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Towards a revision of *Ameira* Boeck, 1865 (Harpacticoida, Ameiridae): reinstatement of *Psammameira* Noodt, 1952

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Both sexes of *Ameira hyalina* (Noodt, 1952) and *A. parasimulans* Lang, 1965 are redescribed. The genus *Psammameira* Noodt, 1952 previously regarded as a junior subjective synonym of *Ameira*, is reinstated to accommodate these two species and a revised diagnosis for the genus is presented. Examination of the type material of *Psammameira reducta* Wells, 1967 and *P. grandis* (Nicholls, 1939) revealed that they should be removed from the genus. The possible relationships of two species of doubtful affinity, *A. exigua* T. Scott, 1894 and *A. simulans* T. Scott, 1912 are reconsidered. The phylogenetic position of *Psammameira* within the Ameiridae is briefly discussed. © 1998 The Norwegian Academy of Science and Letters

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Introduction

One morphological character that is traditionally used in the taxonomy of harpacticoid copepods is the separation or fusion of the antennary basis and proximal endopod segment. Although this character is seldom useless in harpacticoid systematics it has frequently been illustrated incorrectly and in many cases has been improperly assigned excessive taxonomic or phylogenetic weight at the expense of other morphological characters. This has often led to considerable taxonomic confusion in families where the presence or absence of an antennary allobasis has been applied as a generic discriminant. In the Ameiridae for example, it served as one of the major characters to separate *Psammameira* Noodt, 1952 and *Ameira* Boeck, 1865, a genus that is currently under revision (Conroy-Dalton & Huys 1997).

The genus *Psammameira* was proposed by Noodt (1952) to accommodate a new species *P. hyalina* from the Isle of Sylt. The genus was differentiated from *Ameira* on the basis of the presence of an antennary allobasis, the maxilla with three endites (i.e. two endites on the syncoxa), the unusual swimming leg setal formula and the presence of 5 setae on the female P5 baseoendopod. Wells (1967) questioned the taxonomic significance of some of these characters, but regarded the antennary condition of vast importance. He admittedly widened the boundaries of the genus by including *Ameira grandis* Nicholls, 1939 originally described from the St. Lawrence River in Canada (Nicholls 1939) and regarded to hold a problematic systematic position (Lang 1965), and a third newly described species *P. reducta* Wells, 1967 from Inhaca Island (Mozambique). Wells (1967) assumed that the graded series of reduction displayed by these species was merely a reflection of the evolution within the genus. Two more species of doubtful status, *A. exigua* T. Scott, 1894 and *A. simulans* T. Scott, 1912 were also considered as likely members of *Psammameira* since both possess 5 setae on the P5 baseoendopod (Wells, 1967).

Mielke (1975), following Lang (1965), assigned little taxonomic importance to the characters listed by Noodt (1952) and regarded their usefulness as generic discriminants in the Ameiridae rather limited. Upon re-examination of *P. hyalina*, Mielke (1975) claimed that the antenna displayed a genuine basis and, consequently, that the species should be allocated to *Ameira*. Rather than relegating *Psammameira* as a junior subjective synonym of *Ameira*, the author retained Noodt's genus for *P. grandis* and *P. reducta* and designated the latter as '... neue Typusart der Gattung *Psammameira*...'. This is unacceptable nomenclatural practice which is clearly in violation of the Type Concept as stipulated in ICZN Art. 61. Unfortunately, Bodin (1979*a*, 1988) adopted Mielke's designation in his catalogues and fuelled the confusion even further by listing *P. reducta* as the 'néotype' of *Psammameira*.

We have re-examined the syntypes and new material of *P. hyalina* obtained from near the type locality and found several distinct differences with the genus *Ameira* in general, and the *A. longipes*- group in particular, necessitating the resurrection of *Psammameira* as a valid genus. Re-examination of the type material of *A. grandis* revealed that it is an amalgamate of a new species of *Proameira* Lang and a second species of an as yet undescribed genus which does not bear any close relationship to *Psammameira* (Conroy-Dalton & Huys, in prep.). *Psammameira*

reducta differs significantly from *P. hyalina* and should be removed to a new genus which will be dealt with in a forthcoming paper.

The genus *Psammameira* is reinstated here to accommodate the type-species *P. hyalina* and a species previously referred to *Ameira: A. parasimulans* Lang, described from the Californian coast (Lang 1965).

Material and methods

Before dissection, body length measurements were made from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid, and the parts mounted in lactophenol. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a camera lucida on a Leitz Diaplan or Zeiss Axioskop differential interference contrast microscope. The descriptive terminology for body and appendage morphology is adopted from Huys & Boxshall (1991). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. Specimens of *P. hyalina* are deposited in the collections of the Natural History Museum (NHM), London.

Family AMEIRIDAE Monard, 1927

Genus *Psammameira* Noodt, 1952

Diagnosis. Ameiridae. Body cylindrical and slender, without clear demarcation between prosome and urosome; integument not strongly chitinized; without ornamentation dorsally; somatic arthrodial membranes well developed. Somatic hyaline frills plain (cephalothorax and somites and bearing P2–P5) or minutely denticulate (abdominal somites). Female genital and first abdominal somites completely fused forming genital double-somite; original segmentation marked by small, transverse, internal ribs dorsolaterally. Urosome and caudal rami with ventral pattern of distinctive tube pores. Anal operculum smooth. Caudal ramus short and slightly conical; with 7 setae. Sexual dimorphism in body size, antennule, P1 (inner basal spine), P5, P6, and in genital segmentation.

Rostrum small, shorter than first antennulary segment, slender, demarcated at base. Antennulary setae smooth and slender except for single pinnate seta on segments 1 and 2; acrothek on apical segment consisting of aesthetasc and 2 long setae; 8-segmented in ♀, with aesthetasc on segments 4 and 8; 9-segmented and haplocer in ♂, with geniculation between segments 7 and 8 and aesthetasc on segments 5 and 9. Antenna with basis and proximal endopod segment incompletely fused forming allobasis; endopod with 2 lateral and 6 distal elements (outermost one with proximal tuft of setules). Antennary exopod 2-segmented; armature formula [1,2]; exp-1 tapering proximally, bearing 2 groups of spinules and minute-surface frill; exp-2 small. Mandibular palp uniramous, 2-segmented, comprising basis and 1-segmented endopod; basis with 1 flaccid densely plumose and 2 distinctly pectinate elements; endopod with 1 lateral and 4 apical setae. Maxillule with 1 element on coxal endite; basis with 5 naked setae; endopod represented by 2 elements, 1 diminutive and spiniform; exopod absent. Maxillary syncoxa with 2 well developed endites, proximal one expanded distally and with 2 flaccid plumose setae; distal one with 1 pinnate and 2 pectinate elements; allobasis drawn out into a claw and with pectinate spine; endopod 1-segmented, with 2 setae. Maxilliped subchelate; syncoxa with 1 seta; endopod represented by claw with 2 accessory setae.

P1–P4 with 3-segmented rami. P1 inner basal spine of ♂ club-shaped, blunt and with spinules along outer margin. P1 exopod without inner seta on exp-2; exp-3 with 3 outer spines and 2 geniculate setae distally. P1 endopod prehensile, with enp-1 about as long as enp-2 and -3 combined, and shorter than exopod; inner seta of enp-2 well developed. P2–P3 without inner seta on exp-1. P3–P4 enp-3 with 4 armature elements. Armature formula as follows:

	Exopod	Endopod
P1	0.0.023	1.1.111
P2	0.1.123	1.1.[0-1]21
P3	0.1.123	1.1.121
P4	0.1.[2-3*]23	1.1.121

*: when present, distal inner seta minute and displaced onto posterior surface

P5 with separate baseoendopod and exopod in both sexes; baseoendopods fused medially in ♂; ♀ with 5 setae/spines on baseoendopod, middle and distal inner spines serrate apically, exopod with 6 setae; ♂ with 5 setae on exopod, baseoendopod with 1 minute seta and 1 apically serrate spine, inner distal corner of endopodal lobe attenuated forming distinctive process. Female genital field positioned far anteriorly; with wide, medium-sized copulatory pore leading via long, chitinized copulatory duct to paired seminal receptacles; gonopores covered by common, medially incised genital operculum derived from P6, bearing short plumose seta, spiniform element and spinous process on either side. Male P6 asymmetrical, one member fused to somite; each with 3 simple setae, of which middle one longest.

Type-species. *Psammameira hyalina* Noodt, 1952 [by monotypy]

Other species. *Ameira parasimulans* Lang, 1965 = *P. parasimulans* (Lang, 1965) comb. n.

Psammameira hyalina Noodt, 1952

Material examined and type locality. (a) W. Noodt Collection, Christian-Albrechts-Universität Kiel, Germany: 3 damaged slides labelled as: *Parameira hyalina* n.sp., (1) III_2List—Brücke, 29. VI. 51 (2) VI_1List—Süd, 1. VI.51 (3) VI_1List—Süd, 1. VI.51. (b) 5 ♀♀, 2 ♂ ♂ from sandy beach in front of Biological Station, Isle of Sylt, Germany. Interstitial water collected using 63 μm mesh-sieve by Karaman-Chappuis method; coll. R. Huys, 6 August 1996; 1 ♀ dissected on 9 slides (NHM reg. no. 1997. 707); 1 ♂ dissected on 8 slides, A1, A2, cephalosome, P2–P4 and urosome dissected (NHM reg. no. 1997. 708); 4 ♀♀, 1 ♂ in alcohol (NHM reg. no. 1997. 709–713).

Remark. From the detailed collection data on the 3 slides it is clear that they represent the only extant syntypes designated by W. Noodt and that the author had inadvertently mislabelled them as *Parameira hyalina*.

Redescription

Female. (Figs 1, 2A–B, 3, 4, 5, 6A–C). Total body length 447 μm ($\bar{x} = 418$ μm) measured from tip of rostrum to posterior margin of caudal rami. Largest width 78 μm measured at posterior margin of cephalothorax.

