure 9D) six-segmented; suture between fourth and fifth segment incomplete. Second segment bearing small blunt process along outer margin. Majority of setae long and slender; second segment with strong, armed spine near outer margin; certain setae on ultimate segment short and stout. Armature formula as in type species.

Antenna and mouthparts as in type species.

P1 (Figure 8A): exopod one-segmented, bearing six setae. Enp-1 five times as long as exp.

P2–P4 (Figure 8B–D) with three-segmented exopods and two-segmented endopods. Exp-1 and exp-2 equal in length; exp-3 slightly longer. Pattern of spinules as figured. Setal formula in Table I.

P5 (Figure 8E) with separate exopod and baseoendopod. Margins and surface of rami with spinules. Baseoendopod reaching to middle of exopod; bearing one apical and three lateral setae. Exopod ovate; two times as long as wide; bearing five setae.

P6 vestige (Figure 9A) bearing one seta.

Description of male

Total body length 389–402 μm ($n=2$; average=396 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 84 μm.

Habitus as in female; except for fully separated second and third urosomites and lack of lateral extensions in second to fourth urosomites (Figure 9B). Ventral surface of third urosomite densely covered with several rows of spinules. Posteroventral margin

of anal somite with row of small spinules, i.e. without pair of very long spinules as in female.

Antennule (Figure 9E) seven-segmented; sub-chirocer. Shape of first and second segment as in female.

Antenna, mouthparts, and P1–P4 as in female.

P5 (Figure 9F): endopodal lobe of P5 obsolete; without seta. Exopod small; slightly wider than long; bearing one naked and three plumose seta(e).

P6 vestiges (Figure 9B) asymmetrical; each bearing one plumose inner and one naked outer seta.

Variability

The holotype has an aberrant right P3 exopod (0.1.222). The drawing of P3 was made from the female paratype.

Differential diagnosis

The present species exhibits an unusual type of sexual dimorphism, i.e. in the female the posteroventral margin of the anal somite bears a pair of very long (two-thirds length of caudal ramus) and flattened spinules. In the male, these modified spinules are absent. Furthermore, this species has a one-segmented exopod in P1 and bears three outer spines on the ultimate segments of the exopods of P2–P4.

Distribution

Wasini Island, Kenyan coast (present study).

Tapholeon tenuis Gheerardyn and Fiers sp. nov.
(Figures 10–12)

Type locality

Western Indian Ocean, Kenyan coast, Wasini Island (4°40′S, 39°23′E), red (terrigenous?) sediment, water depth 3–4 m.

Material

From type locality: one female holotype dissected on four slides (COP 4737a–d); one male allotype on one slide (COP 4738); two female and three male paratypes dissected on slides (COP 4739–4743), and numerous female and male paratypes preserved in 70% alcohol (COP 4744); collected 28 February 2002 by M. Raes.

From Western Indian Ocean: different locations along Kenyan coast [Diani Beach (4°18′S, 39°35′E), Kisite Island (4°40′S, 39°22′E)], coral sand, water depth from less than 0.5 m to 6 m, three female and four male paratypes (COP 4745) and seven female and 16 male paratypes (COP 4746) preserved in 70% alcohol; collected February 2002 by M. Raes.

Etymology

The specific name *tenuis* (Latin meaning slender) refers to the slender body shape.

