

A review of *Pseudoleptomesochrella* Lang, 1965 (Copepoda, Harpacticoida, Ameiridae), including a redescription of *P. halophila* (Noodt, 1952) from the Black Sea and a key to species

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Abstract

Both sexes of *Pseudoleptomesochrella halophila* (Noodt, 1952) (Copepoda, Harpacticoida, Ameiridae) are redescribed in detail based on material collected from the Black Sea coast of Turkey. Careful comparison revealed that the Turkish specimens are identical with the northwestern European populations originally reported from the Isle of Sylt (Germany) and the Isles of Scilly (U.K.). Re-examination of the type material of *Nitocrella halophila brevifurca* Wells, 1961 confirmed its conspecificity with *P. halophila*. Comparison of the various descriptions indicates the genus comprises two species complexes (Atlantic and *P. halophila* groups) whose members exhibit only cryptic differences, and that the majority of discrepancies reported in the literature are potentially unreal. *Pseudoleptomesochrella pontica* Apostolov, 1969 is removed from its synonymy with *P. halophila* and is reinstated as *species inquirenda*. A dichotomous key to species of *Pseudoleptomesochrella* Lang, 1965 is provided.

Key words: Taxonomy, marine interstitial, cryptic speciation, boreo-pontic distribution, Turkey

Introduction

Ever since its inception the genus *Nitocrella* Chappuis, 1924 (Harpacticoida, Ameiridae) has served as a repository for freshwater, estuarine and marine interstitial taxa that deviated from more traditional ameirid genera in their reduced swimming leg segmentation and armature. The subsequent gradual refinement of the generic diagnosis has resulted in the proposal of numerous new genera and this process appears to be ongoing (Lang 1965; Petkovski 1976; Galassi *et al.* 1999; Lee & Huys 2002; Reid *et al.* 2003; Karanovic 2004, 2006). One marine example is represented by the genus *Pseudoleptomesochrella*, which was proposed by Lang (1965) for three taxa previously attributed to *Nitocrella*: *N. halophila* Noodt, 1952, *N. marina* Chappuis & Rouch, 1961 and *N. halophila brevifurca* Wells, 1961. Lang (1965) claimed the presence of an inner seta on the first segment of P2-P4 exopods not only excluded these taxa from *Nitocrella* but also provided evidence that they could not possibly have been derived from a *Nitocrella*- or *Nitocra*-like ancestor, suggesting an affinity with the genus *Pseudoleptomesochra* Lang, 1965 instead. Noodt (1952) himself remarked that the presence of three outer spines on the distal exopod segment of P2 made *N. halophila* differ from all other *Nitocrella* species known at that time, however, he considered this discrepancy a reflection of the heterogeneity of the genus. Lang (1965) designated *N. halophila* as the type species of *Pseudoleptomesochrella* and upgraded *N. halophila brevifurca* to full species rank based on differences with the nominate subspecies in the

caudal rami, fifth legs and antennary exopod. Mielke (1975) subsequently relegated *N. brevifurca* to a junior subjective synonym of *N. halophila*.

The species originally described as *Paraleptastacus* (?) *incertus* from Bimini (Bahamas) by Chappuis & Delamare Deboutteville (1956), was removed from this genus and the family Leptastacidae (as *Cylindropsyllidae*) by Moore (1975) and provisionally assigned to *Pseudoleptomesochrella* on the basis of the 3-segmented P1 endopod, the presence of an inner seta on the proximal and middle exopod segments of P2-P4, the setation of the female P5 baseoendopod and the shape of the caudal rami. *Pseudoleptomesochrella incerta* (Chappuis and Delamare Deboutteville, 1956) differs from its congeners primarily in the 7-segmented antennule but since this appendage was not figured in the original description additional material needs to be re-examined before this can be confirmed.

Lindgren (1975) described *P. bisetosa* from North Carolina and Mielke (1995) added *P. venezolana* from Venezuela, raising the number of valid species in the genus to five (Wells, 2007), all of which occur exclusively in the intertidal zone of sandy beaches. Based on current records *Pseudoleptomesochrella* appears to be restricted to the Atlantic with outliers in the Black Sea basin, however, one of us (RH) recently discovered an as yet undescribed species from a Kuwaiti beach, indicating a potentially circumglobal distribution of the genus.

Pseudoleptomesochrella halophila was originally described from the Isle of Sylt (Noodt 1952), which has remained the only German locality where the species has been recorded from (Noodt 1956, 1957; Mielke 1975), but the subsequent discovery of populations in southern England and the Black Sea has caused considerable confusion as to its true morphological variability and distribution range. Wells' (1961) specimens from St. Martin's (Isles of Scilly) were assigned to a distinct subspecies *Nitocrella halophila brevifurca* based on differences in female P5 armature and caudal ramus length, a course of action endorsed by Lang (1965) who upgraded it to species rank. Mielke (1975) dismissed the latter character as being of no significance in separating the two species and formally synonymized them. Apostolov (1969) described *P. pontica* from near Lozenets along the southern Bulgarian Black Sea coast whereas Michailova-Neikova & Voinova-Stavreva (1971) reported *P. halophila* (as *N. halophila*) less than 25 km north of the latter's type locality. Marinov (1973) re-examined Apostolov's (1969) material, compared it with his own specimens from Rezovo near the Turkish border and concluded that *P. pontica* is possibly synonymous with *P. halophila*, providing the first evidence for a boreo-pontic distribution of the latter. Wells (2007) continued to treat Noodt's (1952), Mielke's (1975) and Apostolov's (1969) populations as distinct entries in his tabular keys due to differences in the number of armature elements on the baseoendopod of leg 5 in both sexes and the size of the seta on the inner distal corner of P2-P4 exp-3. Noodt's (1952) original description lacks the detail to resolve the issue and the type material of *P. halophila* is no longer extant (A. Ahnert, pers. comm.). Here we present a detailed redescription based on new material from the Turkish Black Sea coast which may serve as a basis for future comparison of other *P. halophila*-like specimens from other localities in Europe. We also review previously published species descriptions and present a dichotomous key to the six currently recognized species in the genus.

Material and methods

Samples from sandy beaches of the Bartın and Kastamonu Provinces along the Black Sea coast of Turkey were collected using the Karaman-Chappuis method (Delamare Deboutteville 1953). Specimens were dissected in lactophenol. Dissected parts were mounted on slides in lactophenol mounting medium. Broken glass fibres were added to prevent the animal and appendages from being compressed by the coverslip and to facilitate rotation and manipulation, allowing observation from all angles. Preparations were sealed with Entellan® (Merck). All drawings were prepared using a camera lucida on Olympus BX-50 or BX-51 differential interference contrast microscopes. Total body length was measured from the anterior margin of the rostrum to

the posterior margin of the caudal rami. Measurements were made with an ocular micrometer. Scale bars in illustrations are in μm . The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: ae, aesthetasc; P1–P6, for swimming legs 1–6; exp (enp)-1 (-2, -3) to denote the proximal (middle, distal) segment of a ramus. Material was deposited in the Mersin University Zoology Museum (MUZM) and the Natural History Museum, London (NHM).