Body cylindrical, slender (Fig. 1A, C), without distinct demarcation between prosome and urosome. Integument

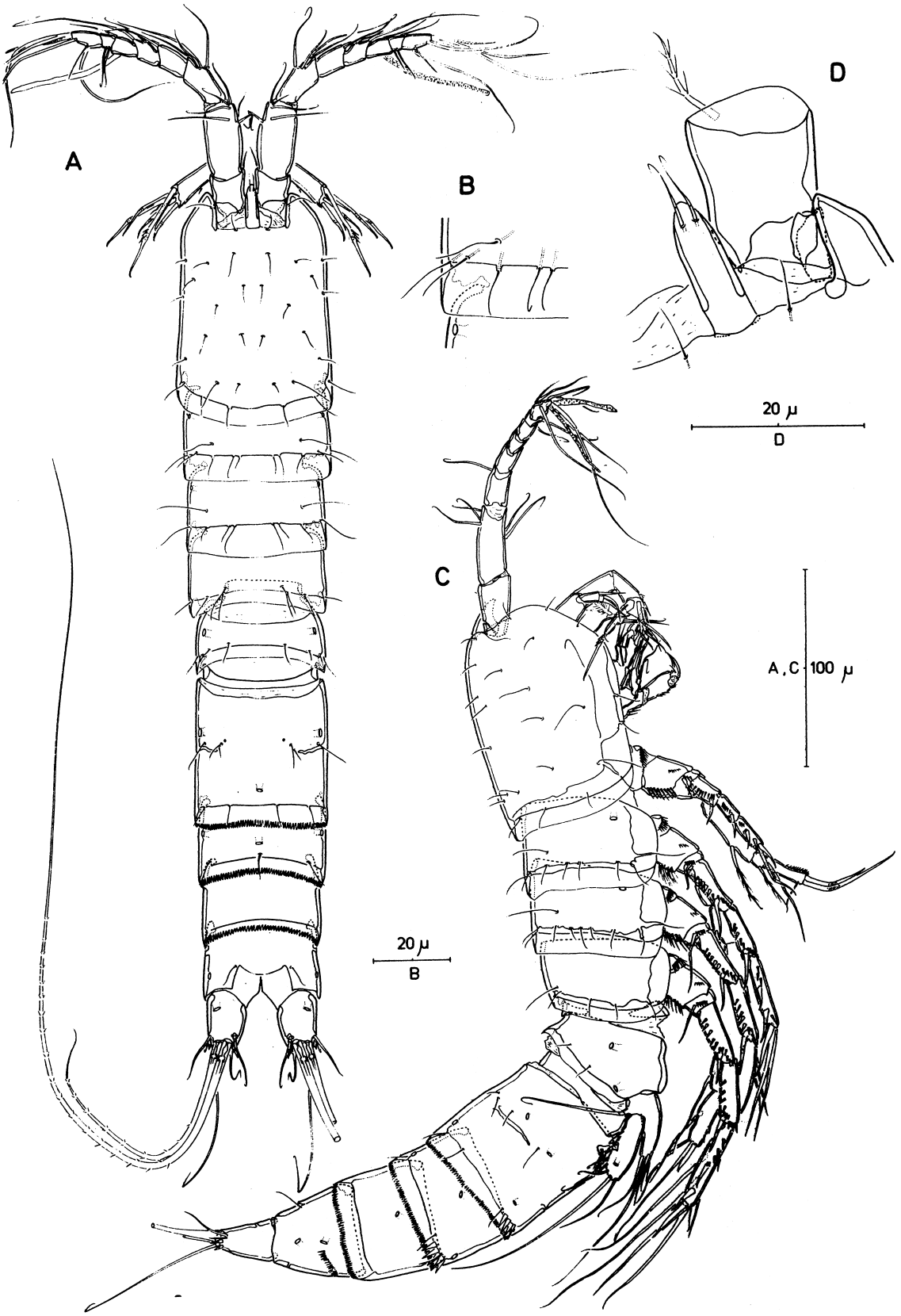

Fig. 1. Psammameira hyalina. A. Habitus ♀, dorsal. *B*. Hyaline frill and sensilla of P2-bearing somite ♀, dorsal. *C*. Habitus ♀, lateral. *D*. Rostrum and antennulary segment 1 ♀, dorsal.

not strongly chitinized. Arthrodial membranes well developed. Hyaline frill of cephalothorax and somites bearing P2–P5 smooth (Fig. 1A–C), minutely denticulate on genital double-somite and abdominal somites (Figs 1A, C, 2A). Cephalothorax and somites bearing P2–P5 with sensillae as only surface ornamentation (Fig. 1A, C). Genital double-somite elongate; original segmentation marked by internal chitinous ribs dorsolaterally only (Figs 1A, C, 2A); posterior margin with paired ventrolateral spinule rows (Fig. 2A). Second abdominal somite (Figs 1A, 2A)

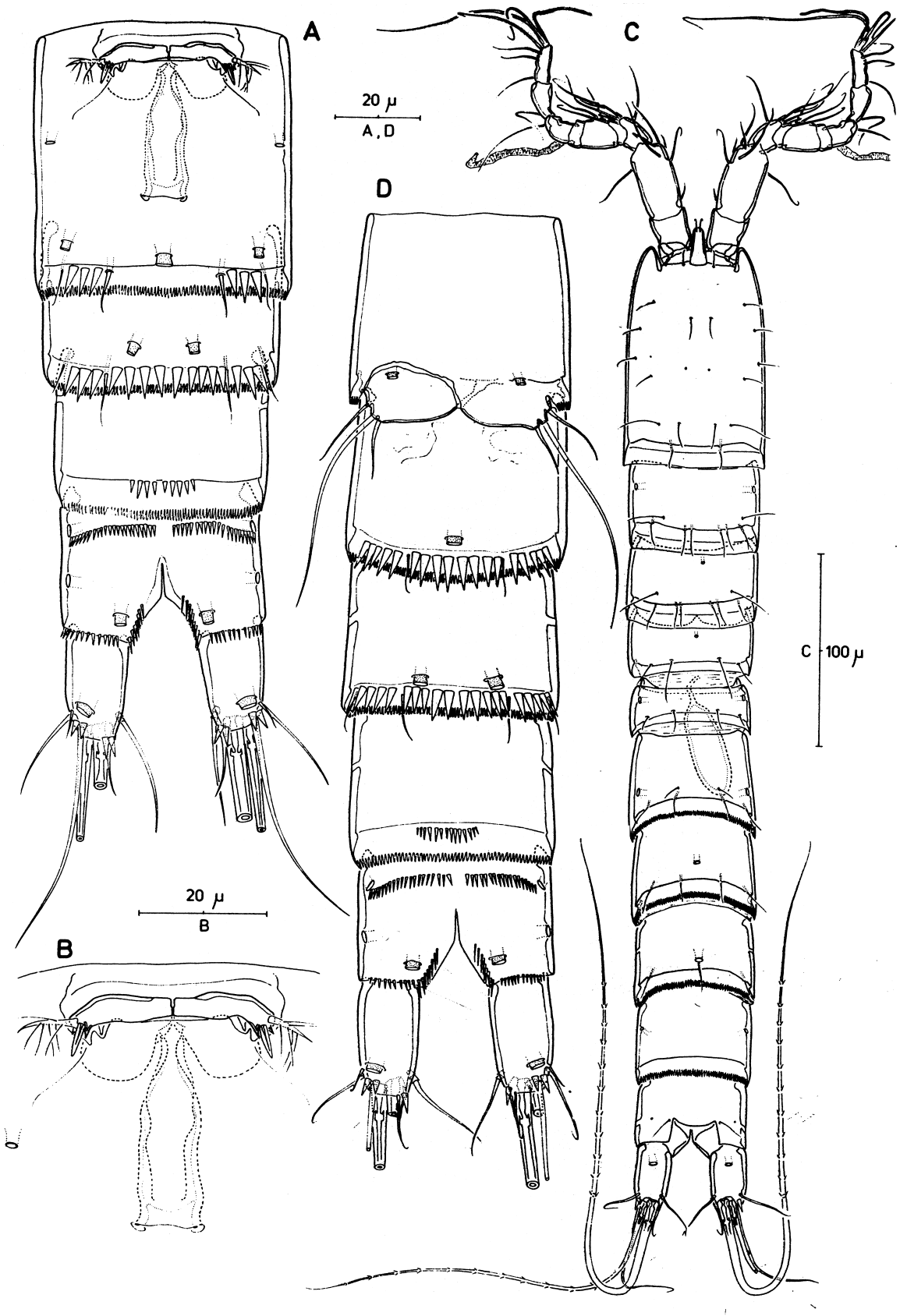

Fig. 2. Psammameira hyalina. A. Urosome ♀ (excluding P5-bearing somite), ventral. *B*. Genital field ♀, ventral. *C*. Habitus ♂, dorsal. *D*. Urosome ♂ (excluding P5-bearing somite), ventral.

with distinct median sensilla dorsally and ventral spinule row. Third abdominal somite (Figs 1A, 2A) with mid-ventral spinule row. Anal somite distinctly cleft medially (Figs 1A, 2A, 6C); with paired ventral spinule rows anteriorly; spinules present around ventral hind margin; anal operculum rounded and bare (Fig. 6C). Caudal rami (Figs 1A, C, 2A, 6C) short, very slightly conical, about 1.8 times as long as average width; few spinules present around ventral hind margin and outer distal corner (Fig. 2A); with 2 secretory pores and 7 setae: seta I diminutive (Fig. 6C);