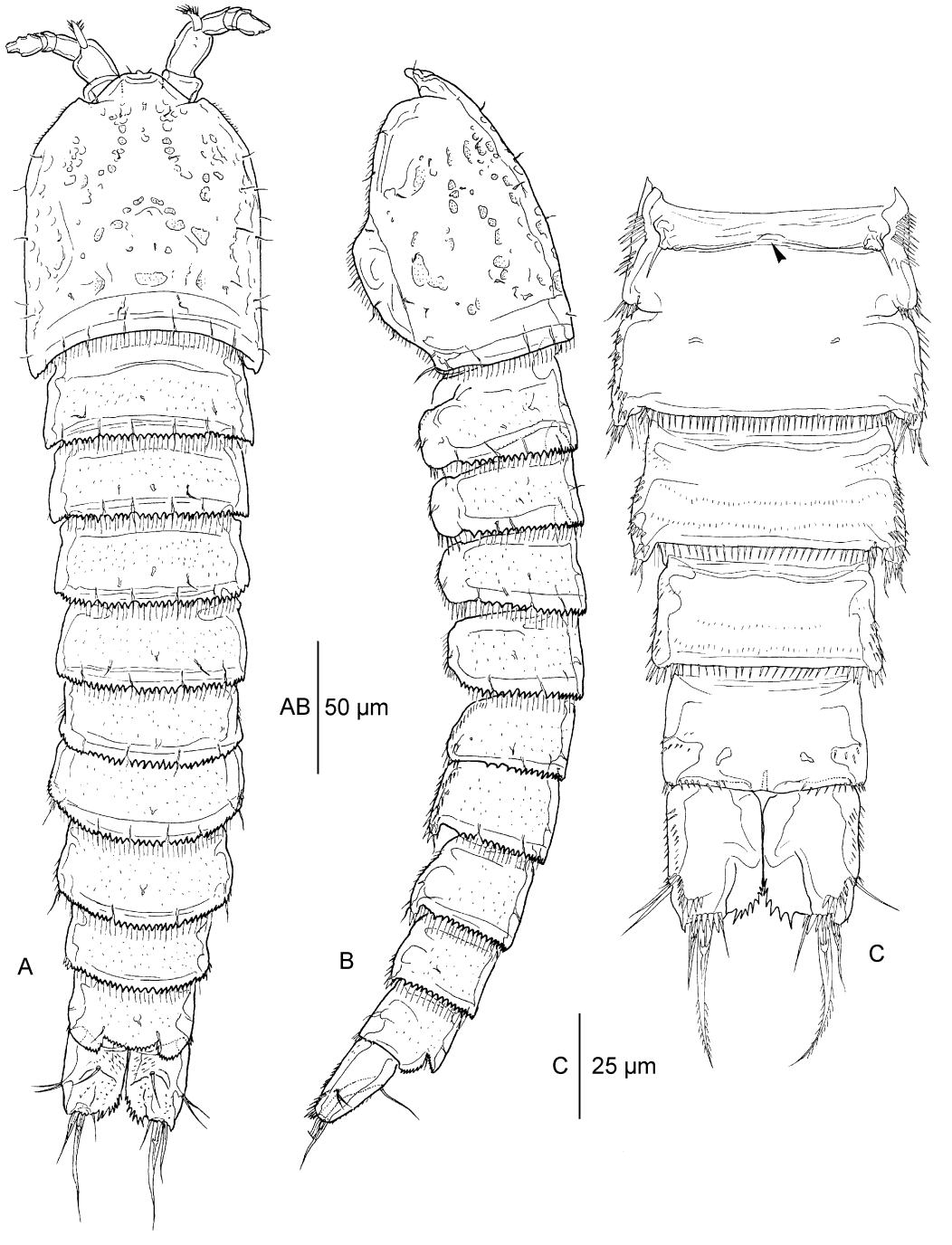

Figure 10. *Tapholeon tenuis* Gheerardyn and Fiers sp. nov. (A) Female habitus, dorsal; (B) female habitus, lateral; (C) female urosome (copulatory pore arrowed), ventral. Scale bars in µm.