Systematics

Order Harpacticoida Sars, 1903

Family Ameiridae Monard, 1927

Genus *Pseudoleptomesochrella* Lang, 1965

Diagnosis (amended). Ameiridae. Body cylindrical and slender, without clear demarcation between prosome and urosome; integument smooth, not strongly chitinized. Hyaline frills of cephalothorax and somites bearing P2–P5 usually plain; those of abdominal somites plain or digitate with rectangular lappets. Female genital and first abdominal somites completely fused to form genital double-somite; original segmentation sometimes marked by dorsolateral, transverse internal ribs. Anal operculum smooth (spinulose in *P. pontica?*). Caudal ramus conical, short; with 7 setae. Sexual dimorphism in body size, antennule, P1 (inner basal spine), P4 endopod, P5, P6, and in genital segmentation.

Rostrum small, not demarcated at base. Antennule slender and elongate; setae smooth; 8-segmented in ♀ (7-segmented in *P. incerta?*), with aesthetasc on segments 4 (extremely long, longer than antennule) and 8; 11-segmented and haplocer in ♂, with geniculation between segments 8 and 9 and aesthetasc on segments 5 and 11. Antenna with basis and proximal endopod segment completely or incompletely separated; endopod with 2 lateral and 6 distal elements (longest geniculate seta fused at base to naked seta). Antennary exopod 2-segmented; armature formula [1,2]; exp-1 without ornamentation; exp-2 minute, with apical seta longer than lateral one. Mandibular palp uniramous, 2-segmented, comprising basis and 1-segmented endopod; basis with 1 pectinate and 2 pinnate setae; endopod with 2 lateral and 3 apical setae. Maxillule with 1 element on coxal endite; basis and rami (endopod; exopod probably absent) partly fused; represented by total of 7 setae. Maxillary syncoxa with 2 well developed endites, proximal one drawn out into apically serrate element and with 1 flaccid plumose seta; distal endite with 1 pinnate and 2 plumose setae; allobasis drawn out into a claw and with pinnate spine; endopod minute, unisetose. Maxilliped subchelate; syncoxa with 1 seta; endopod represented by minutely pinnate claw with 1 accessory seta.

P1–P4 with 3-segmented exopods and 2- (P2–P4) or 3-segmented (P1) endopods. P1 exopod without inner seta on exp-2; exp-3 with 2–3 outer spines and 2 geniculate setae distally. P1 endopod prehensile, with enp-1 at least as long as enp-2 and -3 combined, but shorter than exopod; inner seta of enp-2 short. Inner basal spine of P1 modified in ♂, forming a strong recurved hook. P2–P4 with inner seta on exp-1, exp-2 and enp-1. P4 endopod ♂ slightly modified; inner element on enp-2 reduced in size; distal spine sometimes shorter and recurved (Atlantic complex). Armature formula P1–P4 as follows:

	Exopod	Endopod
P1	0.0.02[2–3]	1.1.111
P2	1.1.02[2–3]*	1.110
P3	1.1.022*	1.110
P4	1.1.222*	1.110

* Note that inner distal seta on exp-3 is thin and minute

P5 with separate baseoendopod and exopod in both sexes; baseoendopods fused medially in ♂; ♀ with 3–4 setae on baseoendopod; exopod semicircular or ovate, with 3–4 setae; ♂ with 1–3 setae on baseoendopod and 3–4 setae on exopod. Female genital field with large copulatory pore leading via chitinized copulatory duct to median seminal receptacle; gonopores covered by common genital operculum derived from P6 with 1 plumose seta and 1 spinous process on either side. Male P6 slightly asymmetrical, with 3 simple setae, of which outer one longest.

Type-species: *Nitocrella halophila* Noodt, 1952 = *Pseudoleptomesochrella halophila* (Noodt, 1952) [by original designation].

Other species: *P. incerta* (Chappuis & Delamare Deboutteville, 1956); *P. marina* (Chappuis & Rouch, 1961); *P. bisetosa* Lindgren, 1975; *P. venezolana* Mielke, 1995.

Species inquirenda: *P. pontica* Apostolov, 1969

***Pseudoleptomesochrella halophila* (Noodt, 1952)**

(Figs 1–4)

Syn.: *Nitocrella halophila* Noodt, 1952; *Nitocrella halophila brevifurca* Wells, 1961; *Pseudoleptomesochrella brevifurca* (Wells, 1961) Lang (1965)

Material examined. 1 ♀ dissected on 8 slides, 2 ♀♀ in alcohol (NHM reg. nos 2008.363–364) and 2 ♀♀ in alcohol (MUZM), collected from Doğanyurt, Kastamonu Province, Turkey, 08 July 2001; 1 ♀ deposited in alcohol (MUZM), collected from Kurucaşile, Bartın Province, Turkey, 08 July 2001; 1 ♂ dissected on 7 slides (MUZM), 2 ♂♂ in alcohol (NHM reg. nos 2008.365–366) and 1 ♂ in alcohol (MUZM), collected from Doğanyurt, Kastamonu Province, Turkey, 14 September 2002. All specimens collected by S. Karaytuğ and S. Sak.

Redescription. FEMALE. Body slender and cylindrical (Fig. 1A–B), without distinct demarcation between prosome and urosome. Total body length from tip of rostrum to posterior margin of caudal rami 450 µm (mean = 427 µm; n = 6). Sensillar pattern of body as figured (Fig. 1A–B). Rostrum (Fig. 1B) small, triangular, tapering distally; with two dorsal sensillae. Pleural areas of cephalothorax not well developed so that cephalic appendages are clearly visible in lateral aspect (Fig. 1A). Hyaline frills of all somites plain.

Genital double-somite (Fig. 1A–B) about 1.5 times longer than wide; original segmentation indicated by paired, chitinous, internal ribs dorsolaterally. Anal somite (Fig. 1A–B) slightly longer than wide; anal operculum (Fig. 1E) slightly rounded, without ornamentation; anal cleft with incised frill as figured.

Caudal rami (Figs 1E, 2A–B) about 1.5 times longer than wide, slightly tapering posteriorly; dorsal surface without crest-like bulge. Each ramus with an integumental pore dorsally, laterally and ventrally (tube-pore); with seven naked setae (indicated by Roman numerals I–VII in Fig. 2A–B; seta I not figured in Fig. 1E); seta I smallest; seta II positioned dorsally to seta I; seta III arising from outer distal corner; seta IV and V located terminally, both with fracture planes; seta V longest; seta VI small and located ventrally, near inner distal corner; seta VII located dorsally, near inner distal corner, tri-articulated at base.

Antennule (Fig. 2C) long and slender; 8-segmented. Segment 1 with tiny seta near anterodistal margin. Segment 2 longest, about twice longer than wide with nine naked setae. Segment 4 with long aesthetasc (L: 133 µm) fused at base with a very long seta. Distal segment with 5 naked setae and apical acrothek. Armature formula 1-[1], 2-[9], 3-[5], 4-[2 + (1 + ae)], 5-[1], 6-[2], 7-[4], 8-[5 + acrothek]. Apical acrothek consisting of an aesthetasc (L: 32 µm) and two slender setae.

