Zoological Journal of the Linnean Society, 2008, **152**, 409–458. With 24 figures

Disentangling the subgeneric division of *Arenopontia* Kunz, 1937: resurrection of *Psammoleptastacus* Pennak, 1942, re-examination of *Neoleptastacus spinicaudatus* Nicholls, 1945, and proposal of two new genera and a new generic classification (Copepoda, Harpacticoida, Arenopontiidae)

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Received 10 November 2006; accepted for publication 18 June 2007

A new generic classification is proposed for the 32 valid species of the interstitial marine family Arenopontiidae (Copepoda, Harpacticoida), primarily based on new observations of type species and reliable descriptions from the literature. The subgeneric division of *Arenopontia* Kunz, 1937 is abolished, and both *Arenopontia* and *Neoleptastacus* Nicholls, 1945 are upgraded to full generic rank. *Arenopontia* is restricted to the *subterranea* group, comprising *Arenopontia subterranea* Kunz, 1937 (type), *Arenopontia problematica* Masry, 1970, *Arenopontia nesaie* Cottarelli, 1975, and *Arenopontia riedli* Lindgren, 1976. The doubtful status of both *Arenopontia pontica* Apostolov, 1969 and recent Egyptian records of *A. nesaie* is discussed, and the alleged cosmopolitanism of *A. subterranea* is reviewed. *Arenopontia* is characterized by the unique morphology of the P1 (prehensile endopod, armature of distal segments of exopod and endopod). The genus *Psammoleptastacus* Pennak, 1942 is reinstated to accommodate *Psammoleptastacus arenaridus* Pennak, 1942 (type), *Arenopontia stygia* Noodt, 1955 and ***Psammoleptastacus barani* sp. nov.** The latter is described from the Turkish Black Sea coast, and had previously been identified as *A. stygia* in Bulgarian waters. The species identified as *A. subterranea* by Rao & Ganapati in 1969 is considered *species inquirenda* in *Psammoleptastacus*. *Neoleptastacus* is resurrected to accommodate all arenopontiids that have an inner spinous process on the P5. The Chilean species *Arenopontia clasingi* Mielke, 1985, *Arenopontia pacifica* Mielke, 1985, and *Arenopontia spicata* Mielke, 1985 are transferred to *Neoleptastacus*. The genus *Pararenopontia* Bodiou & Colomines, 1986 is considered a junior synonym of *Neoleptastacus*, with its type species *Pararenopontia breviarticulata* (Mielke, 1975) being relegated to *species incertae sedis* in this genus. The monotypic genus ***Mesopontia* gen. nov.** is established to accommodate *Arenopontia dillonbeachia* Lang, 1965, which holds an intermediate position between *Arenopontia* and *Neoleptastacus*. Material from Puget Sound identified as *Arenopontia spinicaudata* (Nicholls, 1945) by Chappuis in 1958 is attributed to ***Mesopontia dillonbeachia* comb. nov.** *Psammoleptastacus orientalis* Krishnaswamy, 1957, *Arenopontia intermedia* Rouch, 1964, and *Arenopontia peteraxi* Mielke, 1982 are transferred to a new genus, ***Onychopontia* gen. nov.**, together with ***Onychopontia nichollsi* sp. nov.** (type), which was discovered among type material of *Neoleptastacus spinicaudatus* Nicholls, 1945. Redescriptions are given for *A. nesaie*, *P. arenaridus*, *N. spinicaudatus*, and *M. dillonbeachia*. A key to the five arenopontiid genera as well as keys (or comparative tables) to the species of *Arenopontia*, *Onychopontia*, *Mesopontia*, and the *spinicaudatus* lineage of *Neoleptastacus* are provided. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, **152**, 409–458.

ADDITIONAL KEYWORDS: distribution – generic diagnoses – revision – sexual dimorphism – taxonomy.

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INTRODUCTION

In one of the pioneering papers on the interstitial fauna of coastal groundwater ('Küstengrundwasser') in north-western Europe, Kunz (1937) proposed the genus *Arenopontia* for a new species *Arenopontia subterranea* from Schilksee in the Kiel Bay, Germany. Pennak (1942a) erected the genus *Psammoleptastacus* for a new species, *Psammoleptastacus arenaridus*, from two sandy beaches in the Woods Hole area, USA. Nicholls (1945) established the genus *Neoleptastacus* for its type and only species *Neoleptastacus spinicaudatus*, from Australia. All three genera were originally placed in the Canthocamptidae by their respective authors. Lang (1948) transferred *Arenopontia* to the subfamily Leptopontiinae in the Cylindropsyllidae, and Noodt (1955a) suggested *Psammoleptastacus* should sink as a synonym of this genus. Chappuis (1955) believed the separate generic status of *Neoleptastacus* was not warranted, and also relegated the genus to a junior subjective synonym of *Arenopontia*. Subsequent authors accepted Chappuis' course of action, with the exception of Krishnaswamy (1957) who continued using *Neoleptastacus* as a valid genus, and Wells (1967) who preferred a subgeneric division of *Arenopontia* into the nominate subgenus and *Neoleptastacus*, reflecting the distinct difference in P5 morphology. This subdivision gained wide acceptance (e.g. Kunz, 1971; Mielke, 1975; Lindgren, 1976; Itô, 1978; Bodin, 1979, 1988; Bodiou & Colomines, 1986; Wells & Rao, 1987; Cottarelli, Bruno & Venanzetti, 1994; Karanovic, 2000), but was not universally accepted (Masry, 1970; Cottarelli, 1973, 1975; Mielke, 1982a, b, 1985, 1987). Bodiou & Colomines (1986) proposed a new genus *Pararenopontia* for two *Arenopontia* species with reduced leg segmentation: *Arenopontia breviarticulata* Mielke, 1975 and *Arenopontia trisetosa* Mielke (1982a).

Mielke (1982a) questioned the significance attributed to the P5 morphology as a subgeneric discriminant, as some species exhibit a transitionary condition between the *Arenopontia* and *Neoleptastacus* types of P5. Martínez Arbizu & Moura (1994) argued that the subgenera of *Arenopontia* (*Arenopontia* and *Neoleptastacus*) are not sustainable on grounds of potential paraphyly and/or polyphyly, and that *Pararenopontia* should be synonymized with *Arenopontia*. This amalgamation was disputed by Huys, Bodiou & Bodin (1996a), who resurrected *Pararenopontia*, and by Huys *et al*. (1996b: 35), who maintained the subgeneric classification (although they did not explicitly list the subgenus *Neoleptastacus*). Bodin (1997) offered a compromise by adopting Wells' (1967) original subdivision and adding *Pararenopontia* as a third subgenus (this new rank was erroneously attributed to Martínez Arbizu & Moura, 1994). Finally, Wells (2007) abandoned the subgeneric classification altogether, and maintained *Pararenopontia* as a valid genus.

In this paper we have set out to: (1) redefine the generic boundaries of *Arenopontia*; (2) provide arguments for the resurrection of *Psammoleptastacus* as a valid genus; (3) upgrade *Neoleptastacus* to its original generic rank; (4) propose two new genera for species previously allocated to *Arenopontia*, and (5) describe two new species from the Turkish Black Sea coast and Western Australia, respectively.

MATERIAL AND METHODS

Samples in Turkey were collected using the Karaman–Chappuis method (Delamare Debouteville, 1953). Specimens were cleared in lactic acid and 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 have been prepared using a camera lucida on an Olympus BX-50 or Leica DMR differential interference contrast microscope. Measurements were made with an ocular micrometer. Total body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. The scale bars in the illustrations are in μm. The descriptive terminology is adopted from Huys *et al*. (1996b). Abbreviations used in the text are as follows: ae, aesthetasc; enp, endopod; exp, exopod; exp-1 (enp-1), exp-2 (enp-2), and exp-3 (enp-3) to denote the proximal, middle, and distal segment of a ramus; P1–P6, for swimming legs 1–6. The type material was deposited in the Natural History Museum, London (NHM) and Balıkesir University Zoology Museum (BUZM), and was borrowed from the National Museum of Natural History, Smithsonian Institution, Washington D.C. (NMNH) and the Swedish Museum of Natural History, Stockholm (SMNH).