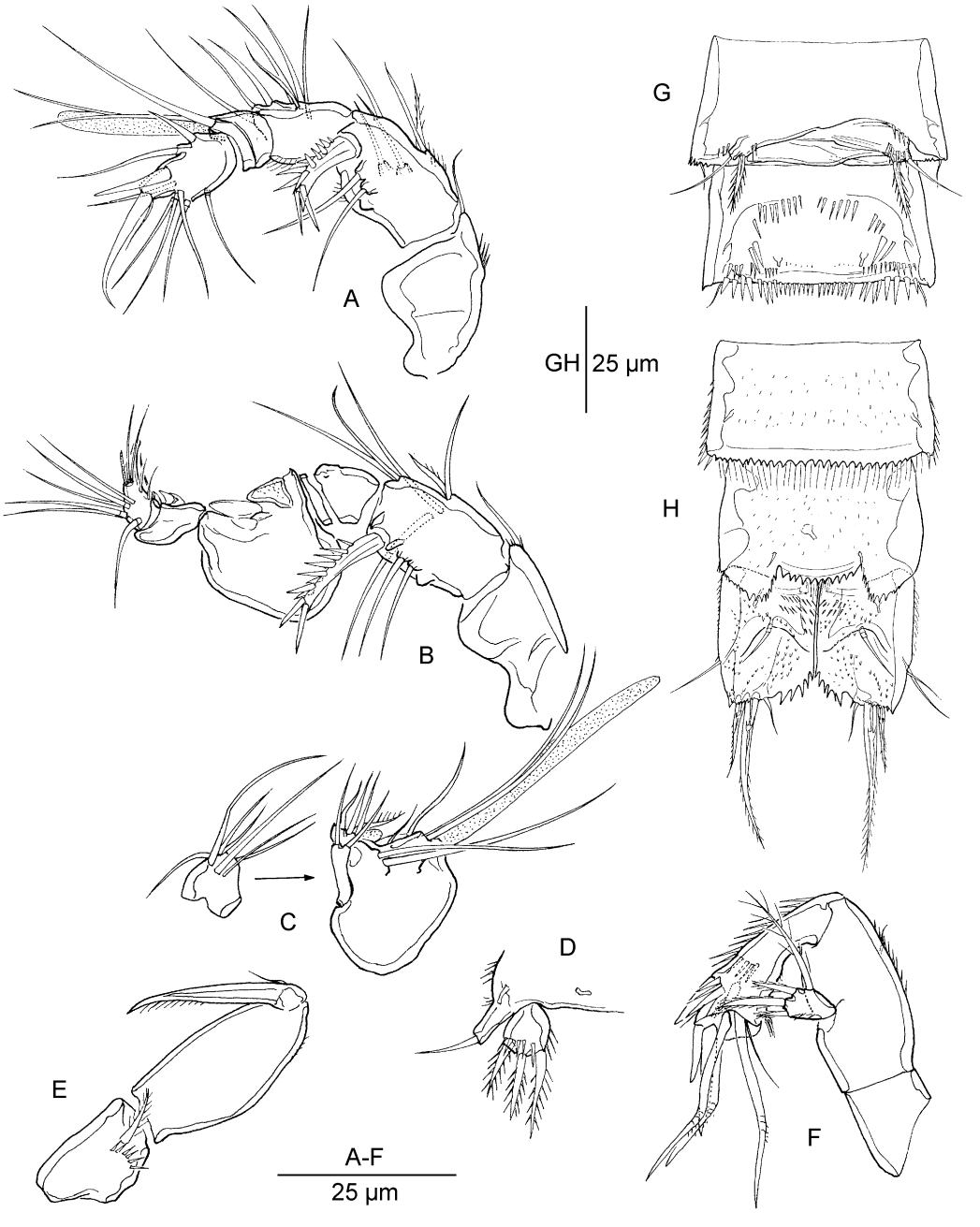

Figure 11. *Tapholeon tenuis* Gheerardyn and Fiers sp. nov. (A) Female antennule, dorsal; (B) male antennule (armature of segments III, IV, and V omitted), dorsal; (C) male antennule (segments III, IV, and V), ventral; (D) male P5, anterior; (E) female maxilliped; (F) female antenna; (G) male second and third urosomite, ventral; (H) female anal somite and caudal rami, dorsal. Scale bars in µm.

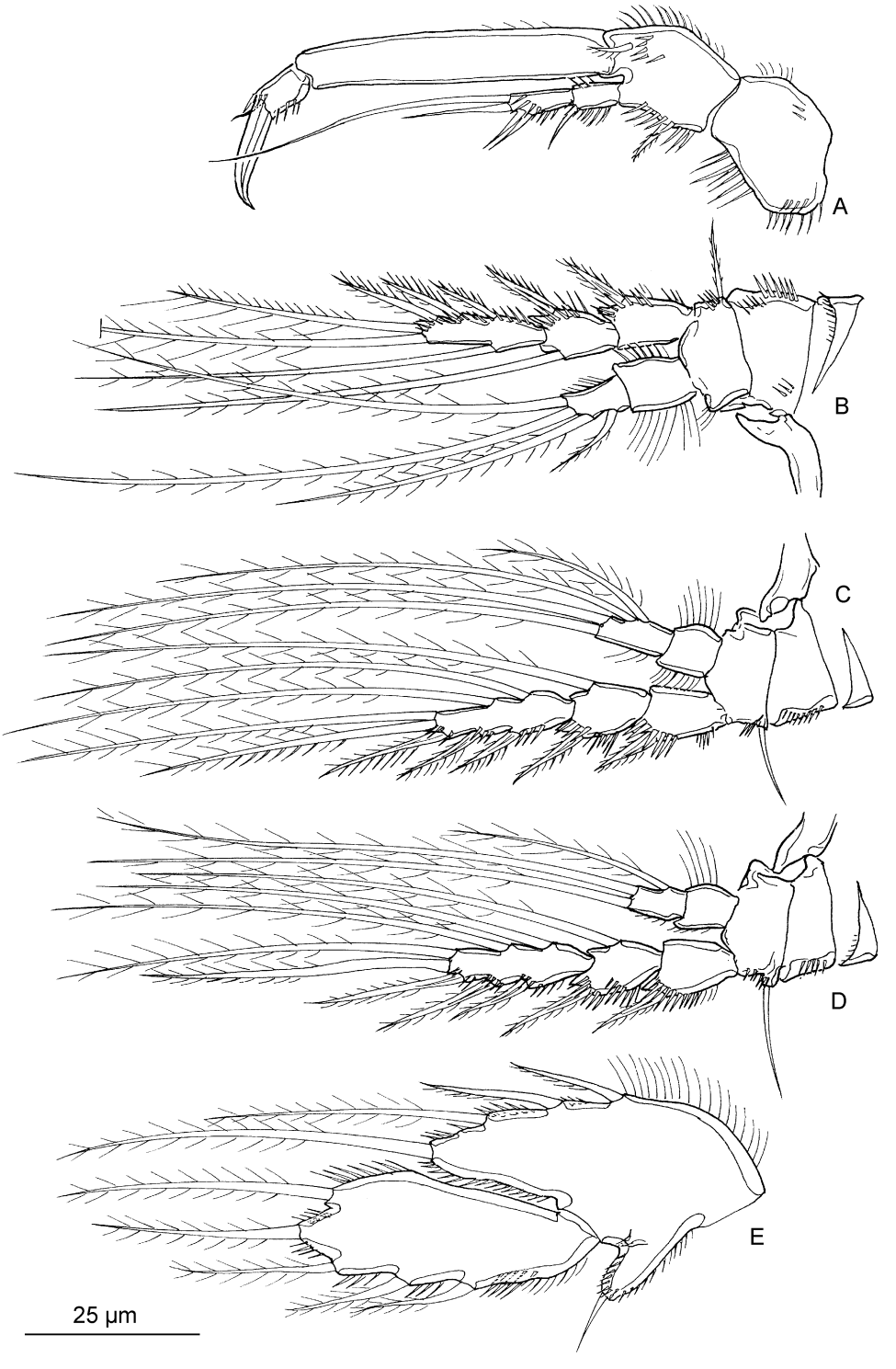

Figure 12. *Tapholeon tenuis* Gheerardyn and Fiers sp. nov. (A) Female P1, anterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior; (E) female P5, anterior. Scale bar in µm.

Description of female

Total body length 354–413 μm (n=10; average=386 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 90 μm.

Rostrum (Figure 10A) broad triangular; fused to cephalothorax.