Antenna (Fig. 3B). Basis small and with two slender spinules along inner margin. Exopod 2-segmented; proximal segment with a bipinnate seta at inner distal corner; distal segment with a slender bipinnate seta along inner margin and a strong, bipinnate seta apically. Proximal endopod segment without ornamentation, twice longer than wide. Distal endopod segment with three spinular tufts along abexopodal margin and a hya-

line frill on anterior surface; lateral armature consisting of one naked and one unipinnate spine; apical armature consisting of five geniculate setae, largest one of which with spinules around geniculation and fused at base to slender seta.

Mandible (Fig. 2D). Gnathobase well developed with series of weakly developed teeth and with a unipinnate seta at dorsal corner. Palp 2-segmented, consisting of basis and 1-segmented endopod. Basis elongate, with two bipinnate (one short, one long) setae and one pectinate seta laterally. Endopod with two lateral and three apical naked setae.

Maxillule (Fig. 2E). Praecoxal arthrite with a spinular row along medial margin and with five spines/setae around distal margin; anterior surface with two parallel setae; posterior surface with spinular row. Coxal endite with one strong pinnate, geniculate spine. Segment boundaries between basis and rami not well expressed; basal endite with three apical setae; endopod (and possibly exopod) represented by total of five naked setae.

Maxilla (Fig. 2F). Syncoxa with two endites (proximal one smaller) and two surface spinular rows; proximal endite with one plumose seta and one apically serrate, basally fused seta; distal endite with one bipinnate and two naked setae. Allobasis drawn out into a claw-like pinnate endite with one accessory seta. Free endopod represented by minute segment with one slender seta.

Maxilliped (Fig. 2G) well developed, subchelate. Syncoxa well developed, with one bipinnate seta. Basis elongate, with two spinular rows along outer distal corner and on anterior surface. Endopod represented by a strong, curved, bare claw accompanied at base by minute naked seta.

P1 (Fig. 1D). Intercoxal sclerite small and squarish, with concave ventral margin (as in male, see Fig. 4E). Coxa with an oblique spinular row on anterior surface. Basis narrower than coxa, with spinules around bases of inner spine and outer seta and between bases of rami; with integumental pore on anterior surface; outer seta bipinnate and inner spine unipinnate. Exopod 3-segmented (exp-3 longest); exp-1 and -2 with spinules around bases of outer spines; outer margins of exp-2 and exp-3 with spinular row; inner margins of segments without ornamentation except for single spinule on exp-2; exp-3 with three spines and two geniculate setae. Endopod 3-segmented, longer than exopod; enp-1 3.8 times longer than wide, with three spinules located halfway along inner margin and with a serrate inner seta in distal third; enp-2 smallest, with bipinnate inner seta and spinules along outer margin; enp-3 with spinular row along outer margin and apical armature consisting of outer curved spine, one geniculate seta and one small naked inner seta.

P2–P4 (Fig. 3C–D) intercoxal sclerites squarish, with concave ventral margins. Praecoxae small and with a spinular row at outer proximal corner (praecoxa of P3 also with spinular row on anterior surface). Coxae rectangular; without any ornamentation except for spinular row on anterior surface of P2. Bases smaller than coxae; anterior surface with a pore near base of outer seta; spinular patterns as illustrated; outer basal element spiniform and bare in P2, setiform and plumose in P3–P4. Exopods 3-segmented; exp-1 and 2 with outer and inner spine; all exopod segments with spinules along outer margins; inner distal element of exp-3 minute (arrowed in Fig. 3C–E). Endopods 2-segmented; segments with spinules along outer margin. Spine and seta formula as follows:

	exopod	endopod
P1	0.0.023	1.1.111
P2	1.1.023	1.110
P3	1.1.022	1.110
P4	1.1.222	1.110

P5 (Fig. 1C). Baseoendopod with two pores on anterior surface; endopodal lobe rectangular, with one long naked seta and three bipinnate spines; outer basal seta plumose; exopod longer than wide; with four naked setae distally and a tube-pore along outer margin.