RESULTS AND DISCUSSION

Family Arenopontiidae Martínez Arbizu & Moura, 1994

Based on the arguments outlined below, a new generic classification is proposed for the family, resulting in the upgrade of the subgenera *Arenopontia* and *Neoleptastacus*, in the resurrection of *Psammoleptastacus*, in the rejection of *Pararenopontia* as a valid genus, and in the proposal of two new genera, *Mesopontia* and *Onychopontia*. Table 1 summarizes

Table 1. Salient features differentiating arenopontiid genera. Apomorphic character states are set in boldface

	Arenopontia	***Mesopontia* gen. nov.**	*Neoleptastacus*	*Psammoleptastacus*	***Onychopontia* gen. nov.**
P1 exp-3 armature	**2 pinnate spines + 1 geniculate seta + 1 penicillate seta**	2 pinnate spines + 2 geniculate setae	1–2 pinnate spines + 2 geniculate setae	2 pinnate spines + 2 geniculate setae	**2 naked setae + 2 geniculate setae**
P1 endopod	**prehensile** longer than exopod	not prehensile **as long as exopod**	not prehensile as long or longer than exopod	not prehensile **shorter than exopod**	not prehensile longer than exopod
P1 enp-2 armature	**1 spine + 1 geniculate claw**	**1 spine + 1 geniculate seta**	**1 spine + 1 geniculate seta***	2 geniculate setae	2 geniculate setae
P2–P3 endopods ♀	two-segmented	two-segmented	one- or two-segmented	two-segmented	two-segmented
P2 enp-2 inner serrate seta	present	present	usually present†	present	**absent**
P3 endopod ♂ segmentation	not modified as in ♀	not modified as in ♀	not modified as in ♀	**modified** two-segmented	**modified one-segmented**
P4 exp-3 inner serrate seta	**absent**	present	usually present‡	**absent**	**absent**
P5 with outer basal seta +	3 or 4 discrete elements	4 discrete elements **(innermost one spiniform)**	1–3 discrete elements + **inner spinous process**	4 discrete elements innermost smaller in ♂	3 or 4 discrete elements in ♀ 3 discrete elements in ♂ (with innermost smaller or fused)

*Except *speluncae* lineage (*N. speluncae* and *N. phreaticus*), which has two geniculate setae.
†Except *N. ornamentus* and *N. reductaspina*.
‡Except *N. australis* and *N. pacifica*; unknown in *N. accraensis*.

Table 2. New classification reflecting restricted taxonomic concept of *Arenopontia* and reallocation of remaining species to *Neoleptastacus*, *Psammoleptastacus*, and two new genera

ARENOPONTIA KUNZ, 1937	*NEOLEPTASTACUS* NICHOLLS, 1945
A. subterranea Kunz, 1937*	*N. spinicaudatus* Nicholls, 1945*
A. problematica Masry, 1970	***N. australis*** (Chappuis, 1952) **comb. nov.**
A. nesaie Cottarelli, 1975	***N. acanthus*** (Chappuis, 1954) **comb. nov.**
A. riedli Lindgren, 1976	***N. longiremis*** (Chappuis, 1955) **comb. nov.**
	N. secundus Krishnaswamy, 1957
PSAMMOLEPTASTACUS PENNAK, 1942	***N. africanus*** (Chappuis & Rouch, 1961) **comb. nov.**
P. arenaridus Pennak, 1942*	***N. accraensis*** (Lang, 1965) **comb. nov.**
P. stygius (Noodt, 1955) **comb. nov.**	***N. indicus*** (Rao, 1967) **comb. nov.**
***P. barani* sp. nov.**	***N. ishikarianus*** (Itô, 1968) **comb. nov.**
	N. angolensis (Kunz, 1971) **comb. nov.**
***ONYCHOPONTIA* GEN. NOV.**	***N. gussoae*** (Cottarelli, 1973) **comb. nov.**
O. orientalis (Krishnaswamy, 1957) **comb. nov.**	***N. trisetosus*** (Mielke, 1982) **comb. nov.**
O. intermedia (Rouch, 1962) **comb. nov.**	***N. clasingi*** (Mielke, 1985) **comb. nov.**
O. peteraxi (Mielke, 1982) **comb. nov.**	***N. pacificus*** (Mielke, 1985) **comb. nov.**
O. nichollsi* sp. nov.	***N. spicatus*** (Mielke, 1985) **comb. nov.**
	N. chaufriassei (Bodiou & Colomines, 1986) **comb. nov.**
***MESOPONTIA* GEN. NOV.**	***N. ornamentus*** (Mielke, 1987) **comb. nov.**
M. dillonbeachia (Lang, 1965) **comb. nov.***	***N. reductaspina*** (Mielke, 1987) **comb. nov.**
	N. phreaticus (Cottarelli *et al.*, 1994) **comb. nov.**
	N. speluncae (Cottarelli *et al*., 1994) **comb. nov.**
	N. huysi (Karanovic, 2000) **comb. nov.**

*Type species of respective genera.
Species inquirendae and *species incertae sedis* is not listed.

the main diagnostic characters for each genus. The updated generic assignment of the 32 valid species in the family is shown in Table 2.

GENUS *ARENOPONTIA* KUNZ, 1937

The genus *Arenopontia* currently contains 32 species allocated to three subgenera (Bodin, 1997; Karanovic, 2000) (or 30 species when the subgenus *Pararenopontia* is attributed full generic rank; see Wells, 2007). The subgenus *Arenopontia* encompasses 13 species and possibly one subspecies [Apostolov (1973) claimed that *Arenopontia pontica* Apostolov, 1969 is a subspecies of *A. subterranea*], whereas Karanovic (2000) listed 17 valid species in the subgenus *Neoleptastacus* [note that *Arenopontia sakagamii* Itô, 1978 was also listed by this author, but according to Wells & Rao (1987) this species is synonymous with *Arenopontia indica* Rao, 1967]. The subgeneric division first proposed by Wells (1967) fell into disuse in the 1980s, when Mielke (1982a, b, 1985, 1987) described several new species from Central and South America without attributing them to either subgenus. Unfortunately, Bodin (1988, 1997) erroneously listed three of those species, *Arenopontia clasingi*, *Arenopontia pacifica*, and *Arenopontia spicata* (all described by Mielke, 1985), under the nominate subgenus *Arenopontia* (*Arenopontia*), as if Mielke (1985) had originally intended such a subgeneric assignment. It is obvious from Mielke's (1985, 1987) descriptions, however, that these species share the *Neoleptastacus* type of P5, and should be assigned to this subgenus if Wells' (1967) subdivision bears any phylogenetic significance. Bodin's (1988, 1997) error unfortunately perpetuated in the literature, as exemplified by Karanovic's (2000) recent key to the subgenus *Neoleptastacus*, which makes no reference to Mielke's (1985) species. *Arenopontia clasingi*, *A. pacifica*, and *A. spicata* are here formally transferred to *Neoleptastacus*, which will be attributed full generic rank (see below).

The subgenus *Arenopontia* currently encompasses the following species: *A. subterranea*; *Arenopontia arenarida* (Pennak, 1942a); *Arenopontia stygia* Noodt, 1955b; *Arenopontia orientalis* (Krishnaswamy, 1957); *Arenopontia intermedia* Rouch, 1962; *Arenopontia dillonbeachia* Lang, 1965; *Arenopontia problematica* Masry, 1970; *Arenopontia nesaie* Cottarelli, 1975; *Arenopontia riedli* Lindgren, 1976; and *Arenopontia peteraxi* Mielke, 1982a. Bodin (1979, 1988, 1997) added *A. subterranea* Kunz? *sensu* Şerban & Eitel-Lang (1957) as a *species incertae sedis*, but the latter should be regarded as a *nomen nudum*. Various Eastern European authors (e.g. Georgescu, Marcus & Şerban, 1962) have repeatedly referred to Şerban &

Eitel-Lang's (1957) paper as 'Notes sur les Copépodes de la Mer Noire. Izdanija, Skopje'; however consistently, no proper citation of volume number or pagination has been given. According to Şerban (1959), the authors were at that time still in the process of submitting the paper ('Une description detaillée en sera publiée par Şerban & Eitel-Lang'), and it has now been confirmed (C. Pleşa, pers. comm. to RH, 1 August 1996) that the manuscript was never published. The reference nevertheless mistakenly persisted in modern literature (e.g. Apostolov & Marinov, 1988).