Habitus (Figure 10A, B) elongate and slender; slightly dorso-ventrally depressed; with distinct convex curvature in lateral aspect. Genital double-somite and following urosomite slightly extended laterally. Second and third urosomite fused to form genital double-somite. Integument of cephalothorax with pattern of relatively large pits; regularly ornamented with small sensilla. Pleurotergites of prosomites and urosomites and dorsal surface of anal somite with irregular pattern of very small denticles. Posterodorsal margin of cephalothorax smooth, of all free somites strongly serrate. Posterodorsal margins of cephalothorax and free somites (except second urosomite) clothed with slender hairs, all bearing number of sensilla (not in penultimate urosomite). Anal operculum convex with slightly serrate margin, not protruding.

Ventral surface (Figure 10C) of genital double-somite smooth. Copulatory pore minute, situated in middle of anterior somite. Ventral surface of following two somites each bearing two rows of very small spinules. Genital double-somite and following two urosomites laterally with spinules. Anal somite smooth ventrally, laterally with few spinules. Ventral surface of caudal rami smooth, with some spinules laterally and two spinular rows apically. Posteroventral margins of genital double-somite and of following urosomites bearing row of spinules.

Caudal rami (Figure 11H) flattened; slightly longer than broad; meeting each other along inner margin. Dorsal surface strongly concave beyond implantation of seta VII. Dorsal surface covered with small denticles; inner margin bearing spinules along proximal half. Distal inner corner rounded and strongly serrate. Seta I, II, and III inserted in distal fourth of outer margin, seta VII near middle of ramus. Seta IV and V not fused, both pinnate and short; all other setae naked. Seta I rudimentary.

Antennule (Figure 11A) six-segmented. First segment with spinules along anterior margin. Second segment bearing small blunt process along posterior margin, and spinules along anterior and posterior margins. Third segment with spinules along posterior margin. Majority of setae long and slender; second segment with strong, armed spine inserted near posterior margin; ultimate segment bearing two stout setae. Armature formula as in type species.

Antenna (Figure 11F): allobasis with one minute abexpodal seta. Exp unisegmented and small, bearing three short bipinnate setae and one long plumose seta. Armature of endopod as in type species.

Mouthparts as in type species.

Maxilliped (Figure 11E): syncoxa with one pinnate seta and a row of spinules. Basis with few spinules along outer margin. Endopod claw-shaped, distally pinnate, with short naked seta at base.

P1 (Figure 12A): exopod two-segmented; exp-2 bearing four setae. Enp-1 three times as long as exp.

P2–P4 (Figure 12B, C, D) with three-segmented exopods and two-segmented endopods. Exp-1 and exp-2 equal in length; exp-3 slightly longer. Segments of endopods and exopods with pattern of spinules as figured. Setal formula in Table I.

P5 (Figure 12E) with separate exopod and baseoendopod. Margins of rami furnished with spinules, surface smooth. Baseoendopod reaching slightly beyond middle of exopod;

bearing one apical and three lateral setae. Exopod ovate; 2.5 times as long as wide; bearing five plumose setae.

P6 vestige (Figure 10C) bearing one seta.

Description of male

Total body length 320–394 μm (n=10; average=356 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 76 μm.

Habitus as in female; except for fully separated second and third urosomites and lack of lateral extensions in second to fourth urosomites (Figure 11G). Ventral surface of third urosomite with several short rows of strong spinules.

Antennule (Figure 11B, C) eight-segmented; sub-chirocer. Shape of first and second segment as in female. Setae on ultimate segment all slender, i.e. without any stout setae as in female. Armature formula: 1-[1], 2-[9], 3-[7], 4-[2], 5-[10(?)+(1+ae)], 6-[0], 7-[1], 8-[8+acrothek]. Apical acrothek consisting of small aesthetasc fused basally to two setae.

Antenna, mouthparts, and P1–P4 as in female.

P5 (Figure 11D): endopodal lobe of P5 obsolete; without seta. Exopod small; about as long as wide; bearing three plumose setae. Inner margin and anterior surface with spinules.

P6 vestiges (Figure 11G) asymmetrical; each bearing one plumose, strong inner and one naked outer seta.

Variability

Some male and female paratypes have a right or left P2 enp with an aberrant setal formula (0.120), the opposite side consistently having a normal setal formula. Two female paratypes were found with an aberrant right and left P2 enp (0.120). One female paratype bears an aberrant P3 enp (0.120) on the left side; one other female paratype has an aberrant P3 exp (0.1.123) on the left side.

Differential diagnosis

The present species bears three outer spines on the ultimate segments of the exopods of P2–P4 and bears four, four and three setae on the second endopodal segments of P2–P4, respectively.

Distribution

Different locations along the Kenyan coast (present study).

Tapholeon uniarticulatus Wells, 1967
(Figure 13)

Type locality

Mozambique, Inhaca Island: Marine Station beach (detritus sand and grass) and off Barriera Vermelha beach (detritus sand) at a depth of 5 m (Wells 1967).