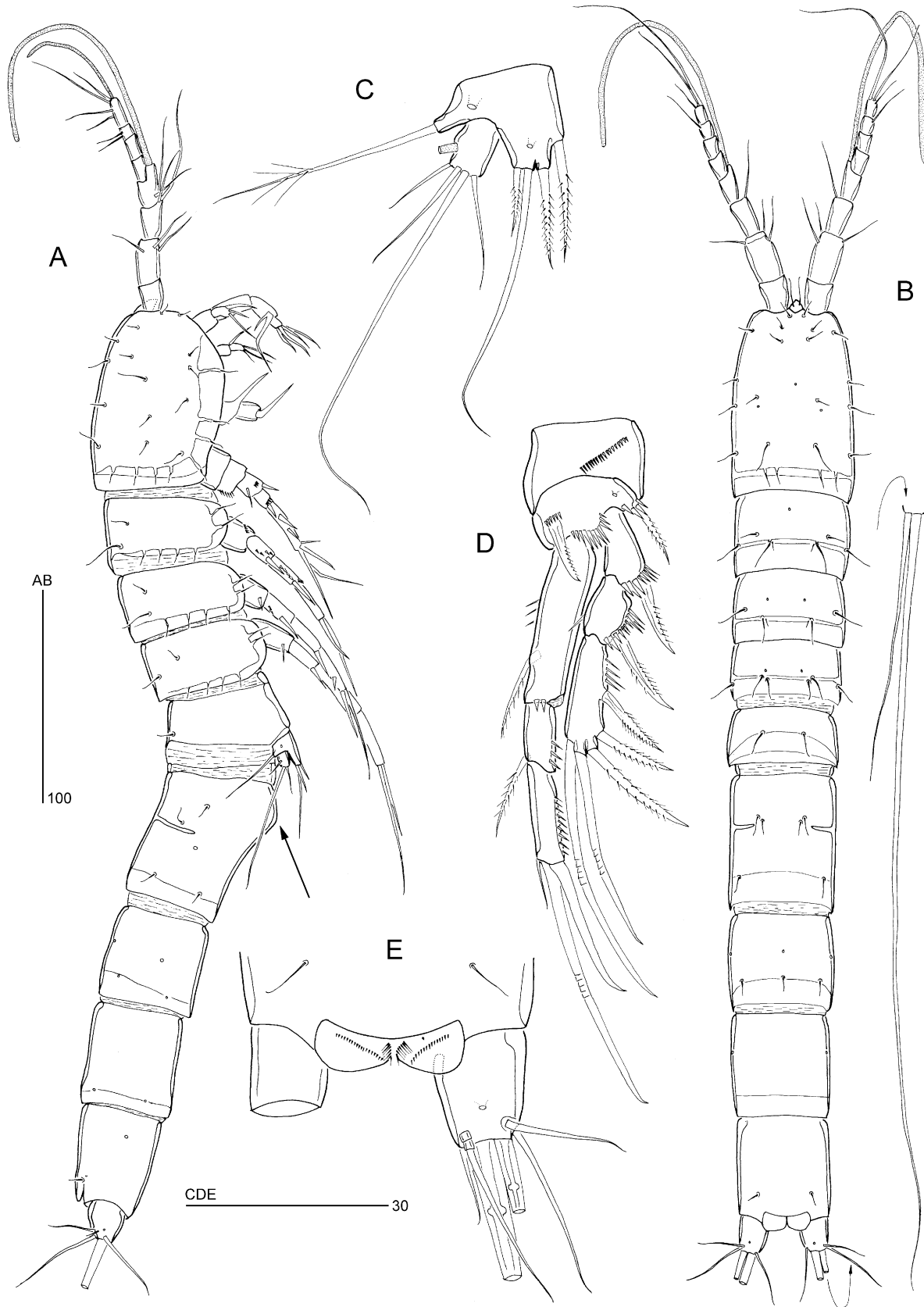


FIGURE 1. *Pseudoleptomesochrella halophila* (Noodt, 1952): (A) habitus ♀, lateral [position of genital field arrowed]; (B) habitus ♀, dorsal; (C) P5 ♀; (D) P1 ♀, anterior; (E) anal somite and caudal rami ♀, dorsal.

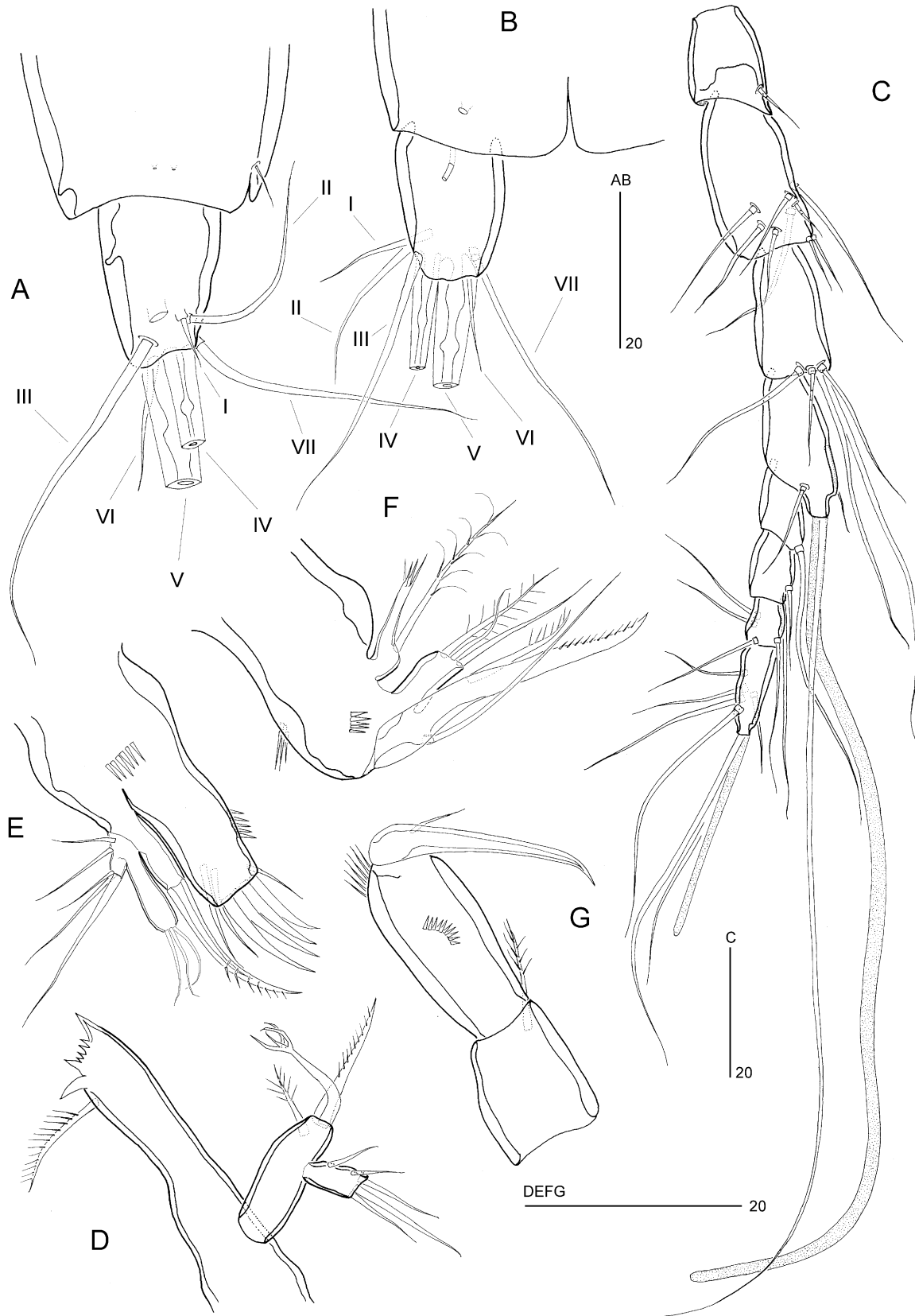


FIGURE 2. *Pseudoleptomesochrella halophila* (Noodt, 1952): (A) anal somite and left caudal ramus ♀, lateral; (B) anal somite and right caudal ramus ♀, ventral; (C) antennule ♀, ventral; (D) mandible ♀; (E) maxillule ♀, posterior; (F) maxilla ♀; (G) maxilliped ♀, anterior.