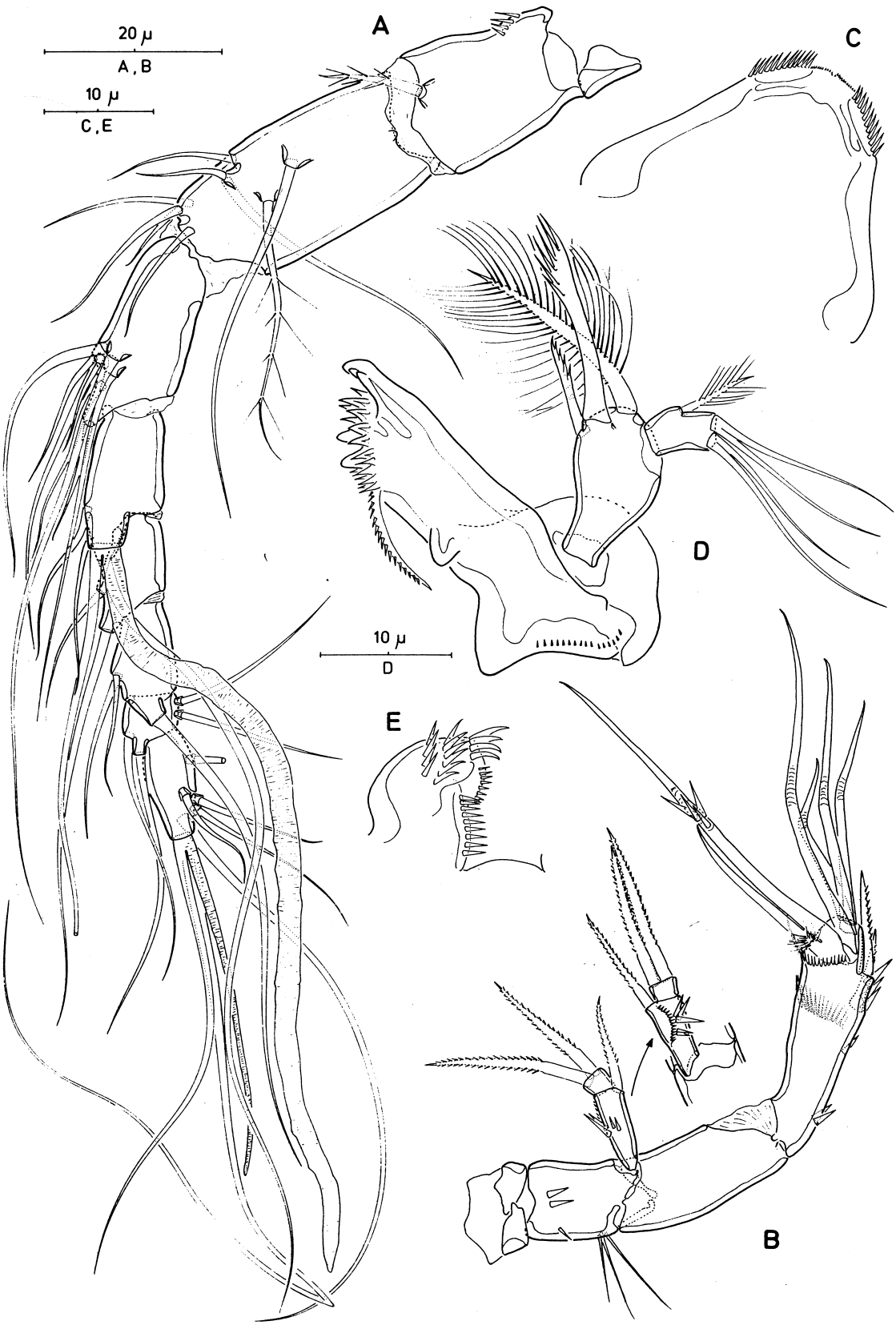

Fig. 3. Psammameira hyalina. A. Antennule ♀, ventral. *B.* Antenna ♀ (arrowed insert indicating lateral view of exopod). *C.* Labrum ♀, anterior. *D.* Mandible ♀. *E.* Left paragnath ♀, anterior.

seta III slightly displaced to ventral distal position (Figs 2A, 6C); setae IV and V well developed and pinnate in distal portion (Figs 1A, 6C); seta VI partially fused to inner distal margin of caudal ramus (Fig. 6C); seta VII triarticulate at base and located at insertion level of setae I–II. Genital double-somite, second abdominal somite, anal somite and caudal rami with large conspicuous tube pores ventrally.

Rostrum (Fig. 1A, D) elongated with rounded tip, demarcated at base; with 2 dorsal sensillae; shorter than first antennulary segment; no pore discernible.

Antennule (Fig. 3A) 8-segmented. Segment 1 with 1

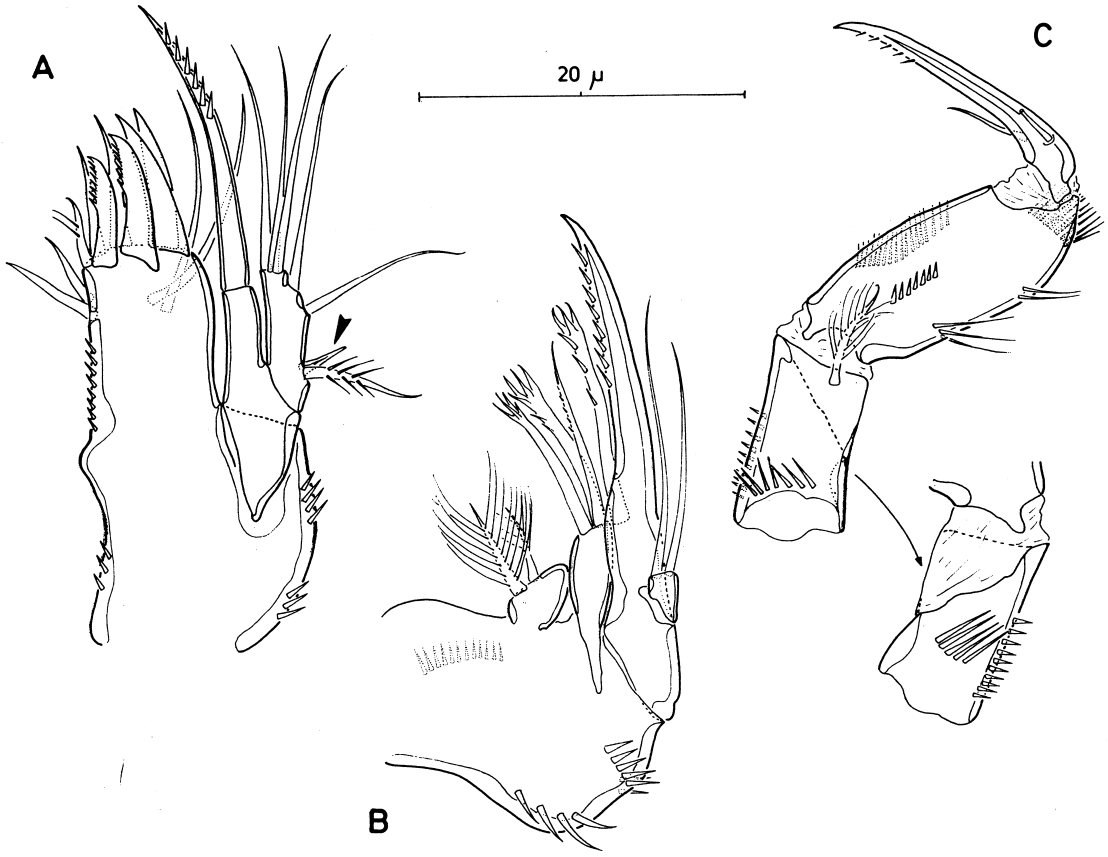

Fig. 4. Psammameira hyalina. A. Maxillule ♀ (arrow indicating diminutive seta). *B.* Maxilla ♀. *C.* Maxilliped ♀, posterior (arrowed insert indicating syncoxa, anterior).

anterior spinule row. Segment 2 longest. Armature formula: 1-[1 pinnate], 2-[1 pinnate +8 bare], 3-[8], 4-[3+(1+ ae)], 5-[2], 6-[3], 7-[4], 8-[5+ acrothek]. Apical acrothek consisting of 2 long setae fused basally to slender aesthetasc.

Antenna (Fig. 3B). Coxa minute, bare. Basis and proximal endopod segment incompletely fused forming allobasis; original segmentation marked by incomplete surface suture; with spinule rows in basal part (Fig. 3B). Endopod with 2 surface frills subdistally; lateral armature consisting of 2 unipinnate spines; apical armature consisting of 5 geniculate setae, with longest one bearing spinules around geniculation and fused basally to smaller seta bearing proximal tuft of fine setules. Exopod 2-segmented (Fig. 3B); armature formula [1,2], all setae bipinnate; exp-1 elongate, tapering proximally, with 2 groups of spinules and tiny surface frill; exp-2 small.

Labrum (Fig. 3C) bell-shaped with spinule rows near distal margin

Mandible (Fig. 3D). Coxal gnathobase with coarse teeth ventrally, 1 pinnate seta dorsally and row of smaller teeth in between; with spinule row proximally. Palp (Fig. 3D) uniramous; 2-segmented, comprising basis and 1-segmented endopod. Basis with 1 flaccid, densely plumose and 2 pectinate setae. Endopod with 1 short pinnate seta laterally, 4 naked setae apically, arranged in 2 basally fused pairs.

Paragnaths (Fig. 3E) paired; with numerous spinule rows around inner and distal margins.

Maxillule (Fig. 4A). Praecoxal arthrite rectangular; with 2 anterior surface setae, 2 lateral elements and distal armature consisting of 4 bare spines, 2 pectinate/serrate spines and 1 pinnate seta. Coxal endite with long distally pinnate spine. Basis with 3 naked setae distally and 2 naked setae laterally. Endopod represented by 1 bipinnate seta and 1 diminutive seta partially fused to basis (arrowed in Fig. 4A). Exopod absent.

Maxilla (Fig. 4B). Syncoxa with 3 spinule rows and 2 well developed (coxal) endites; proximal endite of distinctive shape, expanded distally, with 2 flaccid, plumose setae; distal endite with 1 pinnate and 2 apically pectinate setae. Allobasis drawn out into claw-like pinnate endite; with pectinate pinnate spine at base. Endopod a discrete segment with 2 naked setae.