Morphological comparison revealed a core group of closely related species within the (sub)genus *Arenopontia*, encompassing the type species *A. subterranea*, *A. pontica*, *A. problematica*, *A. nesaie*, and *A. riedli*. These five species differ from other members of the family in their unique P1 morphology, including: (1) the prehensile endopod with enp-1 being distinctly elongate, and with enp-2 bearing an outer spine and an inner geniculate claw, and (2) the modification of the inner distal element of exp-3 into a penicillate seta. Based on these autapomorphies, we here restrict the generic concept of *Arenopontia* to this *subterranea* group. Our unpublished studies based on sandy beach samples from all over Europe revealed that many new species await description (e.g. Sak, Karaytuğ & Huys, in press a), and that the five currently known species only represent the tip of the iceberg. The genus is primarily restricted to the Northern Hemisphere, the only exception being Wells' (1967) doubtful outlier of *A. subterranea* in Mozambique.

Diagnosis: Arenopontiidae. Urosomites without conspicuous surface ornamentation. Anal somite without paired dorsolateral spinous processes. Anal operculum not modified. Hyaline frills of abdominal somites with rectangular digitate lappets. Caudal ramus with dorsolateral spur or raised spinular row near medial margin. P1 exopod: three-segmented; exp-1 with outer spine; exp-3 with two spines, one outer distal geniculate seta, and one inner distal penicillate seta. P1 endopod: prehensile, longer than exopod; enp-2 with one outer distal spine and one inner distal geniculate claw. P2–P3 endopods: two-segmented. P3 enp-2 with outer distal element defined at base or absent. P4 enp-2 with well developed outer distal element. Armature formula as follows:

	Exopod	Endopod
P2	0.0.021	0.110 or 0.120
P3	0.0.021	0.010 or 0.020
P4	0.0.021	0.020

P3 endopod male: not sexually dimorphic, two-segmented. P5 with outer basal seta and three or four discrete elements: innermost one distinctly smaller in males. P6 male with one or two seta(e).

Type species: Arenopontia subterranea Kunz, 1937 (by monotypy).

Other species: Arenopontia problematica Masry, 1970; *Arenopontia nesaie* Cottarelli, 1973; *Arenopontia riedli* Lindgren, 1976.

Species inquirendae: Arenopontia pontica Apostolov, 1969; *Arenopontia nesaie* Cottarelli, 1975 *sensu* Mitwally & Montagna (2001).

Nomen nudum: Arenopontia subterranea Kunz, 1937? *sensu* Şerban & Eitel-Lang (1957).

ARENOPONTIA SUBTERRANEA KUNZ, 1937

Arenopontia (*Arenopontia*) *subterranea* Kunz, 1937: Wells (1967)

Original description: Kunz (1937): pp. 107–110; Abb. 8 (figs 38–42), 9 (figs 43–47), 10 (figs 48–51).

Type locality: Germany, Kieler Förde, Schilksee; 'Küstengrundwasser' (intertidal coastal groundwater).

Arenopontia subterranea has been reported from a wide range of localities throughout Europe, from the Baltic to the Black Sea basin. With additional records from Madeira (Delamare Deboutteville, 1960b), India (Rao, 1967, 1968, 1970, 1980, 1991; Rao & Ganapati, 1968, 1969; Rao & Misra, 1983), Mozambique (Wells, 1967), and North Carolina (Lindgren, 1976) it is not surprising that this species has been regarded as potentially cosmopolitan (Wells, 1967, 1986; Lindgren, 1976). Lindgren (1976) claimed its range might be extended with more investigation of sandy beaches in the Pacific. Unfortunately, the great majority of these records are not accompanied by illustrations, and consequently their authenticity cannot be verified. The discovery of a closely related species from the Isle of Sylt (Sak, 2004) casts further doubt on the validity of most north-western European, and even some German, records. Arlt's (1983) illustrations show that his Baltic specimen does not belong to *A. subterranea* either, raising the suspicion that not all records from east of the Skagerrak necessarily pertain to the type species. There is no doubt that many authors have attributed their material to *A. subterranea* on the sole basis that this species shows extensive intraspecific variability. The true range of the species is as yet unknown, and the only reliable records appear to be restricted to German waters: (1) North Sea coast – Isle of Sylt (Noodt, 1952, 1956, 1957; Mielke, 1975, 1976), Amrum (Noodt, 1956, 1957), Sankt Peter-Ording (Noodt, 1956), and Helgoland (Martínez Arbizu & Moura, 1994); (2) Kieler Bucht – Schilksee (Kunz, 1937; Noodt, 1956), Bottsand, Gelting Birk, Weißenhaus, and Heiligenhafen (Noodt, 1956, 1957).

The type material of *A. subterranea*, as well as the remainder of Kunz' earlier collections, were destroyed during World War II when the Institut für Meereskunde was heavily bombed in 1944 (Schriever, 1984). We have been unable to obtain topotype or other material that could be attributed with confidence to *A. subterranea*, and instead we have selected *A. nesaie* for the model description. Illustrations and text are based on material collected from the Turkish west coast (Marmara Sea), which represents a considerable extension of the range for the species.

Arenopontia nesaie Cottarelli, 1975

Arenopontia (*Arenopontia*) *nesaie* Cottarelli, 1975

Arenopontia nesiae Cottarelli, 1975:

Martínez Arbizu & Moura (1994: 57) (*lapsus calami*)

Arenopontia nessiae Cottarelli, 1975:

Martínez Arbizu & Moura (1994: 63) (*lapsus calami*)

Arenopontia ciplaki Sak, 2004 (*nomen nudum*)

Original description: Cottarelli (1975): pp. 65–70; figures 1–11, 13–16, 18–19, 21–23.

Type locality: Italy, Sardinia, near Cagliari, Bay of Quartu S. Elena, Poetto beach.

Material examined: (1) one ♀ dissected on eight slides (NHM reg. no. 2006. 1953), one ♂ mounted *in toto* on slide (NHM reg. no. 2006. 1954), one ♂ dissected on eight slides (NHM reg. no. 2006. 1955), 22 ♀♀ and 22 ♂♂ preserved in alcohol (NHM reg. no. 2006. 1956–1965); (2) > 50 ♀♀ and > 50 ♂♂ preserved in alcohol (deposited in BUZM). All material was collected from Dutlimanı Beach (Marmara Sea), 40°22.479′N, 28°03.080′E, Balıkesir Province, Turkey; leg. S. Karaytuğ and S. Sak, 18 September 2001.

Redescription

Female: Total body length from tip of rostrum to posterior margin of caudal rami: 341–396 μm (mean = 366 μm, $n = 25$). Maximum width: 38 μm (mean of 20 individuals = 41 μm), measured at posterior margin of cephalothorax. Body: slender and cylindrical, without clear distinction between prosome and urosome (Fig. 1A, B). Hyaline frills of thoracic somites weakly developed and crenulated; those of genital double-somite and free abdominal somites strongly developed, and consisting of rectangular digitate lappets (Figs 1A, B, 2A, B). Genital double-somite (Figs 1A, B, 2A): slightly longer than wide; without chitinous ribs marking original segmentation; with two mid-dorsal, two lateral, and two ventral pores. Anal somite (Fig. 3A, B): with two dorsal and two lateral pores. Anal operculum: with minute pinnules along free distal margin (Fig. 3A). Anus: positioned subterminally between caudal rami. Rostrum (Fig. 1C): small, broadly subtriangular, tapering distally, with two delicate sensillae.

Caudal rami: approximately twice longer than wide (measured in dorsal view), tapering posteriorly; with a proximal pore dorsally (Fig. 3A), one pore near the ventral proximal margin (Fig. 2A), and one pore laterally near the insertion site of seta III (Fig. 3B); outer distal corner produced into posteriorly directed recurved spinous process, accompanied by outer spinular row at base (Fig. 3A, B); dorsal surface with flagellate spur-like process near inner margin, accompanied by a few tiny spinules near base (Figs 1D, 3B). Armature consisting of seven setae: seta I, small; setae II and III, long and naked; seta IV, short, sparsely pinnate, located between seta V and spinous process; seta V, long and with fracture plane; seta VI, small, naked, and located at inner distal corner; seta VII, foliaceous and triarticulate at base.