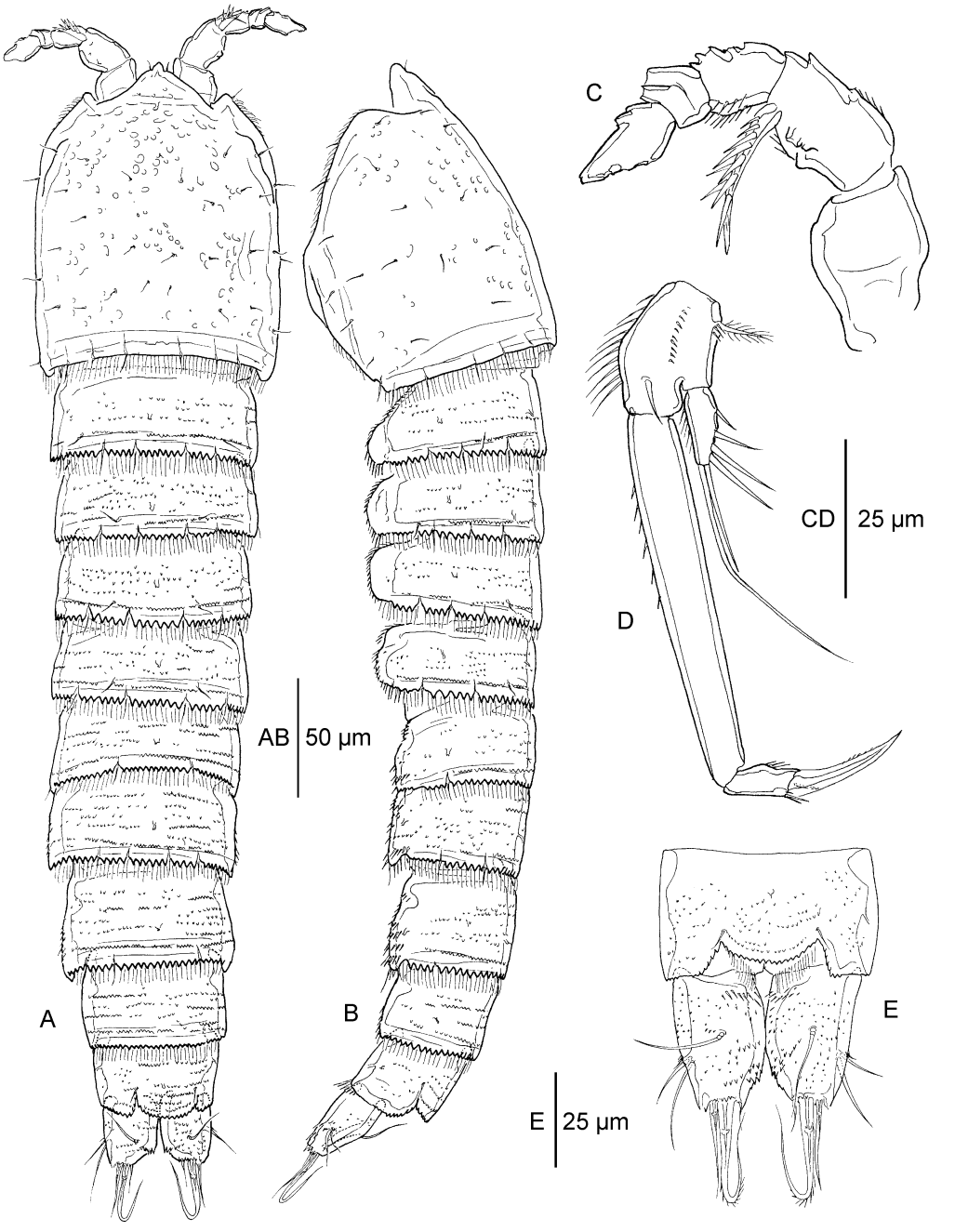

Figure 13. *Tapholeon uniarticulatus* Wells, 1967 (A) Female habitus, dorsal; (B) female habitus, lateral; (C) female antennule (armature omitted), dorsal; (D) female P1, anterior; (E) female anal somite and caudal rami, dorsal. Scale bars in µm.

Type material

Types are deposited in the collections of the British Museum of Natural History, London (Wells 1967).

Material examined

Type material. One female paratype dissected on six slides (NHM 2006.1495), two female and one male paratype in 70% alcohol (NHM 1967.8.4.113).

Diagnosis

Body shape (Figure 13A, B) and proportions as in type species. Body somites scarcely clothed with irregular pattern of small denticles, some of which organized in transversal rows. Posterodorsal margin of cephalothorax smooth, of all free somites serrate. Posterodorsal margins of cephalothorax and free somites clothed with slender hairs, all bearing number of sensilla (not in penultimate urosomite). Caudal rami (Figure 13E) flattened; 1.5 times as long as wide; inner margin slightly convex. Seta IV and V rather short. Antennule (Figure 13C) six-segmented; suture between fourth and fifth segment incomplete. Armature formula as in type species. Second segment with strong, armed spine along outer margin. Antenna and mouthparts as in type species. P1 (Figure 13D) with one-segmented exopod, bearing six setae. Swimming legs P2–P4 with three-segmented exopods and two-segmented endopods. Exp-1 and exp-2 equal in length; exp-3 slightly longer. Setal formula in Table I. Female P5 with four baseoendopodal and five exopodal setae. Baseoendopod almost reaching to middle of exopod. Male swimming legs P1–P4 as in female. Endopodal lobe of male P5 obsolete; without seta. Exopod small; bearing three pinnate and one naked seta(e).

Total body length of female 469–470 μm (n=2; average=470 μm), of male 398–405 μm (n=2; average=402 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax of female 107 μm, of male 84 μm. Measurements by Wells (1967): average length of female 395 μm (range 351–481 μm), of male 348 μm (range 305–396 μm) (measured from base of rostrum to distal edge of last somite, thus excluding caudal rami).