Maxilliped (Fig. 4C) subchelate. Syncoxa with 1 plumose seta; spinule rows on anterior and posterior surfaces. Basis with two groups of long, slender spinules along outer margin, anterior spinule row along inner margin and spinule row on posterior surface. Endopod represented by distally pinnate claw accompanied at base by short tube seta and longer bare seta.

P1 (Fig. 6A) with well developed praecoxa. Coxa with 1 posterior and 3 anterior spinule rows. Basis with bipinnate outer seta and unipinnate inner spine. Exopod 3-segmented; exp-2 without inner seta; exp-3 with 3 outer pinnate spines and 2 geniculate setae distally. Endopod 3-segmented, prehensile; enp-1 about as long as enp-2 and -3 combined and slightly shorter than exopod, with subdistal plumose seta; enp-2 short, inner seta plumose and well developed; enp-3 long, 3.6 times as long as enp-2 (measured

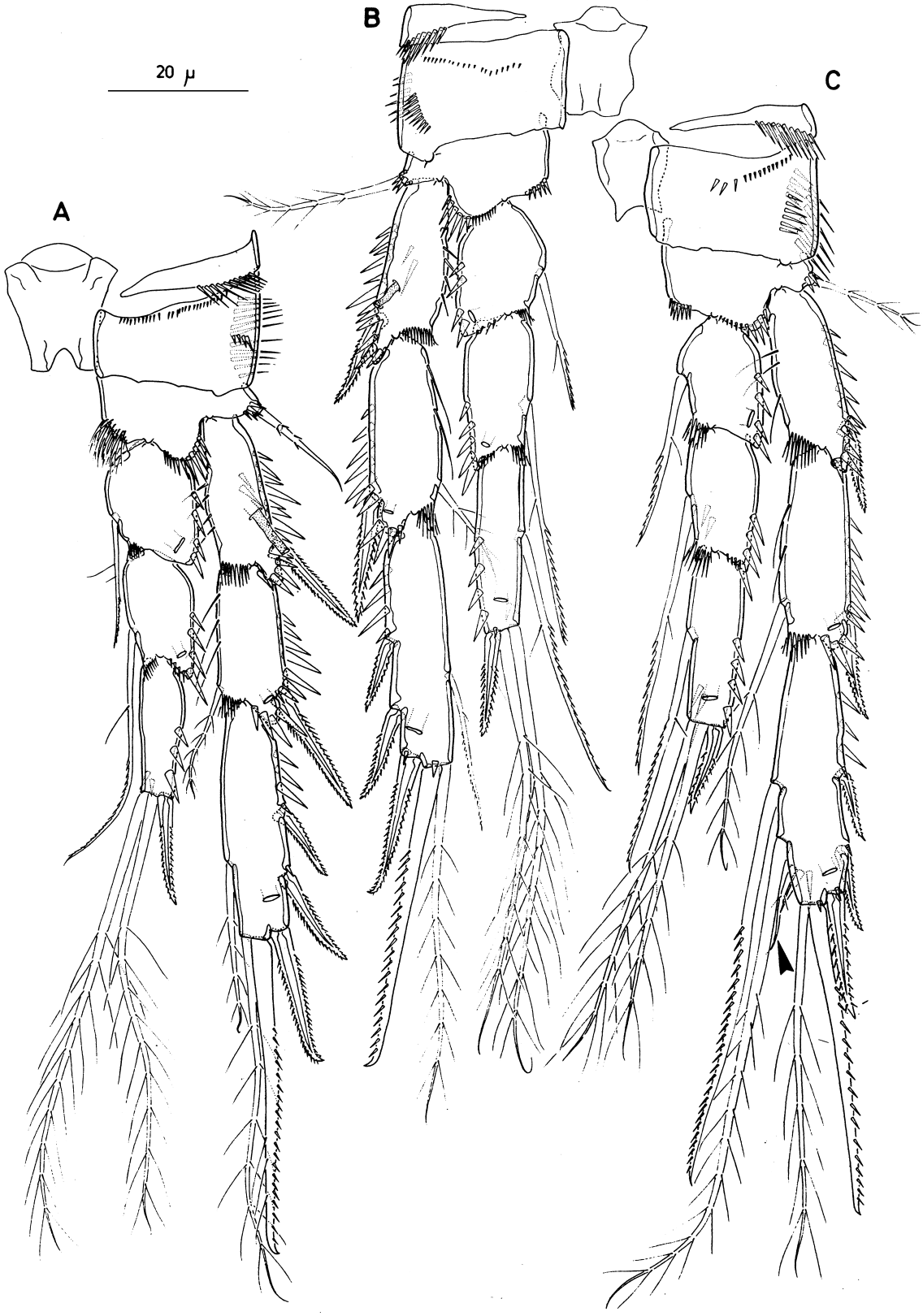

Fig. 5. Psammameira hyalina. A. P2 ♀, anterior. *B.* P3 ♀, anterior. *C.* P4 ♀, anterior (arrow indicating small recurved seta).

along inner margin), with 1 plumose and 2 geniculate setae.

P2–P4 (Fig. 5A–C) with 3-segmented rami; endopods shorter than exopods. P2–P4 exp-3 and enp-3 elongate; enp-1 swollen, with rounded inner margin. Coxae with spinule rows on both anterior and posterior surface. Bases with pinnate (P2) or plumose (P3–P4) outer seta. Anterior surface of most endopodal and exopodal segments with secretory pores; P2–P3 exp-1 with long tube pore. Distal inner seta of P4 exp-3 small, recurved and slightly displaced onto posterior surface (arrowed in Fig. 5C). Armature formula as follows:

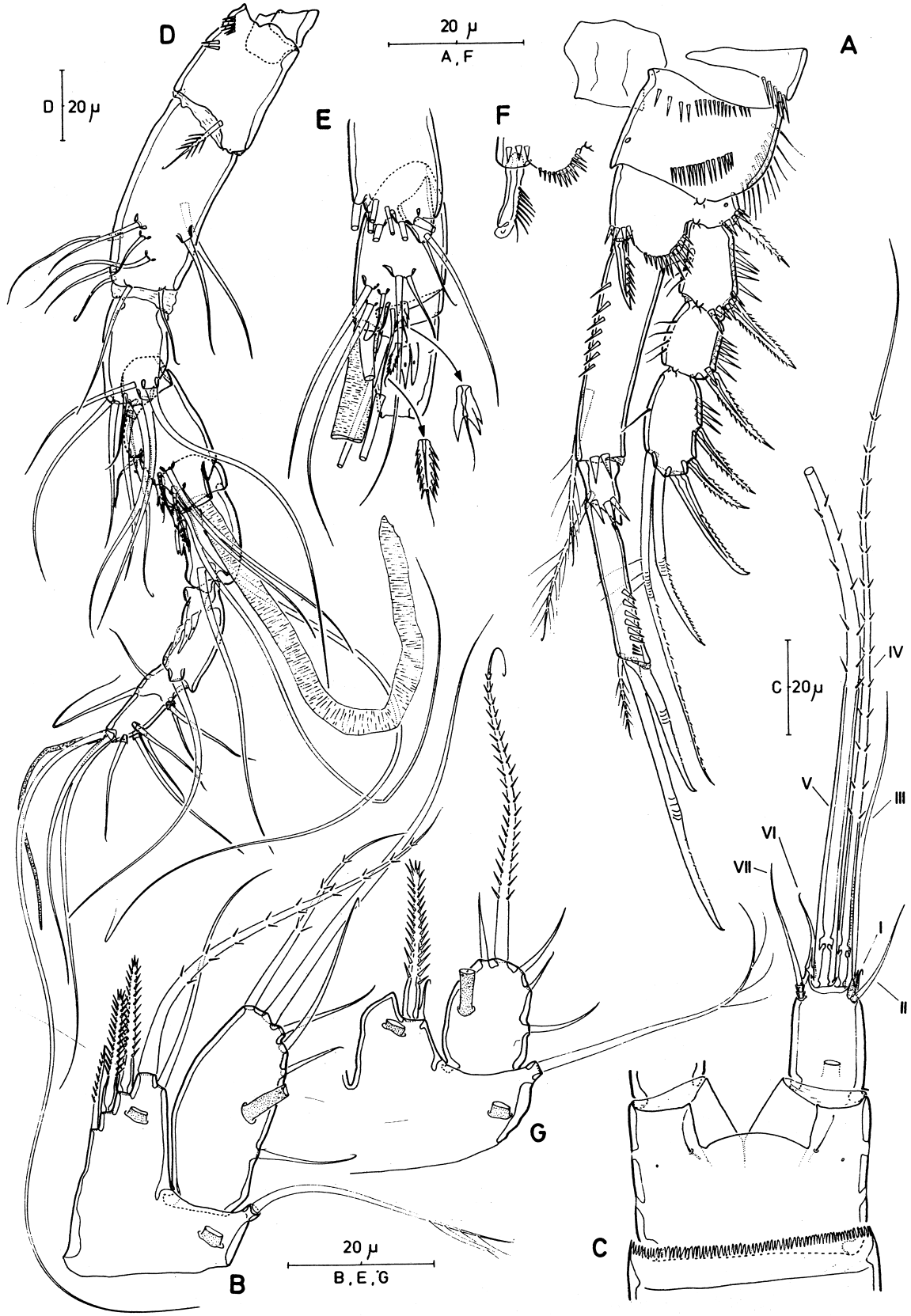

Fig. 6. Psammameira hyalina. A. P1 ♀, anterior. *B.* P5 ♀, anterior. *C.* Anal somite and left caudal ramus ♀, dorsal. *D.* Antennule ♂, ventral. *E.* Detail of antennulary segments 3–7 ♂, lateral (arrowed inserts indicating modified setae). *F.* P1 ♂, inner basal spine, anterior. *G.* P5 ♂, anterior.