Antennule (Fig. 3C): long, six-segmented. Segment 1 with a tiny seta near the anterodistal margin. Segment 2 longest, about 3.5 times longer than wide. Segment 4 with long aesthetasc (32-μm long) fused at base with seta. Distal segment: with seven naked setae (two of which are spatulate) and apical acrothek, consisting of short aesthetasc (20-μm long) and two slender setae. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[7 + acrothek].

Antenna (Fig. 3D, E): coxa small, without ornamentation. Allobasis: about 2.7 times as long as maximum width; original segmentation marked by partial transverse surface suture; with two spinular rows, as illustrated. Exopod one-segmented, elongate, with a naked apical seta (about 3.3 times longer than exopod). Free endopod with two spinular rows on anterior surface, and with finer spinules at outer distal corner; lateral armature consisting of two short spines; apical armature consisting of two spines and three geniculate setae, the longest of which with spinules around geniculation, and fused basally to tiny accessory seta.

Mandible: with two-segmented palp (Fig. 2D); basis elongate with one lateral seta; endopod with one inner, one outer, and three apical setae; all armature elements naked. Gnathobase: with coarse teeth distally, and with one naked seta at dorsal corner.

Maxillule (Fig. 1E): with praecoxal arthrite bearing two setae and five spines around distal margin. Coxal endite: with two long naked setae. Basis with rami entirely incorporated; palp represented by nine naked setae.

Maxilla (Fig. 2E): syncoxa with two cylindrical endites; proximal endite with three setae; distal

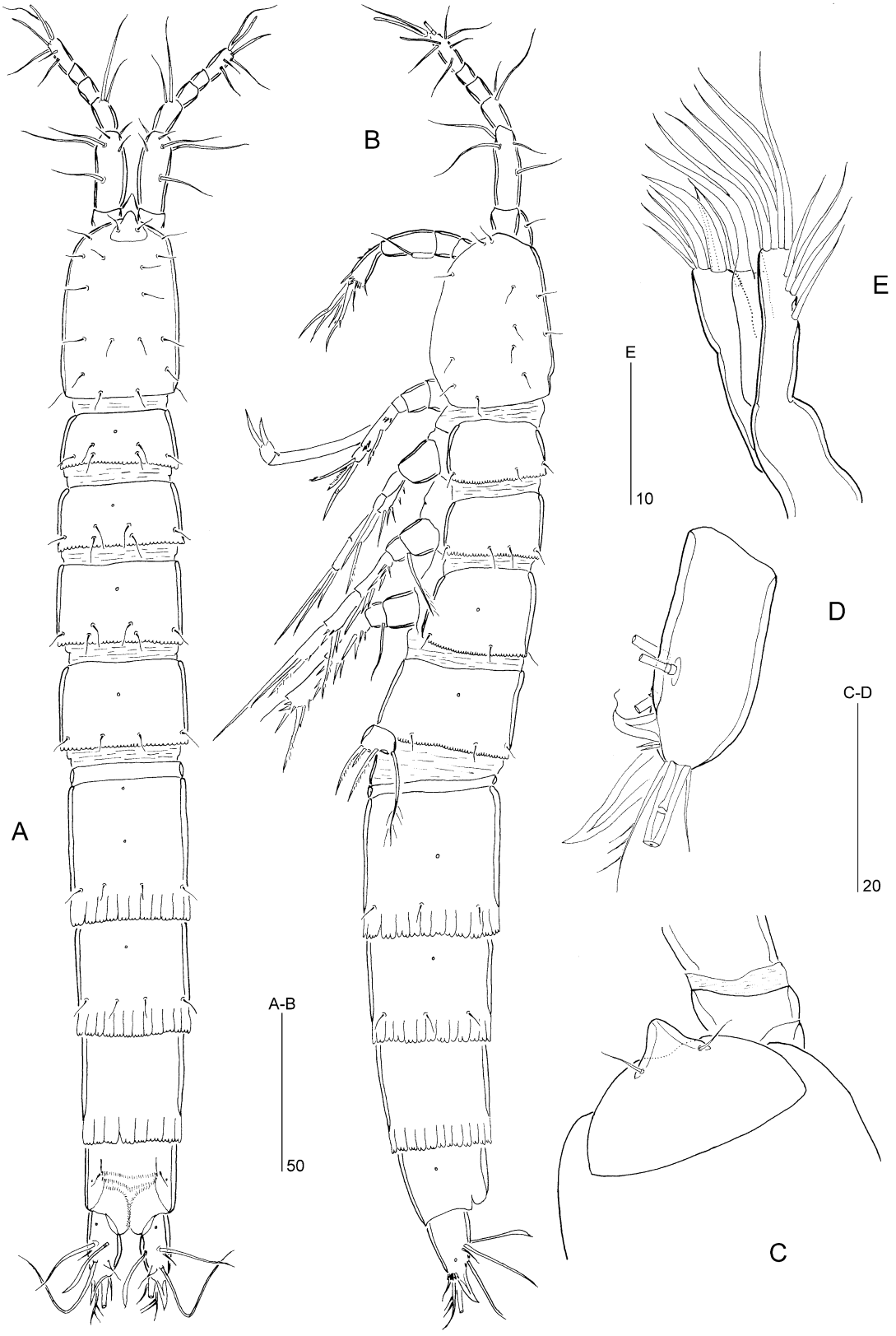

Figure 1. *Arenopontia nesaie* Cottarelli, 1975 (♀). A, habitus, dorsal view. B, habitus, lateral view. C, rostrum, dorsal view. D, left caudal ramus, inner lateral view. E, maxillule.

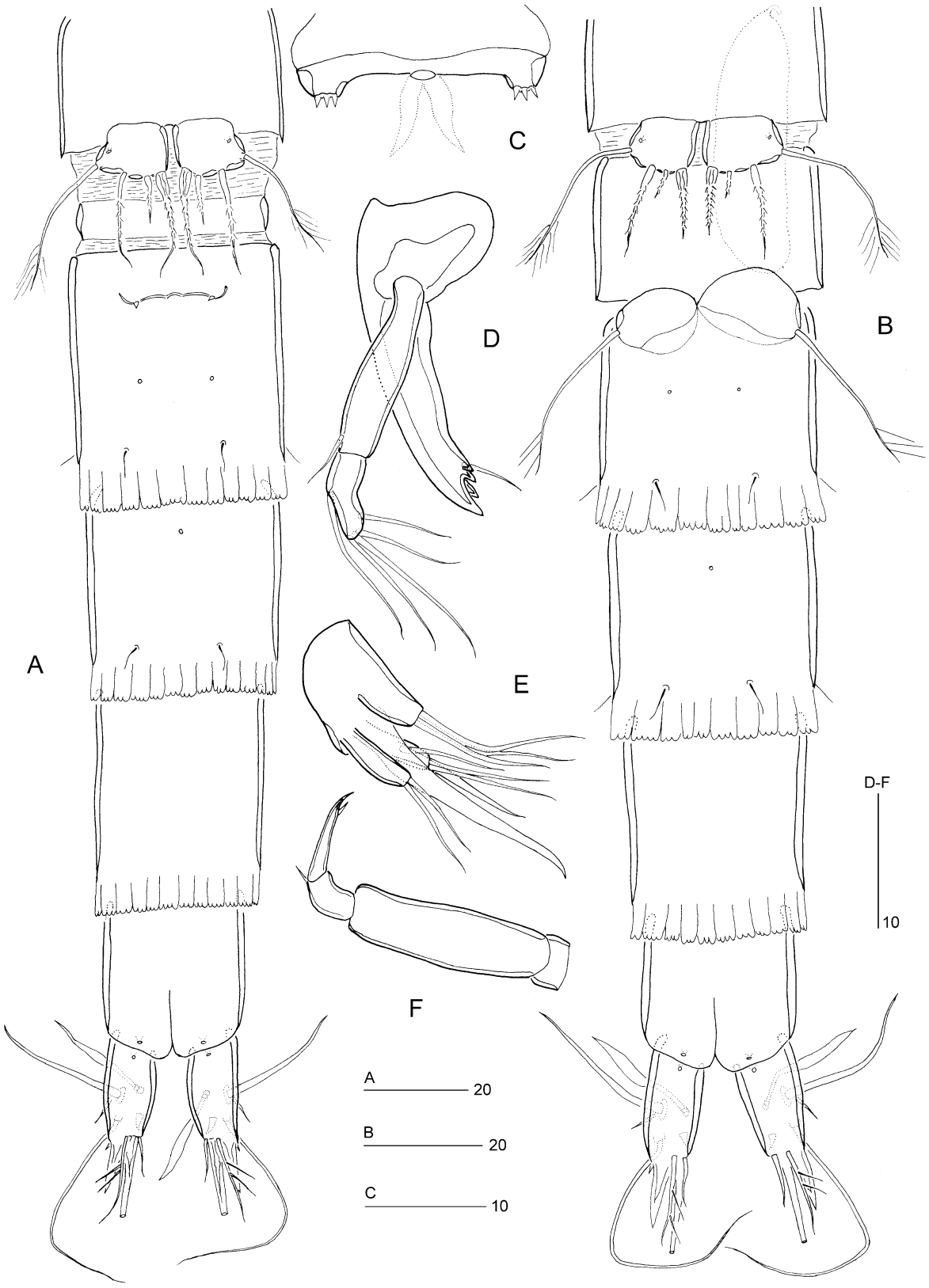

Figure 2. *Arenopontia nesaie* Cottarelli, 1975. A, urosome ♀, ventral view. B, urosome ♂, ventral view. C, genital field ♀. D, mandible. E, maxilla. F, maxilliped.