Remark

Although Wells (1967) describes the P1 exopod as having five setae, his drawing of six setae is correct.

Differential diagnosis

T. uniarticulatus bears two outer spines on the ultimate segments of the exopods of P2–P4 and bears three, four and four setae on the second endopodal segments of P2–P4, respectively. Also, the P1 has a one-segmented exopod.

Distribution

Inhaca Island, Mozambique (Wells 1967).

Key to the species of *Tapholeon* Wells, 1967

1. Exp-3 of P2–P4 each with two outer exopodal spines 2
- Exp-3 of P2–P4 each with three outer exopodal spines. 3

2. Enp-2 of P2–P4 each bearing two setae; exopod P1 two-segmented . . . . . *Tapholeon chappuisius* (Krishnaswamy, 1957) comb. nov.
- Enp-2 of P2–P4 bearing three, four, and four setae, respectively; exopod P1 one-segmented. . . . . *Tapholeon uniarticulatus* Wells, 1967

3. Exp-2 of P4 with inner seta 4
- Exp-2 of P4 without inner seta. 5

4. Enp-2 of P2–P4 bearing three, five, and four setae, respectively . . . . . *Tapholeon inconspicuus* sp. nov.
- Enp-2 of P2–P4 bearing four, four, and three setae, respectively . . . . . *Tapholeon tenuis* sp. nov.

5. Enp-2 of P2–P4 bearing two, three, and three setae, respectively . . . . . *Tapholeon arenicolus* (Chappuis, 1954) comb. nov.
- Enp-2 of P2–P4 bearing three, four, and three setae, respectively. . . . . *Tapholeon ornatus* Wells, 1967

Discussion

The laophontid genus *Tapholeon* was established by Wells (1967) to accommodate two new species: *T. ornatus* Wells, 1967 and *T. uniarticulatus* Wells, 1967, both from Inhaca Island (Mozambique). Since then, no new species were added and, to our knowledge, the two species have not been reported again. Wells (1967) established this genus mainly based on the absence of sexual dimorphism in the natatorial legs. In addition, the following characters form a series of apomorphic features clearly defining this taxon: the elongate and slender, but depressed body, the flattened (not cylindrical) caudal rami, the strong and armed spine on the second segment of the antennule, the reduced antennary allobasal seta and the reduced male P5, with an obsolete endopodal lobe without setae and a small exopod bearing three or four setae.

Within the Laophontidae, the genera *Asellopsis* Brady and Robertson, 1873 and *Tapholeon* are easily recognizable by their lamelliform caudal rami and typical, depressed body shape (although species of *Tapholeon* are more slender and lack well-developed epimeral plates). However, *Asellopsis* can clearly be distinguished from *Tapholeon* by the distinct sexual dimorphism in the endopod of the third leg, i.e. three-segmented with an apophysis on the second segment [except in *A. intermedia* (T. Scott, 1895), in which the male P3 endopod only shows a modified chaetotaxy, as pointed out by Bodin 1970]. In the present study, additional material of the species *Asellopsis arenicola* Chappuis, 1954 revealed the absence of any sexual dimorphism in the swimming legs. Therefore, this species must be assigned to *Tapholeon*. A second species, *A. chappuisius* Krishnaswamy, 1957, also from the Indian Ocean, is assigned to this genus for the same reason.

As a consequence of the transfer of these two species, the genera *Asellopsis* and *Tapholeon* appear to have rather distinct distributions (Figure 14). *Asellopsis* has frequently been reported from various localities in the Mediterranean Sea (including the Black Sea) and along the eastern shores of the North Atlantic Ocean (e.g. Lang 1948; Noodt 1955; Por