	Exopod	Endopod
P2	0.1.123	1.1.021
P3	0.1.123	1.1.121
P4	0.1.323	1.1.121

P5 (Fig. 6B) biramous. Baseoendopod with two large secretory tube pores on anterior surface; outer basal seta arising from short setophore. Endopodal lobe rectangular with stepped inner margin; with anterior secretory tube pore; with 3 bipinnate spines along inner margin, 1 long bipinnate seta apically and 1 outer naked seta; middle and distal inner spines serrate apically. Exopod elongate-oval, 2.2 times as long as maximum width; inner margin with 1 pinnate seta; outer margin with 4 naked setae; apex with 1 long bare seta; anterior surface with 1 large secretory tube pore.

Genital field positioned near anterior margin of genital double-somite (Fig. 2A–B); paired gonopores covered by medially incised genital operculum forming interlocking mechanism derived from fused vestigial sixth legs. P6 with 1 short plumose seta, 1 spiniform element and 1 spinous process (Fig. 2B). Copulatory pore of medium size (Fig. 2B), leading via long chitinized copulatory duct to paired seminal receptacles.

Single median egg-sac.

Male (Figs 2C–D, 6D–G). Larger than female; total body length 490 μm ($\bar{x} = 454\ \mu$m) measured from tip of rostrum to posterior margin of caudal rami. Body (Fig. 2C) cylindrical and slender; ornamentation lacking except for sensillae on dorsal surface; first abdominal somite (Fig. 2D) with ventral spinule row; second abdominal somite with distinct median sensilla dorsally (Fig. 2C). Sexual dimorphism in body size, antennule, P1, P5, P6, abdominal ornamentation and genital segmentation.

Antennule (Fig. 6D–E) slender, 9-segmented and haplocer; geniculation between segments 7 and 8; segment 2 longest; segment 4 represented by U-shaped sclerite; with aesthetasc on segment 5 and as part of apical acrothek on segment 9; apical segment with dorsal, transverse suture marking ancestral fusion plane. Armature formula: 1-[1 pinnate], 2-[10], 3-[7], 4-[2], 5-[6 bare, 1 modified +(1+ ae)], 6-[1 bare], 7-[1+3 modified], 8-[1+3 modified], 9-[9+ acrothek]; see Fig. 6E and arrowed inserts for modified setae on segments 5 and 7.

P1 inner basal spine modified (Fig. 6F); club-shaped with blunt apex; acutely recurved; outer margin with long fine spinules.

P5 (Fig. 6G) biramous. Baseoendopod with outer basal seta arising from short setophore; anterior surface with two secretory pores. Endopodal lobe extending beyond middle of exopod; distal margin with 1 pinnate seta (minutely serrate apically) and a small naked outer seta; inner distal corner attenuated into distinctive pointed process. Exopod much shorter than in female; 1.4 times as long as maximum width; with 5 setae, inner margin with 1 seta, outer margin with 3 setae, apex with 1 long pinnate seta; anterior surface with 1 large secretory pore.

P6 (Fig. 2D) asymmetrical, one member fused to somite, other (functional member) articulating; armature consisting of 3 bare setae, middle one longest.

Spermatophore (Fig. 2C) 43 μm.

Variability. None observed.

Remarks. The original description of *P. hyalina* was based on female specimens only. Mielke (1975) updated Noodt's (1952) observations and provided the first (and only) description of the male. Our material, collected from the vicinity of the type locality, agrees with the original description in most aspects. A number of minor discrepancies were noticed between Noodt's illustrations and the present redescription which are conceivably the result of imperfect dissection or observations: (a) all armature elements of the antennule were figured as naked setae but we found two pinnate setae on segments 1 and 2, respectively; (b) Noodt figured only 1 element on the basis of the mandibular palp as opposed to the 3 highly distinctive elements in the present redescription; (c) P4 exp-3 with 2 inner elements (the tiny distalmost seta being overlooked); (d) the exopodal armature of the P5 was described in the text as 5 well developed setae, although 6 setae are figured (the second outer seta being diminutive); comparison of the figured ♀ P5 (his Abb. 16) with our specimens revealed their morphology to be identical; (e) there appears to be a slight deviation in the caudal ramus length/width ratio, being 1.8 in our specimens as compared to over twice as long as wide in Noodt's description (Noodt 1952); this difference can probably be attributed to the method of mounting and/or drawing as no variability could be detected in our material.

Our male specimens agree closely with Mielke's (Mielke 1975) description in the following aspects: (a) form and shape of the modified inner basal spine of P1; (b) P1–P4 setal formula (the small, distalmost posterior seta of P4 exp-3, however, being overlooked by Mielke); (c) detailed morphology of P5; (d) presence of 3 naked setae on P6. There appears to be some difference in body length, being $\bar{x} = 454\ \mu$m for the redescribed material compared to 300–370 μm for Mielke's specimens. However, the somatic arthrodial membranes are well developed in this genus, and hence the varying degree of telescoping between individual specimens can result in misleading values for body length measurements. The body somites of the female specimen used in this redescription were more telescoped than in the male, causing the false impression that males are larger than females. However, from additional measurements of other specimens there appears to be only a slight difference in body size between sexes. Mielke's (1975) observation that the antenna displays a distinct basis is incorrect and clearly results from a misinterpretation of the incomplete surface suture marking the original segmentation. We suspect that this non-functional remnant of the original segment boundary has been erroneously figured as a solid line in many early ameirid descriptions. On the basis of this character, in conjunction with his conclusion that the swimming leg setal formula and the presence of 5 setae on the ♀ P5 baseoendopod fall well within the realms of the genus *Ameira* as redefined by Lang (1965), Mielke (1975) allocated *P. hyalina* to *Ameira*. The key characters outlined in the generic diagnosis revised above prove the action

taken by Mielke to be unjustified. We consider *Psammameira* to be a distinct genus and consequently reinstate *P. hyalina* as the type species.

Psammameira parasimulans (Lang, 1965) comb. n.

Material examined and type locality.Naturhistoriska Riksmuseet, Stockholm: 9 ♀♀, 1 ♂ and several damaged urosomes in alcohol, labelled 'Syntypes' (reg. no. 2235 (591)): from Dillon Beach, Second Sled Road, California, U.S.A. (type locality). Coll. and det. K. Lang 1960, interstitial water. Lectotype ♀ designated and dissected on 9 slides, paralectotypes are 8 ♀♀ and 1 ♂ in alcohol (all deposited under reg. no. 2235. (591)).

Redescription

Female (Figs 7A–C, 8, 9A–D). Total body length 528 μm ($\bar{x} = 551$ μm) measured from tip of rostrum to posterior margin of caudal rami. Largest width 87 μm measured at posterior margin of cephalothorax.

Body cylindrical, slender (Fig. 7C), without distinct demarcation between prosome and urosome. Integument not strongly chitinized. Arthrodial membranes very well developed. Hyaline frill of cephalothorax and somites bearing P2–P5 smooth (Fig. 7C), minutely denticulate on genital double-somite and abdominal somites (Fig. 7A, C). Cephalothorax and somites bearing P2–P5 with sensillae only as surface ornamentation (Fig. 7C). Genital double-somite elongate; original segmentation marked by internal chitinous ribs dorsolaterally only (Fig. 7A, C); ventral posterior margin with spinule row (Fig. 7A). Second abdominal somite (Fig. 7A,C) with distinct median sensilla dorsally and ventral spinule row. Third abdominal (Fig. 7A) somite with midventral spinule row. Anal somite distinctly cleft medially (Fig. 7A, C); with paired lateroventral and ventrolateral spinule rows anteriorly; spinules present around ventral hind margin; anal operculum rounded and bare (Fig. 7C). Caudal rami (Fig. 7A, C) short, slightly conical, about 1.15 times as long as maximum width; few spinules present around ventral hind margin and outer distal corner; with 2 secretory pores and 7 setae: seta I minute (Fig. 7A); seta III slightly displaced to ventral position (Fig. 7A); setae IV and V well developed and pinnate in distal portion (Fig. 7C); seta VI partially fused to inner distal margin of caudal ramus; seta VII triarticulate at base and located at insertion level of setae I–II. Genital double-somite, second abdominal somite, anal somite and caudal rami with large conspicuous tube pores ventrally.

Rostrum (Fig. 7C) elongate with rounded tip, demarcated at base; with 2 dorsal sensillae; shorter than first antennulary segment.

Antennule (Fig. 9A) as for the type-species. 8-segmented. Armature formula: 1-[1], 2-[9], 3-[8], 4-[3 + (1 + ae)], 5-[2], 6-[3], 7-[4], 8-[5 + acrothek]. Apical acrothek consisting of 2 setae fused basally to slender aesthetasc.

Antenna (Fig. 8A) as for the type-species.

Mandible (Fig. 8B), maxillule, maxilla, maxilliped (Fig. 8C) as for the type-species except for the following: (1) mandible with gnathobase (Fig. 8B) more elongate; basis with fine spinule row; (2) endopod of maxilliped (Fig. 8C) represented by long bare claw accompanied at base by bare seta and tube seta (cf. this seta is shorter in the type-species).

P1 (Fig. 7B) with well developed praecoxa. Coxa with 1 posterior and 3 anterior spinule rows. Basis with bipinnate outer seta and unipinnate inner spine. Exopod as for type-species. Endopod 3-segmented, prehensile; with enp-1 longer than enp-2 and -3 combined and shorter than exopod, with subdistal plumose seta; enp-2 short, inner seta plumose and well developed; enp-3 long, 2.5 times as long as enp-2 (measured along inner margin), with 1 plumose and 2 geniculate setae.