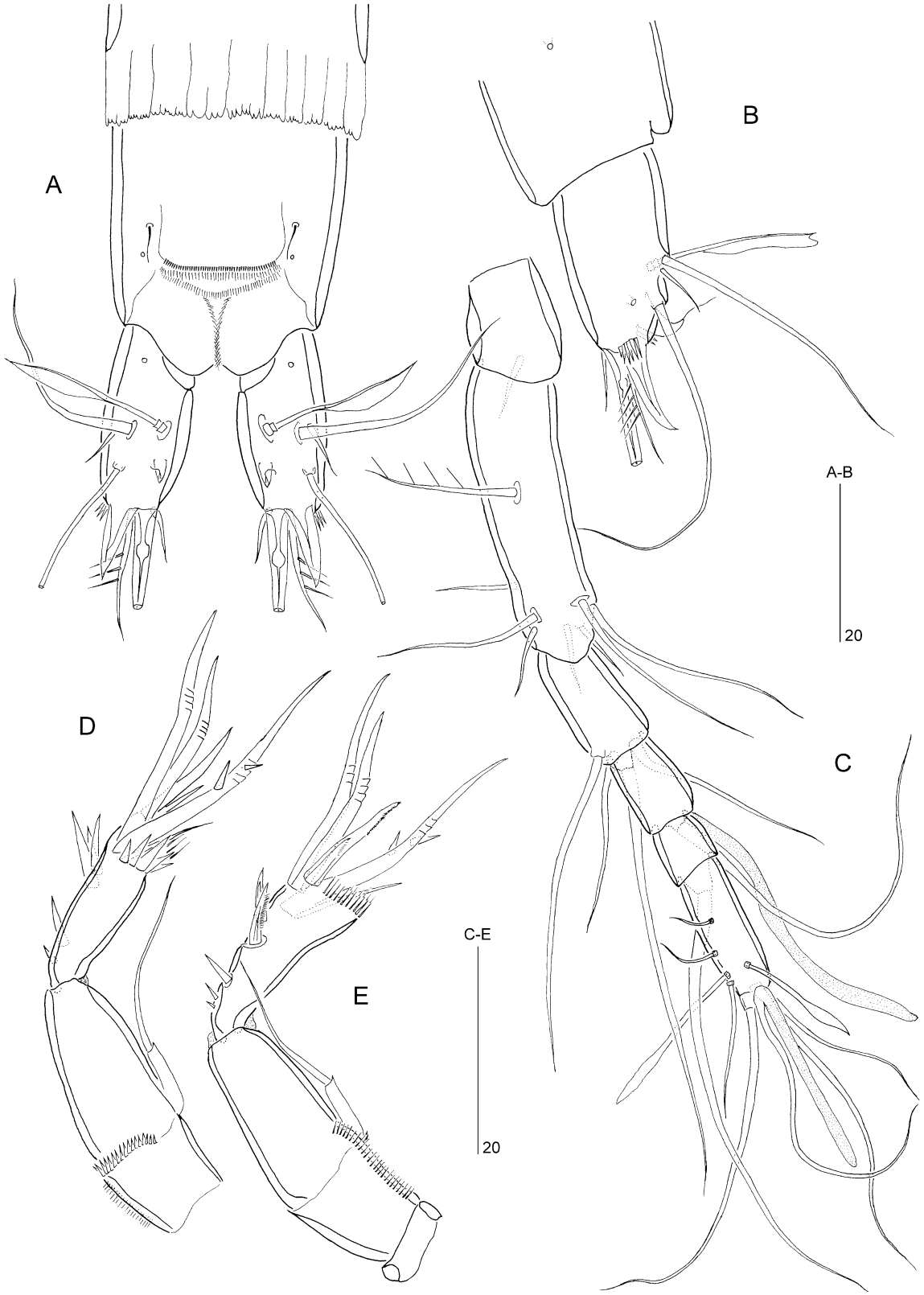

Figure 3. *Arenopontia nesaie* Cottarelli, 1975 (♀). A, caudal rami, anal somite, and posterior margin of penultimate somite, dorsal view. B, left caudal ramus, outer lateral view. C, antennule. D, antenna, outer lateral view. E, antenna, inner lateral view.

endite with two setae. Allobasis: drawn out into long claw; with one accessory setae. Endopod one-segmented , and with three setae. All elements naked.

Maxilliped (Fig. 2F): syncoxa small and unarmed. Basis: elongate and unarmed. Endopod with small accessory seta, and with slightly curved claw bearing subterminal spinule.

P1 (Fig. 4A): intercoxal sclerite long and rectangular. Praecoxa: triangular and naked. Coxa: without ornamentation. Basis: with spinular row near bases of endopod and exopod; anterior surface with a proximal pore and a small inner seta. Exopod: three-segmented; exp-1 and exp-2 with spinules around outer margin; exp-1 longest, with long unipinnate outer spine; exp-2 without outer element; exp-3 with short unipinnate outer spine, a long curved unipinnate spine, and one geniculate seta distally, and one inner, apically penicillate seta subdistally. Endopod: two-segmented, prehensile; enp-1 9.3 times longer than wide, and about twice longer than exopod; with a serrate inner seta in proximal third, and a subdistal spinule along outer margin; enp-2 slightly longer than wide, with a short unipinnate spine, a geniculate claw, and a small inner spinule.

P2–P4 (Fig. 4B–D): intercoxal sclerites naked, wider in P2, but more deeply concave in P3–P4. Praecoxae: small and naked. Coxae: squarish and without ornamentation. Bases: smaller than coxae, with a spinular row near base of endopod (P3–P4); anterior surface with a pore; outer basal seta absent (P2), plumose (P3), or naked (P4). Exopods: three-segmented; segments with spinular ornamentation, as illustrated; inner distal seta of exp-3 sparsely bipinnate, all other elements unipinnate; P3–P4 exp-3 with anterior pore. Endopods: two-segmented; P2–P4 enp-1 about 1.5, 2.2, and 3.0 times longer than their respective distal segments, with few spinules, as illustrated. P2: enp-1 with a long, apically serrate, backwardly directed seta near proximal inner corner. P2–P3: enp-2 with a long, bipinnate, apical seta. P4: enp-2 with apically serrate seta, fused at base, and long unipinnate seta at outer distal corner. Armature formula as follows: P2, exopod, 0.0.021, endopod, 0.110; P3, exopod, 0.0.021, endopod, 0.010; P4, exopod, 0.0.021, endopod, 0.020.

Fifth legs (Fig. 2A) closely set together, but not touching in ventral midline. Baseoendopod and exopod: fused, forming a rectangular plate; distal margin with three pinnate setae, middle one markedly shorter than the others, but not vestigial; outer basal seta, long and plumose.

Genital field: positioned near anterior margin of genital double-somite (Fig. 2A). Genital apertures (Fig. 2C): fused forming median common slit; closed off by fused P6 forming operculum with three minute spinous processes on either side; copulatory pore located midventrally, close to genital slit; seminal receptacles difficult to discern.