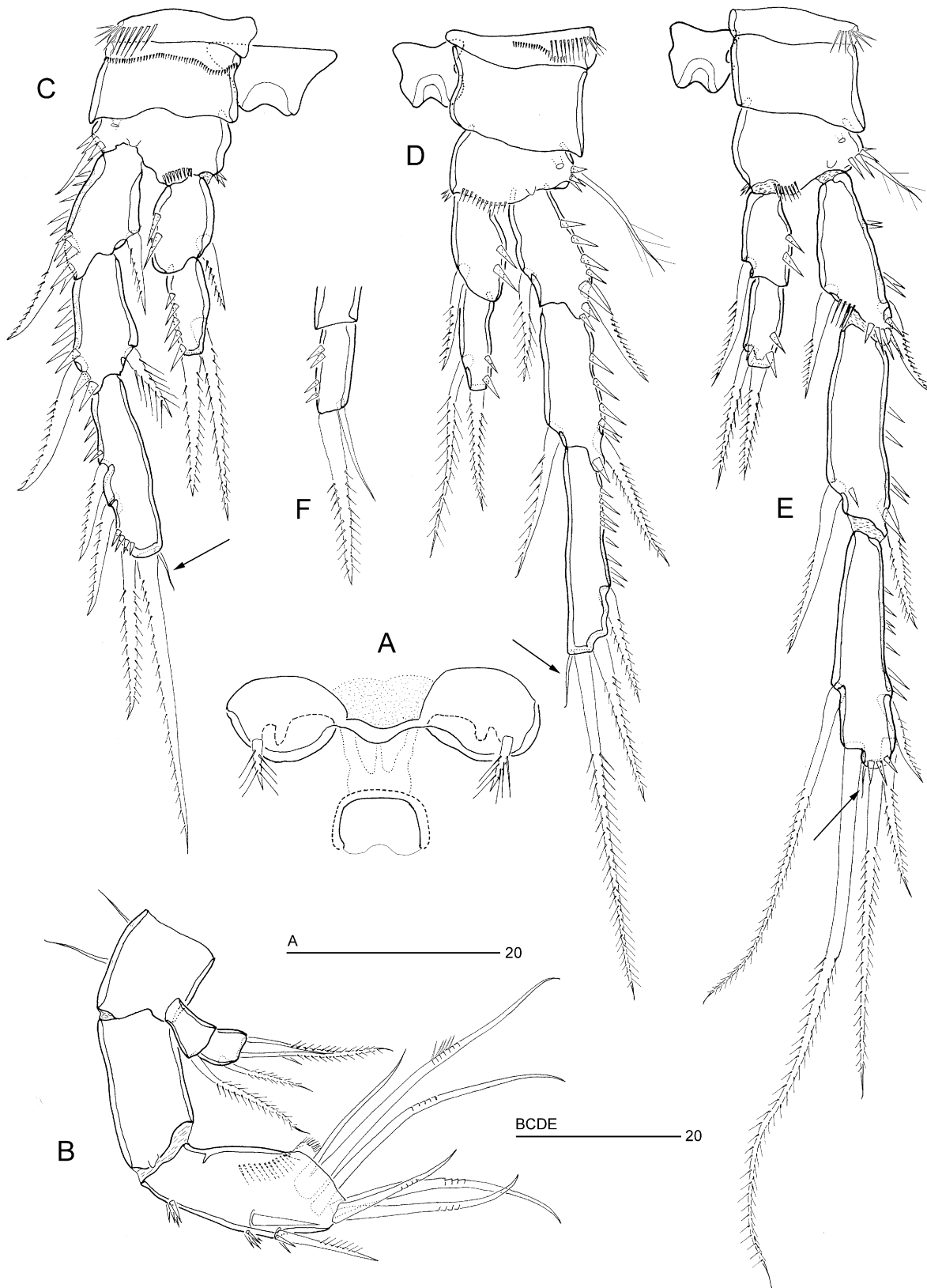


FIGURE 3. *Pseudoleptomesochrella halophila* (Noodt, 1952): (A) genital field ♀; (B) antenna ♀; (C) P2 ♀, anterior; (D) P3 ♀, anterior; (E) P4 ♀, anterior; (F) P4 endopod, distal segment ♂, anterior. [vestigial inner distal element on P2–P4 exp-3 arrowed in C–E].

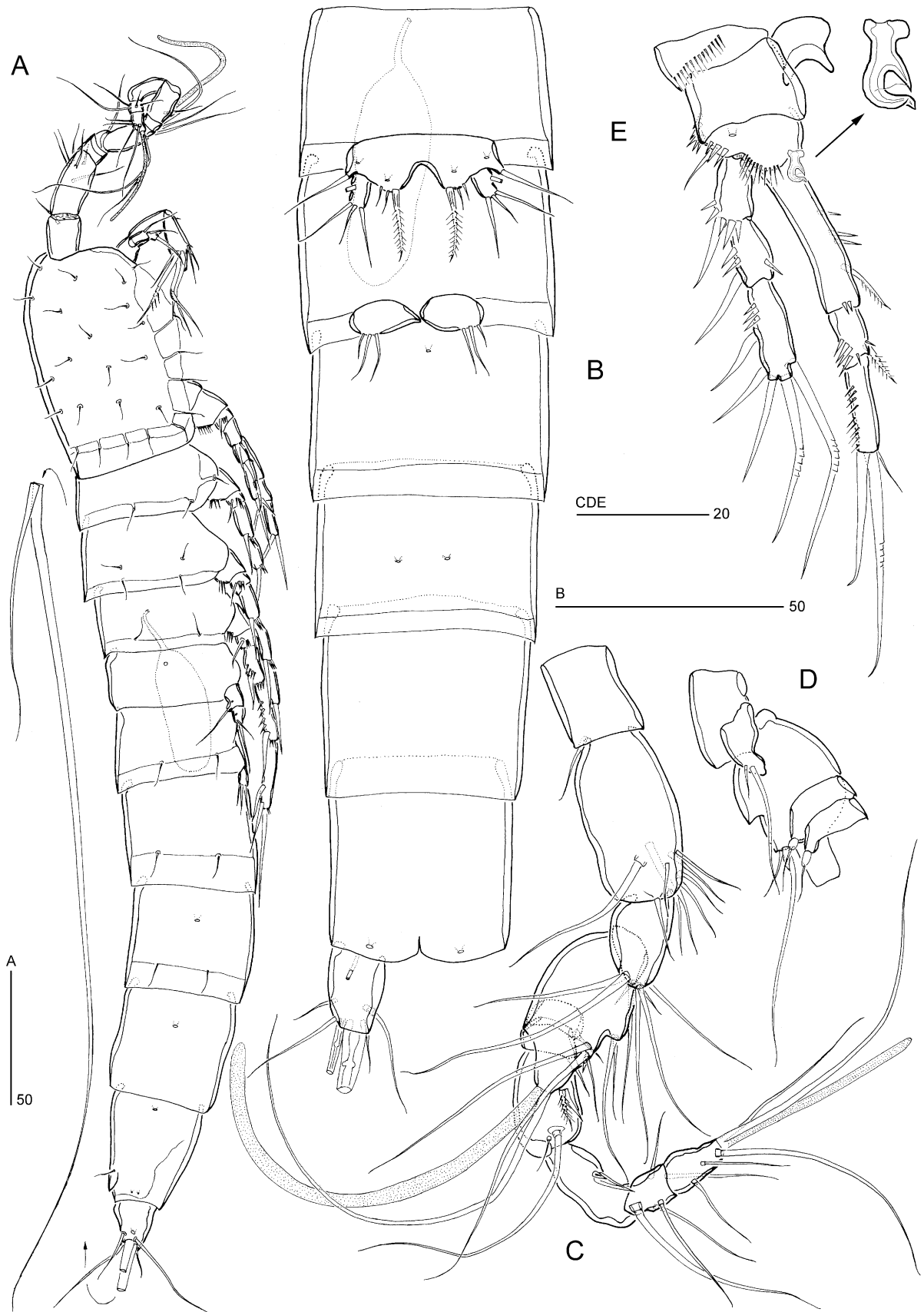


FIGURE 4. *Pseudoleptomesochrella halophila* (Noodt, 1952): (A) habitus ♂, lateral; (B) urosome ♂, ventral; (C) antennule ♂, ventral; (D) antennular segments 3–7 ♂, dorsal; (E) P1 ♂, anterior [insert showing modified inner basal spine].