P2–P4 as for the type-species except for: (1) P2 outer basal seta more stubby; enp-3 with inner seta (Fig. 9B); (2) P4 exp-3 (Fig. 9C) without small recurved posterior seta along inner margin. Armature formula as follows:

	Exopod	Endopod
P2	0.1.123	1.1.121
P3	0.1.123	1.1.121
P4	0.1.223	1.1.121

P5 (Fig. 9D) biramous. Baseoendopod with 2 secretory pores on anterior surface; outer basal seta arising from short setophore. Endopodal lobe rectangular; with 1 unipinnate seta and 2 bipinnate spines along inner margin, 1 long bipinnate seta apically and bare seta along outer margin; middle and distal inner spines serrate apically. Exopod oval, 2.47 times as long as maximum width; inner margin with 1 pinnate seta; outer margin with posterior spinule row and 4 naked setae; apex with 1 long bare seta; anterior surface with 1 secretory tube pore.

Genital field positioned near anterior margin of genital double-somite (Fig. 7A); paired gonopores opening via common midventral slit covered by medially incised genital operculum forming interlocking mechanism derived from fused vestigial sixth legs. P6 with 1 plumose seta, 1 spiniform element and 1 spinous process (Fig. 7A). Copulatory pore narrow (Fig. 7A), leading via long chitinized copulatory duct to paired seminal receptacles.

Single median egg sac.

Male (Figs 7D–E, 9E). Smaller than female. Total body length 490 μm measured from tip of rostrum to posterior margin of caudal rami. Body cylindrical and slender; ornamentation as for type-species. Sexual dimorphism in body size, antennule, P1, P5, P6, and genital segmentation.

Antennule, 9-segmented, as in type-species. Armature formula: 1-[1], 2-[10], 3-[7], 4-[2], 5-[6, 1 modified + (1 + ae)], 6-[1], 7-[1 + 3 modified], 8-[1 + 3 modified], 9-[9 + acrothek].

P1 inner basal spine modified (Fig. 7D); club-shaped and blunt at tip; acutely recurved; outer margin with long fine spinules.

P5 (Fig. 9E) biramous. Baseoendopod with outer basal seta arising from short setophore; anterior surface with 2 secretory pores. Endopodal lobe extending beyond middle of exopod; distal margin with 1 pinnate seta (minutely serrate apically) and a small naked outer seta; inner distal corner attenuated into small, distinctive process. Exopod much shorter than in female; 1.35 times as long as maximum width; with 5 setae, inner margin with 1 seta,

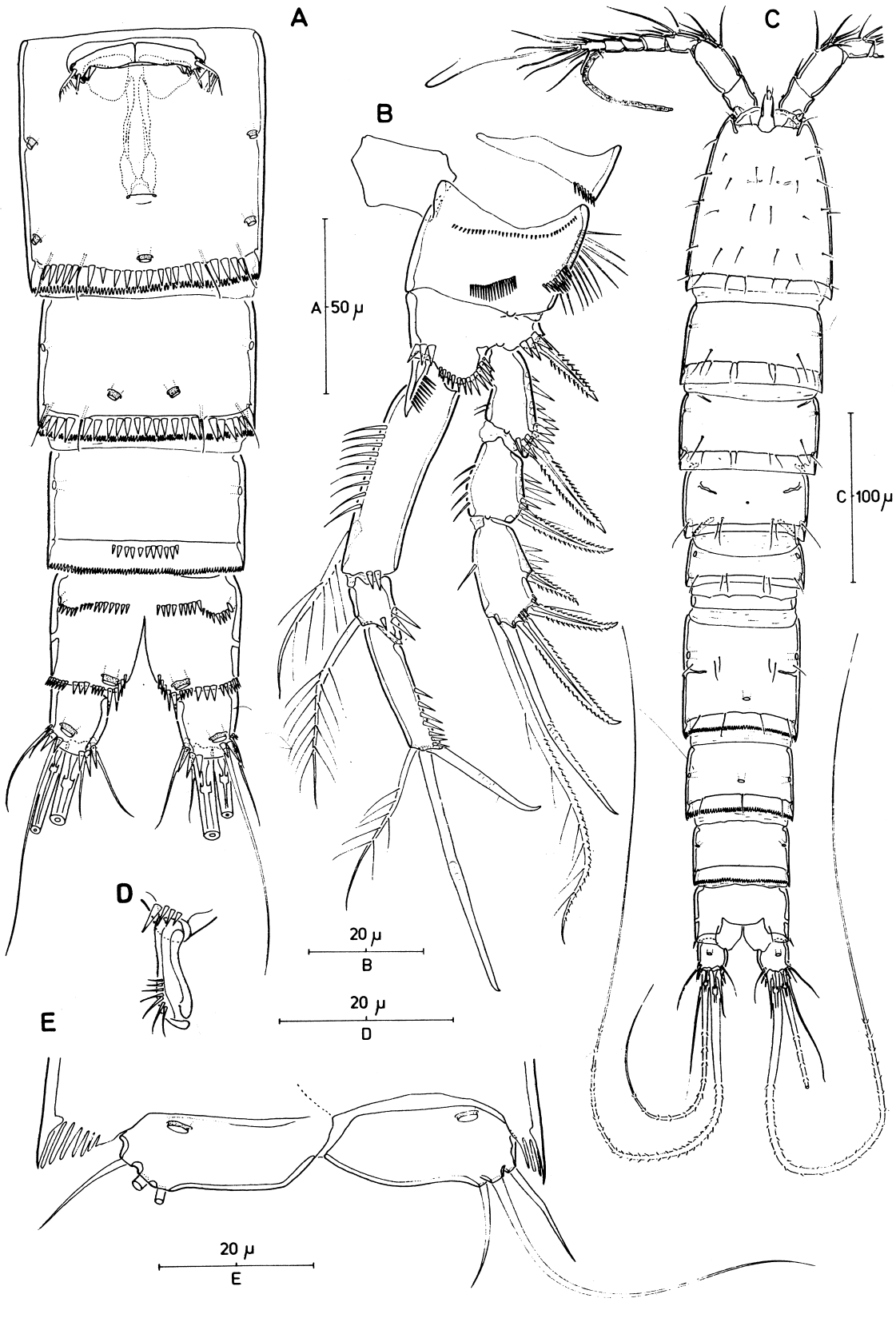

Fig. 7. Psammameira parasimulans comb. n. *A*. Urosome ♀ (excluding P5-bearing somite), ventral. *B*. P1 ♀, anterior. *C*. Habitus ♀, dorsal. *D*. P1 ♂, inner basal spine anterior. *E*. P6 ♂, anterior.

outer margin with 3 setae, apex with 1 long seta; anterior surface with 1 large secretory pore.

P6 (Fig. 7E) asymmetrical, one member fused to somite, other (functional member) articulating; armature consisting of 3 bare setae, middle one longest.

Variability. None observed.

Remarks. This species has never been redescribed nor recorded since its discovery from Dillon Beach in California. Lang's (1965) original description contains a few anomalies

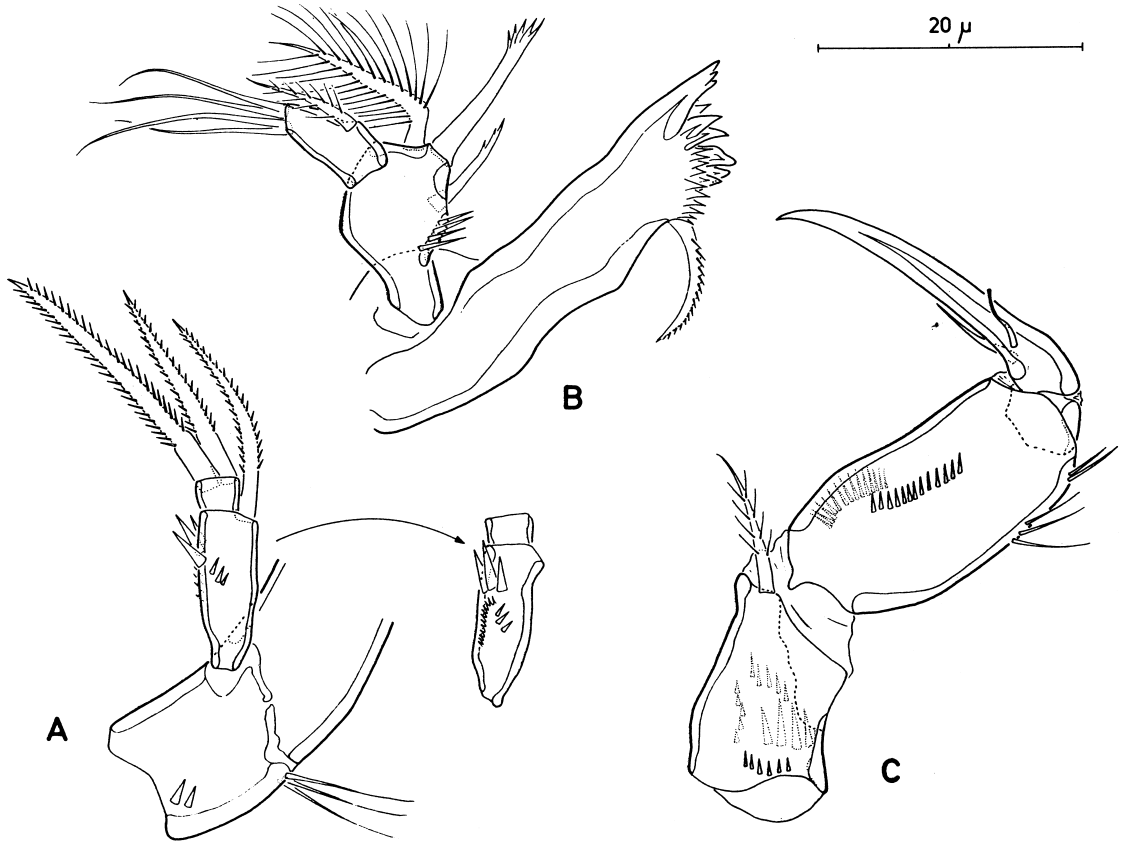

Fig. 8. Psammameira parasimulans comb. n. *A*. Antennary exopod ♀ (arrowed insert indicating lateral view). *B*. Mandible ♀. *C*. Maxilliped ♀, posterior.

compared to the above redescription which can be attributed to omission or misinterpretation of structures and associated elements: (a) body length: the specimens we observed were all considerably expanded with their arthrodial membranes fully exposed which probably accounts for the observed differences in body size; (b) antenna: Lang misinterpreted the incomplete surface suture on the allobasis (Fig. 8A) as a segment boundary separating the basis and proximal endopod segment; (c) mandibular palp: the basal armature was described by Lang as 2 plumose setae: these two setae are distinctly pectinate and the third flaccid plumose seta was overlooked; (d) maxillule: several spines or setae were omitted from the praecoxal arthrite and basis, and the single strong seta on the coxal endite was figured as 2 slender setae; (e) maxilla: the small endopod segment was omitted and the type of setae on the proximal endite misinterpreted; (f) maxilliped: syncoxa was erroneously illustrated with 2 setae as opposed to 1 seta; (g) the asymmetry of ♂ P6 was not shown or described and the ♀ P6 figured with only 1 element.