Male: Total body length from tip of rostrum to posterior margin of caudal rami: 320–374 μm (mean = 346 μm; $N = 25$). Maximum width: 40 μm (mean = 38, $N = 20$), measured at cephalothorax. Body ornamentation (Fig. 5A): essentially as in female. Sexual dimorphism: in antennule, genital segmentation, and P5 and P6. Spermatophore length: approximately 35 μm.

Antennule (Fig. 5B, C): nine-segmented, haplocer; geniculation between segments 7 and 8. Segment 2 longest, and about 2.7 times longer than wide; segment 4 an incomplete sclerite with one modified (fused at base) and one tiny element; segment 5 with three setae plus long aesthetasc (42-μm long) fused basally to a small slender seta; segment 6 with a spinulose spine and long distal seta; segment 7 with three modified spines and a seta; segment 8 with a modified spine; distal segment with seven naked setae (two of which spatulate) and apical acrothek. Setal formula: 1-[1], 2-[7 + 1 plumose], 3-[4 + 2 spines], 4-[1 + 1 modified], 5-[3 + (1 + ae)], 6-[1 + 1 modified], 7-[1 + 3 modified], 8-[1 modified], 9-[7 + acrothek]. Acrothek consisting of short aesthetasc (16-μm long) fused basally to two slender setae.

P5 (Fig. 2B): with armature as in female, but with middle and inner elements comparatively shorter.

Sixth legs (Fig. 2B): asymmetrical, with smallest P6 closing off functional gonopore; each with a long plumose seta.

Remarks: Arenopontia nesaie was originally described from Poetto Beach in the Bay of Quartu S. Elena near Cagliari, Sardinia (Italy). Our material differs from Cottarelli's (1975) description in some aspects, but these are most likely attributable to deficiencies in the original figures. In the type material the marginal spines on the P5 of both sexes appear shorter; however, the flagellate distal parts of these elements are usually difficult to discern, and it seems conceivable that they were not illustrated correctly in the original description. Similarly, Cottarelli (1975) did not illustrate the spinules at the base of the spur and around the terminal process of the caudal ramus, but such morphological minutiae were generally overlooked prior to the advent of differential interference contrast microscopy. The female antennule has fewer setae on the proximal segments than in the Turkish material, but this can be attributed to the fact that Cottarelli viewed the appendage in dorsal aspect and hence overlooked various setae arising from the ventral surface. The three-

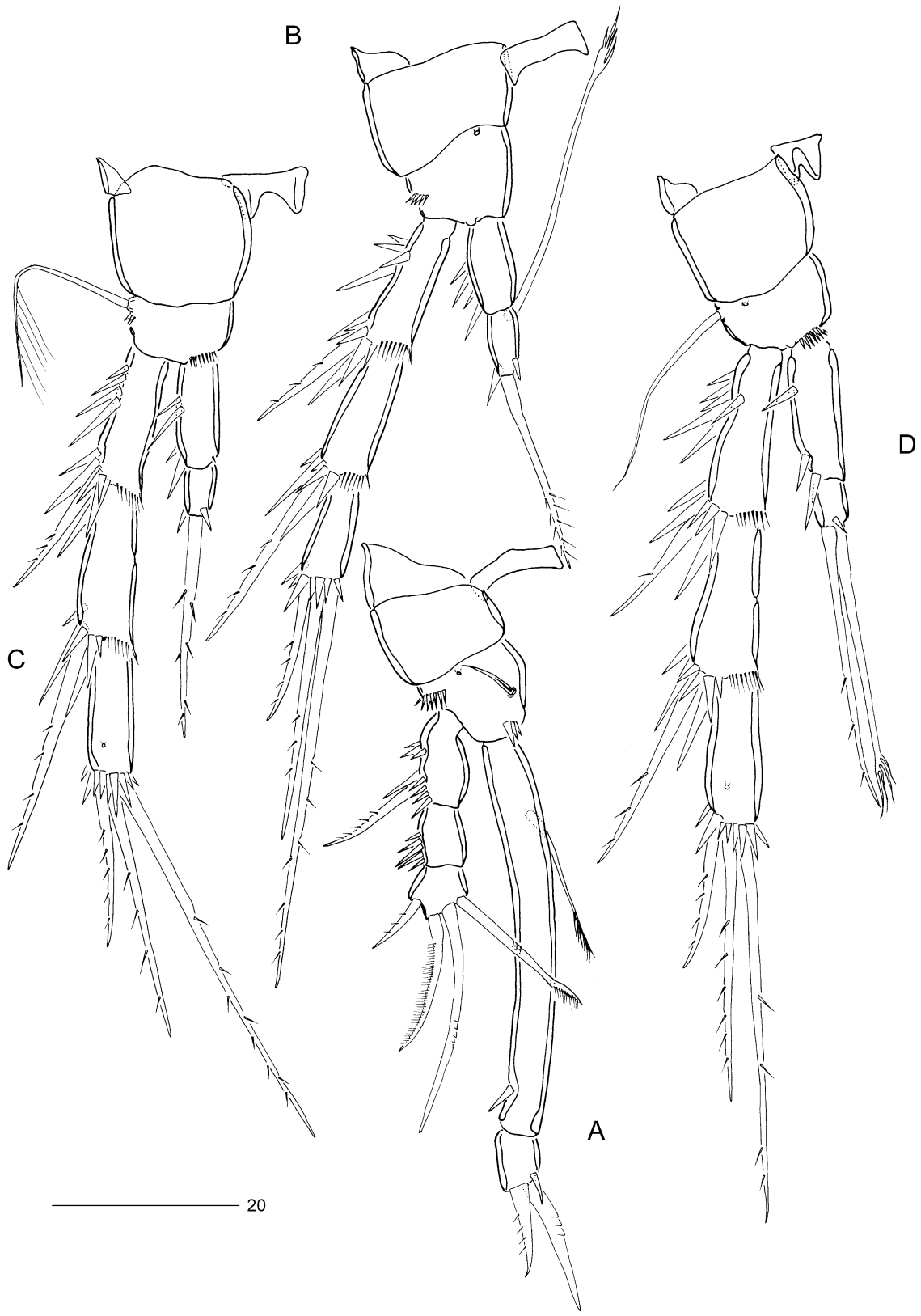

Figure 4. *Arenopontia nesaie* Cottarelli, 1975 (♀). A, P1, anterior view. B, P2, anterior view. C, P3, anterior view. D, P4, anterior view.