Genital field positioned near anterior margin of genital double-somite (position arrowed in Fig. 1A); gonopores fused medially forming common slit, closed off by vestigial P6 (Fig. 3A) with one small plumose spine and one spinous process (internally). Copulatory pore large, leading via copulatory duct to single median receptacle.

MALE. Total body length from tip of rostrum to posterior margin of caudal rami 385 μm (mean=340 μm ; n=4). Ornamentation of body (Fig. 4A) generally as in female. Sexual dimorphism in antennule, genital segmentation, P1 inner basal spine, P4 endopod, P5 and P6. Spermatophore length 46 μm .

Antennule (Fig. 4C–D) haplocer, indistinctly 11-segmented; with geniculation between segments 8 and 9 and aesthetasc on segments 5 and 11. Setal formula: 1-[1], 2-[9], 3-[6], 4-[2], 5-[5 + 1 spine + (1 + ae)], 6-[1], 7-[1], 8-[3 setae + 1 spine], 9-[2 spines], 10-[5], 11-[3 + acrothek). Apical acrothek consisting of aesthetasc fused basally to two setae.

P1 inner basal spine (Fig. 4E) transformed as figured.

P4 distal endopod segment (Fig. 3F) shorter than in female; inner seta displaced to inner distal corner, shorter than in female and naked instead of bipinnate.

P5 (Fig. 4B) biramous, fused medially. Baseoendopod with two pores on anterior surface and with outer basal seta arising from short setophore. Endopodal lobe not extending beyond middle of exopod; distal margin with two minute naked setae and long bipinnate inner seta. Exopod with three setae distally, middle one shortest, and a tube-pore along outer margin.

P6 (Fig. 4B) partially fused and slightly asymmetrical; with three naked seta distally, outermost being shortest.

Discussion

Mielke (1995) distinguished two species groups within the genus *Pseudoleptomesochrella* based on the number of setae/spines on the distal exopod segments of P1 and P2, and the number of elements on the endopodal lobe of the female P5. In the first group he included *P. halophila*, *P. brevifurca* and *P. pontica*, all of which have 5 elements on P1 exp-3, 4 well developed spines (and a vestigial seta) on P2 exp-3 and 4 elements on the female P5 baseoendopod. The second group encompassed *P. incerta*, *P. marina*, *P. bisetosa* and *P. venezolana*, all of which have lost an outer spine on P1–P2 exp-3 and display only 3 elements on the endopodal lobe of the female P5. Species have traditionally been separated on the basis of the number of armature elements on the swimming legs and P5, and caudal ramus length (e.g. Mielke 1995; Wells 2007) but the reliability of these characters has hardly been scrutinized. Comparison of the various descriptions indicates the genus comprises two species complexes whose members exhibit only cryptic differences and that the majority of discrepancies reported in the literature are potentially unreal.

Atlantic species complex

Mielke (1995) provided an excellent description of *P. venezolana* which serves as a basis for comparison with other Atlantic species. His assumption that the inner distal accessory seta on P2–P4 exp-3 is present in all members of the genus is likely to be correct even though it has only been recorded in some descriptions of *P. halophila* (Mielke 1995; present account) and *P. pontica* (Apostolov 1969, 1972; P2–P3 only and not included in the armature formula!). Given that this seta is also present in the as yet undescribed species from Kuwait (R. Huys, pers. obs.) we believe this character to be uniform throughout the genus which would remove one of the alleged differences separating *P. venezolana* and *P. incerta*–*P. marina*–*P. bisetosa*. In addition to the latter, Wells (2007) also used the number of elements on P2–P4 exp-2 to differentiate these species. Typically, the distal endopod segment has a distal spine and an inner seta which originates from the posterior surface of the segment and is often concealed by it and the distal spine. This pattern has been documented for *P. halophila*, *P. pontica* and *P. venezolana*, but for none of the other Atlantic species.

Lindgren (1975) described *P. bisetosa* from North Carolina and named the species after the "... unique terminal segment of P2–P4 with two outer setae" (it should be noted that these setae do not feature in the setal formula of P2, which is tabulated correctly; his Table 3). Comparison with Mielke's (1995) illustrations of *P. venezolana* shows that these outer elements are in reality mere coarse spinules along the outer margin of the segment and not genuine armature elements (see also *P. hyalina*: Fig. 3D–E). Lindgren's (1975) formulae of P3–P4 enp-2 (112 and 012) should therefore be corrected to account for this reinterpretation. In addition, the inner seta of P4 enp-2 (which is often small and partly concealed beneath the segment; e.g. Mielke (1975: Fig. 9A)) was almost certainly overlooked in Lindgren's description (as well as the accessory setae on P2–P4 exp-3 which are of a similar size), implying that the swimming leg setal formulae are identical in *P. venezolana* and *P. bisetosa*. Both species also show virtually complete congruence in the shape and armature of the fifth legs in both sexes; note that Lindgren (1975) interpreted the outer tube-pore on the exopod as an additional seta and that the minute outer seta on the endopodal lobe of the male was not figured. It is clear that *P. bisetosa* and *P. venezolana* are very closely related and potentially conspecific. Except for the presence of a crest-like dorsal bulge on the caudal ramus in the latter (discernible in lateral aspect only which was not figured by Lindgren (1975) or for any other Atlantic species), the only noticeable differences are of a morphometric nature: proportional length of P1 enp-1 vs exopod, P2–P4 endopods are shorter and more robust in *P. venezolana* and minute setal length differences in the male P6. In the absence of any data on intraspecific variability we consider it premature to synonymize both species and are inclined to view the observed variation between the North Carolina and Venezuelan "populations" as indicative of cryptic speciation rather than conspecificity.

Pseudoleptomesochrella marina was described on the basis of two males collected from a sandy beach near Accra (Ghana) and is the only member of the genus occurring along the eastern seaboard of the South Atlantic (Fig. 5). The original description by Chappuis & Rouch (1961) is deficient in that several small armature elements were almost certainly omitted from the illustrations, including the distal inner seta on P1 enp-3, the accessory distal inner seta on P2–P4 enp-2, the inner vestigial seta on the endopodal lobe of P5, and possibly the inner seta on P2–P3 enp-2. Given this uncertainty, differentiation of this species should preferably not be based on swimming leg setation characters since it is conceivable that it shares the same armature pattern with *P. venezolana* and *P. bisetosa*. The illustrations of the P4 show that *P. marina* exhibits a similar type of sexual dimorphism as in *P. venezolana*, the distal spine being typically recurved and the inner seta represented by a vestigial element (figured as a spinule). Chappuis & Rouch (1961) also claim that there is an outer spine on the proximal endopod segment of P3–P4 but from their illustrations it is evident that they have misinterpreted the large spinule, typically present in that position, as an armature element. It should also be noted that their Figures 42–43 both refer to the P5 in the legend whereas the former in reality depicts the P6. The text description states that the P5 exopod bears 5 setae, the maximum recorded in the genus. Although the short outermost element unmistakably represents the tube-pore recorded in other congeners, the minute element near the inner distal corner is clearly unique within the genus. It is, however, unlikely that it represents an ornamentation element since no other species has spinules or setules in that position. *Pseudoleptomesochrella marina* resembles *P. venezolana* very closely in the proportional segment lengths of P1–P3 endopods and in the general structure of the caudal ramus. The only reliable feature differentiating the two species (in addition to the P5 exopod setation) is the male P4 endopod which has a distinctly longer proximal segment in *P. marina*. It may be very difficult to separate females of *P. marina* and *P. venezolana*.