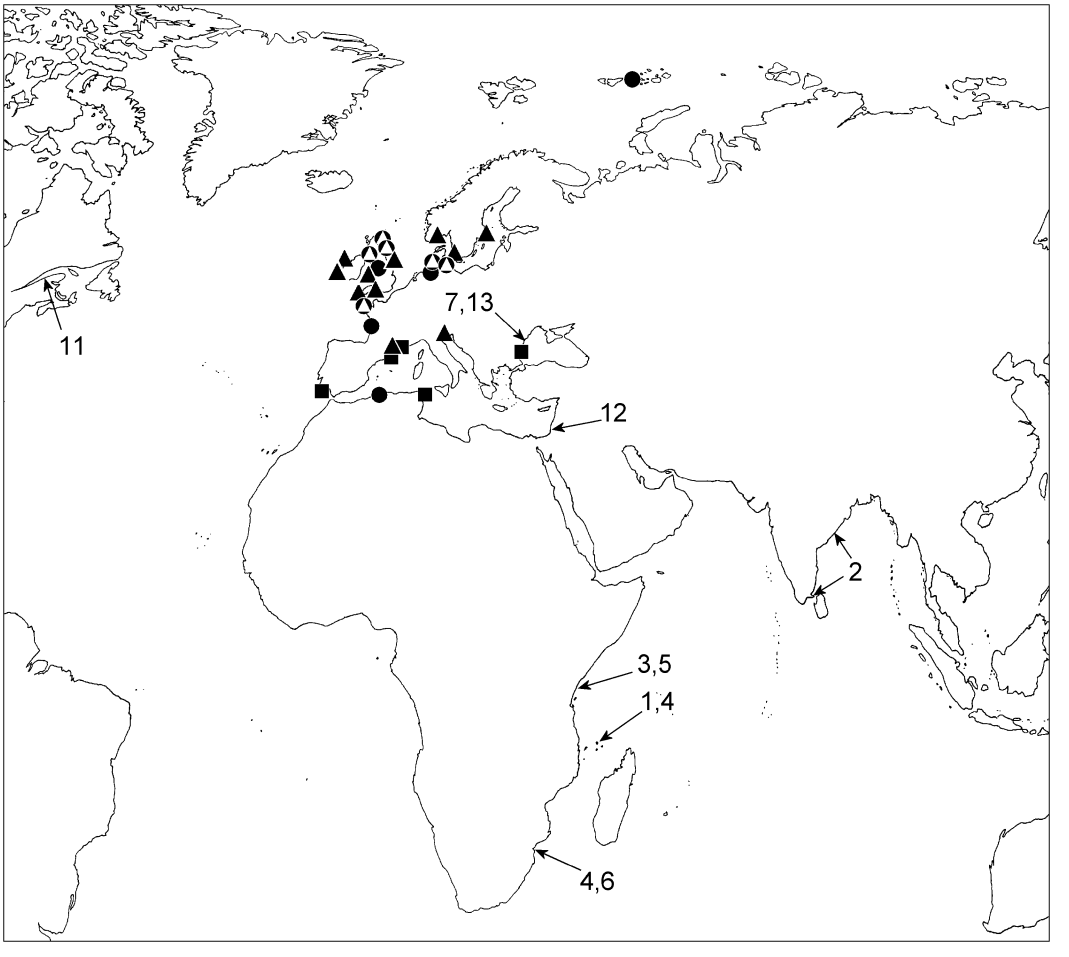

Figure 14. Sampling locations of the presently known species of *Tapholeon* Wells, 1967 and *Asellopsis* Brady and Robertson, 1873, based on the original descriptions and the reports in Lang (1948) and Bodin (1997). (1) *Tapholeon arenicolus* (Chappuis, 1954); (2) *T. chappuissius* (Krishnaswamy, 1957); (3) *T. inconspicuus* Gheerardyn and Fiers sp. nov.; (4) *T. ornatus* Wells, 1967; (5) *T. tenuis* Gheerardyn and Fiers sp. nov.; (6) *T. uniarticulatus* Wells, 1967; (7) *Asellopsis bacescui* Por, 1959; (8) *A. duboscqui* Monard, 1926 (■); (9) *A. hispida* Brady and Robertson, 1873 (▲); (10) *A. intermedia* (T. Scott, 1895) (●); (11) *A. littoralis* Nicholls, 1940; (12) *A. penicillata* Por, 1964; (13) *A. sarmatica* Jakubisiak, 1938.

1959, 1964; Griga 1963; Guille and Soyer 1966; Marinov 1971; Mielke 1975; Bodiou 1980; Gee and Warwick 1984), and mostly occurs in sandy and muddy bottoms. The only representative from the western shore of the North Atlantic Ocean is *A. littoralis* Nicholls, 1940, described from the shore of the River St. Lawrence (at Trois-Pistoles) (Nicholls 1940). The type locality of *A. intermedia*, at Franz-Josef Land in the Arctic Ocean (Scott 1898), represents the most northern limit of the genus *Asellopsis*. The genus *Tapholeon* (now containing six species) shows a limited distribution confined to the southwestern part of the Indian Ocean (Mozambique, Kenya, Comoros) and the Bay of Bengal. The occurrence of *T. chappuisius* comb. nov. in the Bay of Bengal might indicate a much wider distribution of *Tapholeon* in the Indian Ocean. Apart from the report of *T. arenicolus* comb. nov. in a

sample of gravel with coral rubble and shell debris (Chappuis 1954), all six species have been found in sediments (Chappuis 1954; Krishnaswamy 1957; Wells 1967; Rao and Ganapati 1969; present report). The distinct differences in sexual dimorphism and the remote distribution of *Tapholeon* and *Asellopsis* are indications that the strong resemblances in body shape and form of the caudal rami are the result of convergence and that the two genera are not directly related to each other. Therefore, body shape and caudal rami might have evolved similarly in response to similar environmental conditions, i.e. the similar substrate in which members of both genera are found.

The flattened caudal rami also occur in two species of *Paralaophonte* Lang, 1944 (i.e. *P. asellopsiformis* Lang, 1965 and *P. aenigmaticum* Wells, Hicks and Coull, 1982). Furthermore, their body shape is typical asellopsiform and quite unlike other species of *Paralaophonte*, as stated by Wells et al. (1982). These two species, however, are typical members of the genus *Paralaophonte* as illustrated by the dimorphic features in P2 and P3. Lang (1965) ascribes the similarities with *Asellopsis* to ecological convergence, as *P. asellopsiformis* (and *P. aenigmaticum*) are sediment dwellers in substrata similar to those inhabitated by species of *Asellopsis*. Wells et al. (1982), however, warn that a thorough phylogenetic analysis is still necessary before the homogeneity of *Paralaophonte* can be addressed.

Apart from the flattened caudal rami and the characteristic body shape, *P. asellopsiformis* and *P. aenigmaticum* furthermore bear a thickened seta on the second antennular segment. These shared characteristics might indicate a strong affinity of *Tapholeon* with *Paralaophonte*. However, *Tapholeon* is clearly differentiated by the lack of sexually dimorphic features in the endopods of P2 and P3 and the exopods of P2–P4. Whether the similarities have to be attributed to a shared ancestry or to convergence has to be decided on the basis of a thorough phylogenetic analysis.