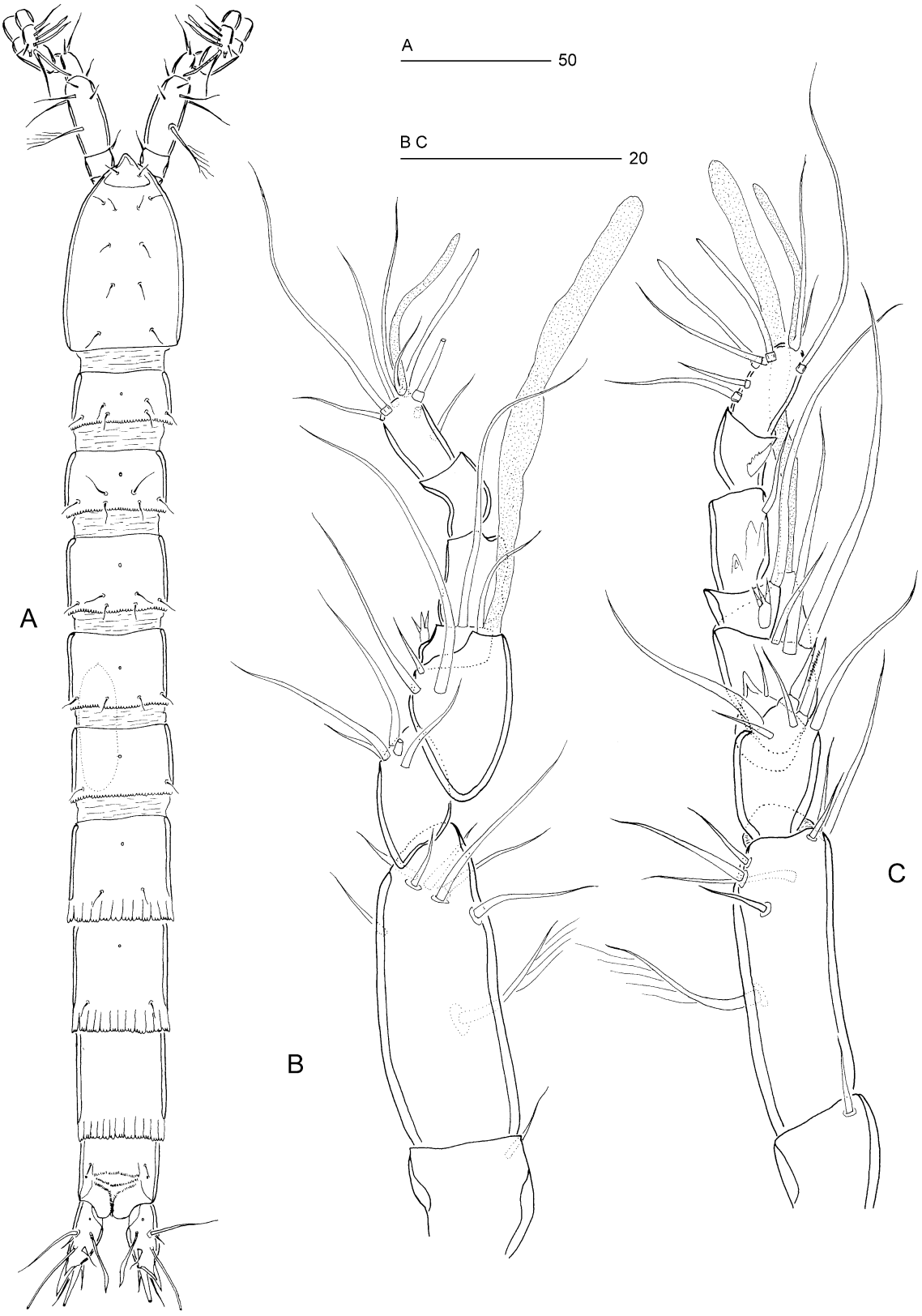

Figure 5. *Arenopontia nesaie* Cottarelli, 1975 (♂). A, habitus, dorsal view. B, antennule, ventral view. C, antennule, anterior view.

segmented mandibular palp, which was considered diagnostic for *A. nesaie*, was not observed in our material, and requires confirmation. The extra segment boundary indicates a two-segmented endopod, which has thus far not been reported for any other oligoarthran harpacticoid (but see Mitwally & Montagna, 2001; cf. below). It is also noteworthy that Cottarelli (1975) had accidentally rotated exp-3 in his drawing of the P2. His drawing of the female genital field superimposes external and internal structures; for a more accurate interpretation see Fig. 3C and Martínez Arbizu & Moura (1994: fig. 2c, as *A. nessiae*). The Sardinian specimens are somewhat smaller [334 μm (♀), 285–300 μm (♂)] than the Marmara population [341–396 μm (♀), 320–374 μm (♂)], but it is questionable whether this size discrepancy has any significance beyond the range of intraspecific variability.

Arenopontia nesaie appears to be widely distributed in the Mediterranean, with confirmed intertidal records from El Saler (Valencia, Spain) by Martínez Arbizu & Moura (1994, as *A. nesiae*), Sardinia (Cottarelli, 1975), the mouth of the Trigno River on the Adriatic coast (Molise, Italy) by Bruno, Cottarelli & Berrera (1998), and Dutlimanı beach (Sea of Marmara, Turkey) by Sak (2004, as *A. ciplaki*; present account). Mitwally & Montagna (2001) provided a redescription of *A. nesaie* based on specimens collected from three beaches (Bir Masoud, El Mamoura, and El Shatby) near Alexandria, Egypt, but the many deficiencies in their illustrations make it difficult to validate their identification. According to Wells (2007), Mitwally & Montagna (2001) make statements about the setation of P1–P4 that, if true, mean that their material cannot belong to *Arenopontia*. It is obvious that their atypical setal formula results from a failure to distinguish between ornamentation elements (such as long spinules) and genuine setae/spines. Their reports of an outer seta on P1 enp-1 and P3–P4 enp-1, as well as their claim of four elements on P2 exp-3, are false and do not reflect deficiencies in Cottarelli's (1975) original description, as claimed by the authors. The elements on the female P5 are distinctly longer than in *A. nesaie* (but are similar to our specimens), and the caudal ramus appears shorter. The variability illustrated for the male P5 suggests that Mitwally & Montagna (2001) had an amalgam of *Arenopontia* species in their samples. No information was given on the number of setae on the male P6. The distal segment of the P4 exopod appears rotated in their Fig. 11G. Finally, the mandibular palp is erroneously illustrated as three-segmented (see above). Pending re-examination of more material of the Egyptian populations, *A. nesaie* Cottarelli (1975) *sensu* Mitwally & Montagna (2001) is considered *species inquirenda* in *Arenopontia.*

ARENOPONTIA PONTICA APOSTOLOV, 1969

Original description: Apostolov (1969): pp. 125–127; Abb. 36–45.

Type locality: Bulgaria, south of Lozenetz, Düni Beach; 5 m from low-tide mark.

Remarks: Apostolov's (1969) description of *A. pontica*, from the Bulgarian Black Sea coast, is a taxonomic nightmare because of several internal inconsistencies between the text and illustrations. Apostolov (1969: 111) claimed to have found two females (although on p. 125 he stated that three females were recorded), but for some inexplicable reason provided a brief diagnosis of the male. He referred to Figure 46 in his description of the male P5, but this figure is not printed. His illustrations of the female show several extraordinary features not found in any other member of the Arenopontiidae: (1) the antennary exopod is bisetose – in all species of *Arenopontia* this ramus displays only one apical seta; (2) P1 exp-2 bears an outer spine – the absence of this spine is a high-level diagnostic, being a synapomorphy linking the Parastenocarididae, Leptopontiidae, and Arenopontiidae (Martínez Arbizu & Moura, 1994); (3) P1 enp-1 lacks an inner seta – this seta is present in all species, except for the inadequately described *A. problematica* and *Arenopontia accraensis* Lang, 1965 – we have been able to confirm its presence in the types of *A. problematica*; (4) P2–P3 exp-3 with four elements, i.e. with two outer spines and two terminal setae – all Arenopontiidae have only one outer spine and share a [021] setal formula on the distal exopod segment – note that Apostolov (1969) contradicts himself in the setal formula table on p. 125 (three elements), his Figure 42 (four elements), and the comparative table on p. 127 (four elements); (5) P2–P3 exp-2 bears a long inner seta – the latter seta is absent in all other arenopontiids, except for *Arenopontia angolensis* Kunz, 1971, which according to Kunz' (1971) setal formula possesses a seta on P2 exp-2. However, as Kunz neither illustrated the P2 nor mentioned this character in the text or the table comparing *Arenopontia africana* f. *africana* and *A. africana* f. *angolensis* (he does state that the P2 is as in the nominate subspecies, apart from the ornamentation of the inner seta on enp-2), we strongly suspect that his report is based on a slip of the pen in his table, rather than on an observational error.

Apostolov (1969) recognized a close relationship with *A. subterranea*, *A. indica* and *A.* sp. *sensu* Griga (1964) [the latter was later identified as conspecific with *Stenocaropsis valkanovi* (Marinov, 1974), family Cylindropsyllidae]. In our opinion it is impossible to make any positive statement on the identity and

Table 3. Diagnostic characters of *Arenopontia* species

	P1 enp-1:exp	P2 enp	P3 enp	P5♀♂	P6♂	CR	An Op
A. riedli	1.4	0.120	0.020	5	2	Spur	Smooth
A. nesaie	2.0	0.110	0.010	4	1	Spur	Pinnate
A. subterranea	1.5	0.110	0.010	4	2?*	Spinules	Smooth
A. problematica	1.5†	0.110‡	0.010‡	4	2?*	Spinules	Smooth

*According to Kunz (1937) and Masry (1970) the P6 is a minute plate bearing three elements, but it is likely that these claims are based on observational errors.
†Based on Sak's (2004) redescription.
‡Masry (1970) claimed there are two distal elements on P2–P3 enp-2 but this has been corrected by Sak (2004). CR = caudal ramus; An Op = anal operculum.

possible relationships of *A. pontica* other than that this species can be assigned to the genus *Arenopontia* as diagnosed herein. Pending redescription, *A. pontica* is considered here as *species inquirenda*. This course of action is in contrast to Marinov's (1971) suggestion to relegate *A. pontica* to a junior subjective synonym of *A. subterranea*. Marinov rightly pointed out some of the weaknesses in Apostolov's (1969) description, but it remains a mystery how he reconciled the many differences between the latter and his own illustrations of *A. subterranea* from the Bulgarian coast.