Chappuis & Delamare Deboutteville's (1956) description of *P. incerta* (as *Paraleptastacus* (?) *incertus*) is very concise, presenting illustrations only of the P1, P3 endopod, caudal ramus and P5 of both sexes. Their text description does not make any statement about the male. The antennule was described as 7-segmented but this requires confirmation. There appears to be some confusion surrounding the armature formula of P2–P3 in this species. Wells (2007: 137) separated *P. incerta* on the basis of the number of outer spines on P2–P4 exp-3, which he considers to be 1, 1 and 2, respectively. This observation is obviously based on Chappuis &

Delamare Deboutteville's (1956) misleading statement that the distal segment of P2–P3 has "... une épine dorsale subapicale et 2 soies apicales". However, in all members of the genus the distal outer spine of P2–P3 exp-3 is typically displaced to the subdistal corner of the segment, creating the deceiving impression that it is distal in position (e.g. Mielke 1995: Figs 8A–B); moreover, none of the species has two well developed elements around the distal margin of exp-3, suggesting that the armature formula of P2–P3 exp-3 in *P. marina* is 022 as in other members of the Atlantic species complex. *Pseudoleptomesochrella incerta* resembles *P. venezolana* in the facies of the P1 endopod, enp-1 being as long as the other segments combined, and in the armature formula of P2–P4 (as in most species descriptions the inner accessory seta on exp-3 was not observed). It differs from this species in subtle characters, including the more slender P4 endopod which apparently lacks the short inner seta (resembling more *P. bisetosa* in this respect), the elongate P5 exopod in the female, and some setal length differences on the P5 baseopod in both sexes. According to Chappuis & Delamare Deboutteville (1956) only one female displayed 3 setae on the endopodal lobe (which they figured), the rule being 4 or 5 in the other individuals. Mielke (1975) reported a similar variability for the male endopodal lobe in *P. halophila*. The "soie minuscule" figured on the inner margin of P1 exp-2 (and mentioned in the text description of *P. incerta*) was also referred to by Mielke (1995) in his description of *P. venezolana*.

Boreo–Pontic P. halophila complex

Wells (1961) established *Nitocrella halophila brevifurca* based on material collected from Old Quay beach on St. Martin's Flats, Isles of Scilly. He identified three differences with the type population from the Isle of Sylt (Noodt 1952): (a) antennary exopod 2-segmented instead of 1-segmented, (b) P5 of female with four terminal setae and one small outer seta on exopod (instead of four in total), and with four setae on the baseopod, the outer one being small (instead of three in total), and (c) caudal ramus only as wide as long instead of longer than wide. This suite of differences was regarded sufficient by Lang (1965) to attribute *N. halophila brevifurca* full specific status. However, Mielke's (1975) partial redescription of *P. halophila* from the Isle of Sylt removed the first difference, showing that the antennary exopod is clearly 2-segmented in both populations. He also showed that Noodt (1952) had overlooked the short outer seta on the P5 endopodal lobe, thus agreeing with Wells' (1961) specimens, and confirmed the presence of a "Doppelstruktur" on the outer margin of the exopod which corresponds with the supernumerary seta in the Isles of Scilly material (representing the tube-pore). Mielke's (1975) and Wells' (1961) illustrations both show the caudal ramus in ventral aspect and agree remarkably well in length:width ratio. Noodt (1952) figured the caudal ramus in dorsal aspect which may account for the length difference, thus removing the last difference between the German and English "populations". Mielke (1975) saw no reason in maintaining the Isles of Scilly subspecies and sank it as a junior subjective synonym of *P. halophila*. We have re-examined Wells' (1961) type material, consisting of two female syntypes mounted *in toto* on slides (NHM reg. nos 1960.11.14.1–2), and can confirm they agree in every aspect with Mielke's (1975) redescription.

Apostolov (1969) described *P. pontica* from the Bulgarian Black Sea coast but did not present any differential diagnosis or factual justification for establishing this species. *Pseudoleptomesochrella pontica* differs from its congeners primarily in the presence of a well developed inner seta on P1 exp-2. Michailova-Neikova & Voinova-Stavreva (1971), apparently unaware of Apostolov's (1969) paper, reported the northwestern European *P. halophila* from Arkutino, less than 25 km south of the type locality of *P. pontica*. Their only figure, depicting the female P4, suggests they were dealing with the same species occurring along the Turkish Black Sea coast (this study). Marinov (1973) attempted to resolve the anomaly by comparing Apostolov's (1969) type material of *P. pontica* with his own specimens from near the Bulgarian–Turkish border, concluding that both populations were morphologically identical and almost certainly conspecific with *P. halophila*. He pointed out several observational errors in Apostolov's (1969) description, including (a) P1 exp-2 lacks the inner seta, (b) P1 enp-3 is considerably longer than enp-2 instead of equally long, and (c) the distal segment of the antennary exopod is much shorter instead of as long as exp-1. Surprisingly, Apostolov (1972) had already

rectified these mistakes in his new illustrations of *P. pontica*, published as part of a catalogue to the marine harpacticoids of Bulgaria but not cited by Marinov (1973). The fact that these figures are entirely out of sequence, being the last ones in the catalogue and without any textual reference to them, suggests they were added as a last-minute revision subsequent to consultation with T.M. Marinov when his 1973 paper had already been submitted (31 August 1971). Contrary to Bodin's (1988, 1997) claim, Marinov (1973) did not formally synonymize *P. pontica* with the type species, presumably on the sole ground that there was an additional seta on the female P5 baseoendopod in the Bulgarian species (the correct number of setae was not known until Mielke's (1975) redescription). Although Marinov (1973) identified his material with *P. halophila*, the concept of *P. pontica* as a valid species perpetuated in the literature until recently (Mielke 1975, 1995; Wells 1976). Apostolov & Marinov (1988) finally appeared to have settled the issue in their Fauna Bulgarica by citing *P. pontica* as a synonym of *P. halophila*; the illustrations used are based on Marinov (1973). Wells (2007) accepted this synonymy, however, faced with the intraspecific variability displayed by *P. halophila*, continued to use the Black Sea populations as a separate entry in his tabular keys.