There is no doubt that *A. parasimulans* is closely related to *P. hyalina* and should be placed in *Psammameira*. The Californian species can be readily distinguished by the additional seta on the distal endopod segment of the P2, the absence of the small posterior inner seta of the P4 exp-3, the ventral body ornamentation of the ♀ genital double-somite and the shorter but more square caudal rami.

Discussion

A great deal of confusion surrounds the taxonomic status of the genus *Psammameira*. The genus was established by Noodt (1952) to accommodate *P. hyalina* as its type and only species and was considered by the author as most closely related to *Ameira*. Wells (1967) allocated two additional species to this genus, *P. reducta* Wells, 1967 and *Ameira grandis* Nicholls, 1939 and tentatively suggested that *A. exigua* T. Scott, 1894 and *A. simulans* T. Scott, 1912 (both placed as '*species incertae et incertae sedis*' in *Ameira* by Lang (1948)), could also possibly be removed to *Psammameira*. Wells (1967) recognized the increased morphological heterogeneity within the newly diagnosed genus, however regarded this as a mere reflection of a continuous evolutionary reduction trend within *Psammameira*.

Noodt (1952) diagnosed his genus on the basis of the antennary allobasis, the number of maxillary endites, the swimming leg setal formulae and the armature of the ♀ P5 baseoendopod. Following Lang's (Lang 1965) revised diagnosis of *Ameira*, Mielke (Mielke 1973, 1975) considered the latter three characters to be of negligible taxonomic importance at the generic level and, moreover, interpreted the antennary basis and proximal endopod segment as discrete segments. Mielke (1973) initially suggested to exclude *Ameira listensis* Mielke, 1973, *A. parasimulans*, *P. hyalina* and related species from *Ameira* and to regard them as part of a distinct lineage (possibly of generic rank). In his later account (Mielke 1975) the author did not reiterate this view, but formally transferred *P. hyalina* to *Ameira*. Within *Ameira* he regarded *A. hyalina* to be very closely related to the sympatric species *A. listensis*, and considered the setal formula of the swimming legs as the only reliable character to distinguish both species. The taxonomic position of *A. listensis* is beyond the scope of this paper and will be dealt with in a future publication

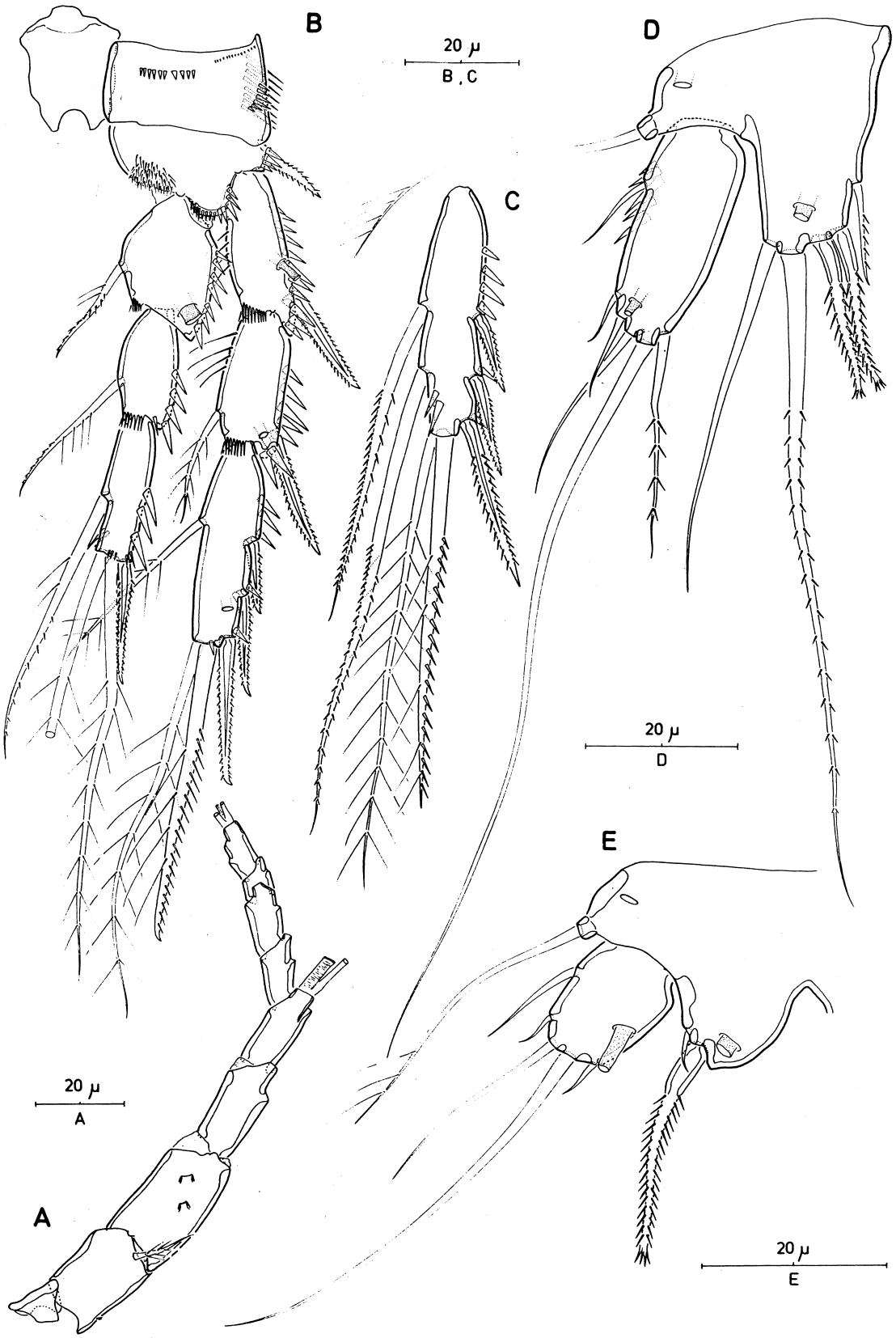

Fig. 9. Psammameira parasimulans comb. n. *A*. Antennule ♀, ventral (armature omitted). *B*. P2 ♀, anterior. *C*. P4 exp-3 ♀, posterior. *D*. P5 ♀, anterior. *E*. P5 ♂, anterior.

(Conroy-Dalton & Huys, in prep). However, the reduced armature of P2–P4 of *A. listensis* is unique within *Ameira sensu lato* and does not point to a close relationship with either of the currently recognized *Psammameira* species. Other apparent similarities such as the presence of 5 setae on the baseoendopod of the ♀ P5 and the structure of the ♂ P6 represent plesiomorphic character states which are of no significance in determining evolutionary affinity.

Mielke's (1975) course of action had unfortunate nomenclatural consequences. By removing the type species *P. hyalina* to *Ameira*, *Psammameira* Noodt, 1952 became an invalid name as a junior subjective synonym of *Ameira*.

The author also recognized that the two remaining species, *P. reducta* and *P. grandis*, should be placed in a separate genus for which he erroneously maintained the name *Psammameira*. It was obviously not Mielke's (Mielke 1975) intention to formally synonymize *Psammameira* with *Ameira*, however, instead of creating a new generic name and proposing new combinations for both *P. reducta* and *P. grandis*, he further compounded the confusion by designating *P. reducta* as the new type of *Psammameira*. This is in clear violation with the Type Concept (Art. 61) of the ICZN. Since '*Psammameira* Mielke, 1975' is at best a junior homonym of *Psammameira* Noodt, 1952 and no valid replacement name has been proposed since, both *P. reducta* and *P. grandis* are currently floating in status.

Psammameira hyalina and *P. parasimulans* differ significantly from the *Ameira longipes*-group in the following key characters: (1) body vermiform and slender, with little ornamentation in general and total lack of spinules dorsally; (2) rostrum demarcated at base; (3) structure of antenna (Conroy-Dalton & Huys (1997) discuss the significance of the exopod as an important diagnostic character in comparison to the previously heavily weighted presence/absence of allobasis); (4) maxillulary endopod completely incorporated in basis and represented by 2 setae; (5) P1 morphometry and morphology, including type of modification of inner basal spine in ♂; (6) setal formula of P2–P4; (7) armature of ♀ P5; (8) P6 ♀ with a plumose element as in the *A. longipes*-group, but the second element, normally being a well developed seta, is diminutive; (9) P6 ♂ asymmetrical with one member fused to somite wall; (10) ♀ genital field and copulatory pore; (11) inner chitinized ribs marking original segmentation of genital double-somite very small and present only dorsolaterally. The clearly demarcated rostrum is a noteworthy feature since it is usually fused to or largely incorporated into the cephalic shield in most ameirid genera. It is however highly probable that considerable misinterpretation of this character has occurred in the past.