Acknowledgements

The first and last authors acknowledge grants, as aspirant and postdoctoral fellow, respectively, from the Fund for Scientific Research (FWO-Flanders, Belgium). The sampling campaign in Kenya was organized in the frame of the research project G.0199.03 'A Comparative Study of the Meio-Epifauna Associated with Tropical and Cold-water Coral Reefs', sponsored by the same Fund for Scientific Research. Miranda Lowe (Natural History Museum, London) is kindly thanked for lending the type material examined in this study. Dr P. J. Hayward and two anonymous reviewers are thanked for checking our manuscript.

References

Bodin P. 1970. Copépodes Harpacticoïdes marins des environs de La Rochelle. 1—Espèces de la vase intertidale de Chatelaillon. Tethys 2(2):385–436.

Bodin P. 1997. Catalogue of the new marine Harpacticoid Copepods (1997 edition). Studiedocumenten van het K.B.I.N. 89:1–304.

Bodiou JY. 1980. Copépodes Harpacticoïdes (Crustacea) des sables fins infralittoraux de Banyuls-sur-Mer. II. Variations saisonnières qualitatives du peuplement. Vie et Milieu 30(3/4):269–274.

Chappuis PA. 1954. Recherches sur la faune interstitielle des sédiments marins et d'eau douce à Madagascar: IV. Copépodes Harpacticoïdes psammiques de Madagascar. Mémoires de l'Institut Scientifique de Madagascar 9:45–73.

Gee JM, Warwick RM. 1984. Preliminary observations on the metabolic and reproductive strategies of harpacticoid copepods from an intertidal sandflat. Hydrobiologia 118:29–37.

Gheerardyn H, Fiers F, Vincx M, De Troch M. 2006a. *Peltidiphonte* gen. n., a new taxon of Laophontidae (Copepoda: Harpacticoida) from coral substrates of the Indo-West Pacific Ocean. Hydrobiologia 553:171–199.

Gheerardyn H, Fiers F, Vincx M, De Troch M. 2006b. *Paralaophonte harpagone* sp. n. (Copepoda: Harpacticoida), a laophontid with an extremely specialised maxilliped. Organisms, Diversity and Evolution 6:323–324.

Griga RE. 1963. Harpacticoids of the benthonic biocenoses in the southern coast of the Crimea and Caucasus. Trudy Sevastopol'skoy Biologicheskoy Stantsii 16:159–172.

Guille A, Soyer J. 1966. Copépodes Harpacticoïdes de Banyuls-sur-Mer. IV. Quelques formes des gravelles à Amphioxus. Vie et Milieu 17(B):345–387.

Huys R, Gee JM, Moore CG, Hamond R. 1996. Marine and brackish water harpacticoid copepods. Part 1. Shrewsbury: Field Studies Council. 352 p. (Synopses of the British fauna (new series); 51).

Huys R, Lee W. 2000. Basal resolution of laophontid phylogeny and the paraphyly of *Esola* Edwards. Bulletin of the Natural History Museum London (Zoology Series) 66(1):49–107.

Krishnaswamy S. 1957. Studies on the Copepoda of Madras [PhD dissertation]. Madras: University of Madras. 168 p.

Lang K. 1948. Monographie der Harpacticiden. Lund: Håkan Ohlssons Boktryckeri. 1683 p.

Lang K. 1965. Copepoda Harpacticoidea from the Californian Pacific coast. Kungliga Svenska Vetenskapsakademiens Handlingar (4)10(2):1–566.

Marinov T. 1971. Harpacticoids of the Bulgarian Black Sea coast. Proceedings of the Research Institute of Oceanography and Fisheries, Varna 11:43–87.

Mielke W. 1975. Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt. Mikrofauna Meeresbodens 52:1–134.

Nicholls AG. 1940. Marine harpacticoids and cyclopoids from the shores of the St. Lawrence. Fauna et Flora Laurentianae 2:241–316.

Noodt W. 1955. Marine Harpacticoiden (Crust. Cop.) aus dem Marmara Meer. Istanbul Universitesi Fen Fakultesi Mecmuasi 20(1/2):49–94.

Por FD. 1959. Harpacticoide noi (Copepoda, Crustacea) din milurile Marii Negre. Studii si Cercetari de Biologie, Seria Biologia Animala 4(11):347–368.

Por FD. 1964. A study of the Levantine and Pontic Harpacticoida (Copepoda Crustacea). Zoologische Verhandelingen, Leiden 64:1–128.

Rao CG, Ganapati PN. 1969. On some interstitial copepods from the beach sands of Waltair coast. Proceedings of the Indian Academy of Sciences 70:262–286.

Scott T. 1898. Report on the marine and freshwater Crustacea from Franz-Josef Land, collected by Mr. William S. Bruce, of the Jackson-Harmsworth expedition. Journal of the Linnean Society of London, Zoology 27:60–126. Plates 3–9.

Wells JBJ. 1967. The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. Transactions of the Royal Society of Edinburgh 67(7):189–358.

Wells JBJ, Hicks GRF, Coull BC. 1982. Common harpacticoid copepods from New Zealand harbours and estuaries. New Zealand Journal of Zoology 9:151–184.