It would be unwise to attribute specific status to the Turkish populations based solely on differences in the P2–P4 armature formula since it is highly conceivable that none of the Bulgarian descriptions (Apostolov 1969, 1972; Michailova-Neikova & Voinova-Stavreva 1971; Marinov 1973) is devoid of observational errors (see above and Mielke 1995). Unfortunately the type material of *P. pontica* is no longer extant (A. Apostolov, pers. comm.) and no topotypes could be obtained so that any discrepancies between Apostolov's (1969, 1972), Marinov's (1973) and our descriptions have to remain unresolved. One character of particular interest is what appears to be a dorsal crest on the caudal ramus of *P. pontica* (illustrated in both Apostolov descriptions). Such structure is reminiscent of the condition in *P. venezolana* but is definitely absent in the Turkish specimens. Other potentially significant differences include the well developed spinular row on the anal operculum (Apostolov 1972, Fig. 210), the spinular ornamentation on the outer margin of P1 enp-1 (Apostolov 1969, Abb. 5; 1972, Fig. 218), the longer outermost seta on the female P5 exopod (Apostolov 1969, Abb. 9; 1972, Fig. 222), and the absence of the paired minute setae on the male P5 baseoendopod (Apostolov 1969, Abb. 12; 1972, Fig. 223). Pending the collection of topotype material we prefer to remove *P. pontica* from its synonymy with the type species and reinstate it as *species inquirenda* in *Pseudoleptomesochrella*.

Similarly, the type material of *P. halophila* is no longer available for detailed comparisons, however, Mielke (1975) provided a partial but accurate redescription based on material from Sylt (the type locality). Except for the caudal rami which are shorter than in the Turkish specimens, all other illustrations (antennary exopod, P1, P5 of both sexes) agree closely with the present description. Although some characters require confirmation in the Sylt material (e.g. sexual dimorphism of P4 endopod) there appears to be no substantial evidence at present that would refute conspecificity with the Black Sea material. At present the distribution of *P. halophila* in the Black Sea Basin appears to be restricted to the southern part of the Bulgarian coast and the northwestern part of the Turkish coast (Fig. 5). In their comparative study on the spatial variability of the structure of harpacticoid assemblages in intertidal and shallow-water zones of the European Seas (including the Black and Azov Seas), Chertoprud *et al.* (2007) recorded the genus *Pseudoleptomesochrella*, however, it is not clear which sea basin they were referring to.

The Black Sea is arguably the world's most isolated sea, connected to the Atlantic Ocean via the Mediterranean Sea through the Bosphorus, Dardanelle and Gibraltar straits, and linked with the Sea of Azov in the northeast through the Kerch Strait. The fauna of the Black Sea is extremely sensitive to the expansion of immigrant species due to the high diversity of habitats and the low diversity of native species. Unoccupied ecological niches and the absence of natural competitors or enemies provide favourable conditions for exotic invaders. Native populations originating from the Mediterranean are a significant source of enhancement for the Black Sea fauna, and in this way the Black Sea is also enriched with warm-water species of Atlantic origin. This is particularly the case for ostracods and larger crustaceans (see review by Gönllügür-Demirci 2006). The current boreo-pontic distribution of *P. halophila* is however, difficult to explain since there are no pub-

lished records from the Mediterranean and extensive sampling of sandy beaches along the entire Mediterranean coast and most of the Aegean coast of Turkey failed to recover any *Pseudoleptomesochrella* species (S. Karaytuğ & S. Sak, unpublished data).

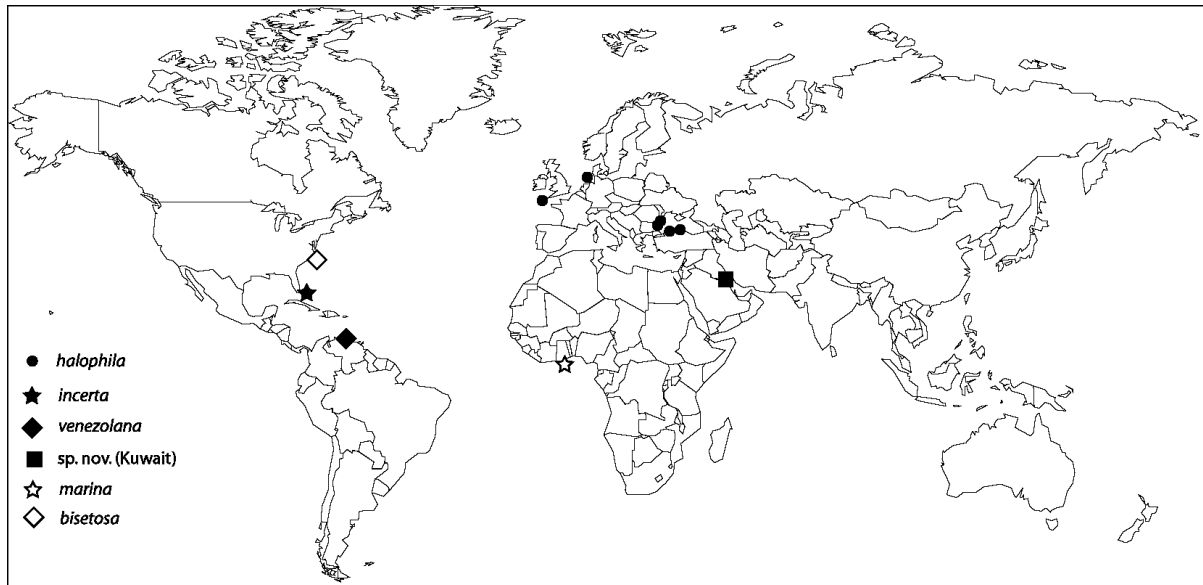


FIGURE 5. Distribution of *Pseudoleptomesochrella* species.

Key to species

1. P1 exp-3 with 5 setae/spines; P2 exp-3 with 4 spines and 1 vestigial seta; P5 endopodal lobe ♀ with 4 elements.....2.
 P1 exp-3 with 4 setae/spines; P2 exp-3 with 3 spines and 1 vestigial seta; P5 endopodal lobe ♀ with 3 elements.....3.
2. Caudal ramus with dorsal crest-like bulge; anal operculum spinular; proximal outer seta of P5 exopod ♀ at least twice the length of adjacent outer one; P5 endopodal lobe ♂ with one long seta.....*P. pontica*.
 Caudal ramus without dorsal crest-like bulge; anal operculum smooth; proximal outer seta of P5 exopod ♀ about the same length as adjacent outer one; P5 endopodal lobe ♂ with one long and 2 small setae
 *P. halophila*.
3. P1 enp-1 1.6 times length of enp-2 and -3 combined.....*P. bisetosa*.
 P1 enp-1 1.0–1.1 times length of enp-2 and -3 combined4.
4. P5 exopod ♀ distinctly longer than wide; longest element on P5 endopodal lobe ♂ about as long as exopod *P. incerta*.
 P5 exopod ♀ semicircular; longest (or only) element on P5 endopodal lobe ♂ distinctly longer than exopod5.
5. P4 ♂ enp-1 distinctly longer than enp-2; P5 exopod ♂ with 4 elements; caudal ramus likely without dorsal bulge *P. marina*.
 P4 ♂ enp-1 and -2 about equally long; P5 exopod ♂ with 3 elements; caudal ramus with crest-like dorsal bulge*P. venezolana*.

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