Contrary to earlier contentions (Wells 1967; Mielke 1975), we find no evidence to suggest that *P. reducta* and *P. grandis* are at all related and/or belong to the same genus. *Psammameira reducta*, which is known only from females, proved upon re-examination of the types (NHM reg. nos 1967.8.4.58–59) to differ significantly from *P. hyalina* in the following characters: (1) rostrum (not demarcated at base); (2) setal counts on all the mouthparts; (3) P1 morphology; (4) setal formulae of P2–P4; (5) ♀ P5 baseoendopod with 4 setae, exopod with 5 setae; and (6) ♀ genital field and position of copulatory pore. On the basis of this suite of characters *P. reducta* should be removed from *Psammameira* and be placed in a new genus (Conroy-Dalton & Huys, in prep.).

Nicholls' (1939) types of *P. grandis* (NHM reg. nos 1940.5.1.19–28), proved upon re-examination to contain two different species. Unfortunately, Nicholls' (Nicholls 1939) original description appears to be based on this amalgamate, comprising the female, a new species of *Proameira* Lang, 1944 and the male representing a new genus (Conroy-Dalton & Huys, in prep.). Both species differ from *Psammameira* in important diagnostic characters including: (a) for the female: antennary exopod; syncoxa of maxilliped with two elements; setal formula of swimming legs; anal operculum furnished with spinules, and (b) for the male: setal formula of swimming legs; structure of P5; anal operculum with spinules. Hence both components of this composite are to be removed from *Psammameira*, and will be dealt with in greater detail in a forthcoming paper.

The genus *Psammameira* belongs to a lineage of small-sized ameirids which live interstitially in the littoral zone of sandy beaches and whose precise relationships are yet to be resolved. This lineage further encompasses *A. listensis* and the species of the '*A. atlantica*-group', comprising *A. atlantica* Noodt, 1958, *A. atlantica mediterranea* Kunz, 1974 and *A. reducta* Petkovski, 1954. All species are characterized by (1) ornamentation of antennary exopod consisting of group(s) of spinules and a minute surface frill on exp-1 (in *A. longipes*-group typically with cluster of 2-4 coarse spinules around outer lateral margin and with supplementary spinular rows and/or frills); (2) coxal endite of maxillule with only one well developed element (i.e. the seta is absent); (3) a short P1 endopod, the proximal segment being at most as long as, but usually distinctly shorter than, the exopod; (4) the typical shape of the endopodal lobe on the ♂ P5; (5) a 1.1.121 endopodal formula on P4; (6) denticulate or incised hyaline frill on urosomites. Four of these apomorphies (1,3,4,6) are also displayed by the species identified as *A. pusilla* T. Scott, 1903 by Bodin (1979b) which on account of the more primitive setal formula on P2–P4 is regarded here as the outgroup of the *Psammameira*-lineage. Within the latter *Psammameira* occupies the most primitive position and shares a sistergroup relationship with the *A. listensis-atlantica* clade. A unique apomorphy for *Psammameira* is the posteriorly displaced copulatory pore (and long copulatory duct).

The retention of the plesiomorphic state of the ♀ P5 baseoendopod (i.e. with 5 elements) in some species of the *Psammameira*-lineage is remarkable since in interstitial copepods the P5 is likely to undergo reduction (as clearly expressed in the swimming legs) as a result of heterochrony or similar underlying mechanism. This ancestral 5-setae condition is further only found in the primitive genera *Stenocopia* Sars, *Sarsameira* C.B. Wilson, *Pseudameira* Sars, *Ameiropsis* Sars, *Nitokra* Boeck and *Proameira*. Within the latter, *P. hiddensoensis* (Schäfer, 1936) is of particular interest since it is (together with the imperfectly described *P. phaedra* (Monard, 1935)) the only member of the genus that has lost the inner seta on P2–P4 exp-1 (Schäfer's (Schäfer 1936) text and illustrations contradict on this matter; Kunz (1954) lists correct setation). *P. hiddensoensis* shows a striking similarity with *Psammameira* in the segmental proportions of the P1 endopod, the shape and setation of the ♀ P5 and ♂ P6, but differs in the presence of a spinulose anal operculum and the more primitive setal formulae on P2–P4. Schäfer (1936) expressed some doubts about its generic affinity and Kunz (1954), who found the species in *Amphioxus*-gravel, pointed out that it is primarily interstitial, this being in contrast to other *Proameira* species. It is conceivable that *P. hiddensoensis* represents a transitionary stage between *Proameira* and the lineage leading to *A. pusilla* and the mesopsammic *Psammameira*-group and therefore should be attributed separate generic status.

Status of *A. exigua* T. Scott, 1894 and *A. simulans* T. Scott, 1912

Both these species were regarded as *species incertae* in *Ameira* by Lang (1948: 795, 798) but Wells (1967) briefly considered the possibility that they could belong to *Psammameira* because of the presence of 5 setae on the baseoendopod of the ♀ P5. Surprisingly, Wells (1967) did not include *A. parasimulans* in his discussion on *Psammameira*.

The similarity recognized by Lang (1965) between *P. parasimulans* and *A. simulans* rests solely on the shared armature of the P4 and P5 baseoendopod in the female. Lang himself pointed out differences between both species in the number of exopodal setae on the ♀ P5 and the general morphology of the P1 and caudal rami. *Ameira simulans* has never been recorded or redescribed since its discovery from the South Orkneys and any discussion on its relationships is severely hampered by the lack of detail in T. Scott's (Scott 1912) concise description. Provided that T. Scott has not reversed P2 and P4 (as previously questioned by Lang (1948)) it seems impossible to maintain the species in *Ameira* as it displays a 1.1.121 formula on the P4 endopod and 5 setae on the endopodal lobe of the ♀ P5. The combination of these characters is found only in *Psammameira* and *A. listensis*. The species may represent a distinct genus (cf. Lang 1948), however, in view of the complete lack of information on mouthparts and P2–P3 it is removed here from *Ameira* and placed as *species incertae sedis* in *Psammameira*.

Ameira exigua, described from off St. Monans (Scotland) and never recorded again, is very similar to *A. simulans* in the structure of the P1, caudal rami and P5 baseoendopod but differs from the latter in the 1.1.221 formula on the P4 endopod and the number of setae on the P5 exopod. On the basis of T. Scott's (Scott 1894) fragmentary description it is impossible to place this small species in any of the currently recognized ameirid genera. Lang (1948) suggested a relationship with *Proameira* but did not substantiate his view. A position within this genus would seem unlikely as the elongate P1 endopod of *A. exigua* is quite different from the abbreviated type displayed by the various *Proameira* species (e.g. Lang 1948: Abb. 321). Although T. Scott (1894) did not mention the precise number of setae on the P5 exopod, his illustration (Plate VI, Fig. 22) clearly shows a total of seven elements. It is highly probable that a spinule has been misinterpreted as a seta since no other known ameirid possesses more than 6 setae on this segment. The rostrum shown in the lateral habitus view is remarkably large for an ameirid and is more reminiscent of most Diosaccidae. Another unusual feature is the short P4 endopod, a feature not found in any of the ameirids that have retained 5 setae on the ♀ P5 baseoendopod. On the basis of the mouthparts *A. exigua* is retained in the Ameiridae as *incertae sedis*, however, a more precise allocation at generic level will require thorough redescription.

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References

Bodin, P. (1979a). *Catalogue des nouveaux Copépodes Harpacticoïdes marins. (Nouvelle édition)*. Brest: Université de Bretagne occidentale. Laboratoire d'Océanographie biologique.

Bodin, P. (1979). Copépodes Harpacticoïdes marins des environs de la Rochelle. V. Espèces nouvelles ou incertaines. *Vie et Milieu, (A) 27(3)*, 311–357.

Bodin, P. (1988). *Catalogue des nouveaux Copépodes Harpacticoïdes marins. (Édition 1988)*. Brest: Université de Bretagne occidentale. Laboratoire d'Océanographie biologique.

Conroy-Dalton, S., & Huys, R. (1997). Towards a revision of *Ameira* Boeck, 1865 (Harpacticoida, Ameiridae): re-examination of the *A. tenella*-group and the establishment of *Filexilia* gen. n. and *Glabrameira* gen. n. *Zoologica Scripta 25(4)*, 317–339.

Huys, R., & Boxshall, G. A. (1991). *Copepod Evolution*. London: The Ray Society.

Kunz, H. (1954). Beitrag zur Kenntnis der Harpacticoiden der Deutschen Bucht. *Kieler Meeresforschungen 10*, 224–228.

Lang, K. (1948). *Monographie der Harpacticiden*. Lund: Håkan Ohlsson.

Lang, K. (1965). Copepoda Harpacticoida from the Californian Pacific coast. *Kungliga Svenska Vetenskapsakademiens Handlingar (4)10(2)*, 1–560.

Mielke, W. (1973). Zwei neue Harpacticoida (Crustacea) aus dem Eulitoral der Nordseeinsel Sylt. *Mikrofauna des Meeresbodens 17*, 1–14.

Mielke, W. (1975). Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt. *Mikrofauna des Meeresbodens 52*, 1–134.

Nicholls, A. G. (1939). Marine harpacticoids and cyclopoids from the shores of the St. Lawrence. *Le Naturaliste canadien 66*, 241–316.

Noodt, W. (1952). Marine Harpacticiden (Cop.) aus dem eulitoralen Sandstrand der Insel Sylt. *Abhandlungen der mathematisch-naturwissenschaftlichen Klasse. Akademie der Wissenschaften und der Literatur in Mainz 1952(3)*, 105–142.

Schäfer, H. W. (1936). Harpacticoiden aus dem Brackwasser der Insel Hiddensee. *Zoologische Jahrbücher für Systematik 68(6)*, 545–588.

Scott, T. (1894). Additions to the fauna of the Firth of Forth. *Report of the Fishery Board for Scotland 12(3)*, 231–271.

Scott, T. (1912). The Entomostraca of the Scottish National Antarctic Expedition, 1902–1904. *Transactions of the Royal Society of Edinburgh 48*, 521–599.

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