Inspired by the variability reported for French mediterranean (Chappuis, 1954a) and Romanian populations (Şerban, 1959) of *A. subterranea*, but apparently unaware of Marinov's (1971) paper, Apostolov (1973) claimed that *A. pontica* may well be a synonym of the latter. He further proposed that the Black Sea specimens represent a new subspecies of *A. subterranea*, but refrained from formally naming it. Apostolov stated that considerable variability was found in the caudal rami, the P1 exopod, and the P5, but it is conceivable that this is at least partly attributable to his failure to discriminate between two or more coexisting species. His drawings of the female P5 clearly refer to two different species: his Figure 5 shows a fifth leg of the *subterranea* type, whereas Figure 6 was almost certainly based on the species previously identified by Marinov (1971) as *A. stygia* (and described below as *Psammoleptastacus barani* sp. nov.). In accordance with Şerban's (1959) observations, Apostolov (1973) maintained that his material did not display the foliaceous seta VII, or the penicillate seta on P1 exp-3.

Key to species: A simple dichotomous identification key is difficult to construct; however, species can be reliably identified by considering the salient diagnostic characters summarized in Table 3.

GENUS *PSAMMOLEPTASTACUS* PENNAK, 1942A

Pennak (1942a) proposed this genus for a new species, *P. arenaridus*, collected from two sandy beaches near Woods Hole, and placed it without any further comment in the Canthocamptidae. He remarked on the superficial resemblance with other interstitial genera (*Leptastacus*, *Paraleptastacus*, and *Arenopontia*), but considered the differences in the antenna, maxillipeds, P5, and caudal rami sufficient for generic distinction. Pennak's (1942a) paper remained largely unnoticed until Noodt (1955b) synonymized *Psammoleptastacus* with *Arenopontia*, a course of action that was endorsed by Lang (1965) but was overlooked by Krishnaswamy (1957), who added a second species, *Psammoleptastacus orientalis* Krishnaswamy, 1957 from the Madras coast. As noted by Wells (1967), Lang's (1965) statement that *P. orientalis* belongs to *Arenocaris* (Leptastacidae) is obviously a slip of the pen.

Noodt (1955b) considered *A. stygia* to be most closely related to *A. arenarida*, recognizing some subtle differences in the caudal rami and P2–P4, whereas Lindgren (1976) suggested *A. stygia* is potentially '. . . an intraspecific variation of *A. arenarida*'. The genus *Psammoleptastacus* is reinstated herein for the latter two species and a new species, *P. barani* sp. nov., from the Turkish Black Sea coast, which had previously been misidentified as *A. stygia* by Marinov (1971). *Arenopontia subterranea* Kunz, 1937 *sensu* Rao & Ganapati (1969) is regarded as a *species inquirenda* in *Psammoleptastacus*, and *P. orientalis* is transferred to *Onychopontia* gen. nov. *Psammoleptastacus* differs from *Arenopontia* and other arenopontiid genera in the small size of the P1 endopod, which is shorter than the exopod. It is most closely related to *Onychopontia*, with which it shares the sexual dimorphism on the P3 endopod (apomorphic) and the presence of two geniculate setae on P1 enp-2.

Diagnosis: Arenopontiidae. Urosomites: without conspicuous surface ornamentation. Anal somite: without

paired dorsolateral spinous processes. Anal operculum: not modified. Hyaline frills of abdominal somites with rectangular digitate lappets. Caudal ramus: with dorsolateral spur near medial margin. P1 exopod: three-segmented; exp-1 with outer spine; exp-3 with two spines and two geniculate setae. P1 endopod: not prehensile, shorter than exopod; enp-2 with two geniculate setae. P2–P3 endopods: two-segmented. P3 endopod: with outer distal element defined at base. P4 endopod: with well-developed outer distal element. Armature formula as follows:

	Exopod	Endopod
P2	0.0.021	0.120
P3	0.0.021	0.020
P4	0.0.021	0.020

P3 endopod male: sexually dimorphic, two-segmented; enp-1 unarmed; enp-2 minute, with strong spinule on outer margin, curved spine distally (sometimes fused at base), and fine seta on inner margin. P5: with outer basal seta and four discrete elements; innermost one distinctly smaller in male. P6 male: with two setae.

Type species: Psammoleptastacus arenaridus Pennak, 1942a (by monotypy).

Other species: Arenopontia stygia Noodt, 1955b = *P. stygius* (Noodt, 1955b) comb. nov.; *P. barani* sp. nov.

Species inquirenda: Arenopontia subterranea Kunz, 1937 *sensu* Rao & Ganapati (1969)

PSAMMOLEPTASTACUS ARENARIDUS PENNAK, 1942A

Psammoleptastacus arenardius Pennak, 1942a: Coull (1977) (*lapsus calami*)

Arenopontia arenarida (Pennak, 1942a) Noodt (1955a)

Arenopontia (*Arenopontia*) *arenarida* (Pennak, 1942a): Wells (1967)

Arenopontia arenardia (Pennak, 1942a): Coull (1971, 1977) (*lapsus calami*)

Arenopontia stygia Noodt (1955b) *sensu* Coull (1971) and Lindgren (1976)

Original description: Pennak (1942a): pp. 275–278; plate I, figures 1–11.

Type locality: USA, Massachusetts, Woods Hole. Pennak (1942a) collected material from both Nobska and north Cape Cod beaches, but did not specify the type locality; sand washings in vicinity of high tide mark.

Material examined: NMNH: one ♂ syntype mounted *in toto* on slide, and partly remounted by one of us (RH); erroneously labelled '*Paraleptastacus arenaridus* n.g. n. sp.'; Cat. no. 81982; leg. R.W. Pennak, September 1939.

Partial redescription

Male: Total body length from tip of rostrum to posterior margin of caudal rami: 325 μm. Body: slender and cylindrical, without clear distinction between prosome and urosome. Hyaline frills of thoracic somites weakly developed and crenulated (Fig. 6A, B); those of abdominal somites strongly developed and consisting of rectangular digitate lappets (Fig. 6A).

Caudal rami (Fig. 6A, C): approximately 2.8 times longer than basal width, tapering posteriorly; with one pore dorsally, one pore near ventral proximal margin, and two pores laterally near outer spinules; outer distal corner produced into posteriorly directed recurved spinous process, accompanied by ventral spinular row at base; dorsomedial surface with posteriorly directed spinous process. Armature consisting of seven setae: seta I, small; setae II and III, long and naked; seta IV, short, sparsely pinnate, located between seta V and distal spinous process; seta V, long and with fracture plane; seta VI, small, naked, and fused at base to seta V; seta VII, weakly foliaceous and triarticulate at base.

Rostrum (Fig. 6D): small, broadly subtriangular, tapering distally, with two delicate sensillae and subapical pore.

Antennule (Fig. 7A): nine-segmented, haplocer; geniculation between segments 7 and 8. Segment 2 longest; segment 4 an incomplete sclerite with one modified (fused at base) and one tiny element; segment 5 with long aesthetasc fused basally to seta; segments 6–8 with one seta and one basally fused spiniform element. Setal formula: 1-[1], 2-[7 + 1 plumose], 3-[4 + 1 pinnate spine], 4-[1 + 1 modified], 5-[2 + (1 + ae)], 6-[1 + 1 modified], 7-[1 + 1 modified], 8-[1 + 1 modified], 9-[7 + acrothek]. Acrothek consisting of short aesthetasc fused basally to two slender setae.

P1 (Fig. 7B): coxa without ornamentation. Basis: with spinular row near bases of endopod and exopod; anterior surface with inner naked seta. Exopod: three-segmented; about 1.3 times the length of endopod; all segments with spinules along outer margin; exp-1 longest, with long unipinnate outer spine; exp-2 without outer element; exp-3 with two unipinnate spines and two geniculate setae of different lengths. Endopod: two-segmented, not prehensile; enp-1 slightly longer than exp-1, with a serrate seta at about halfway along the length of the inner margin, and with two subdistal spinules along outer

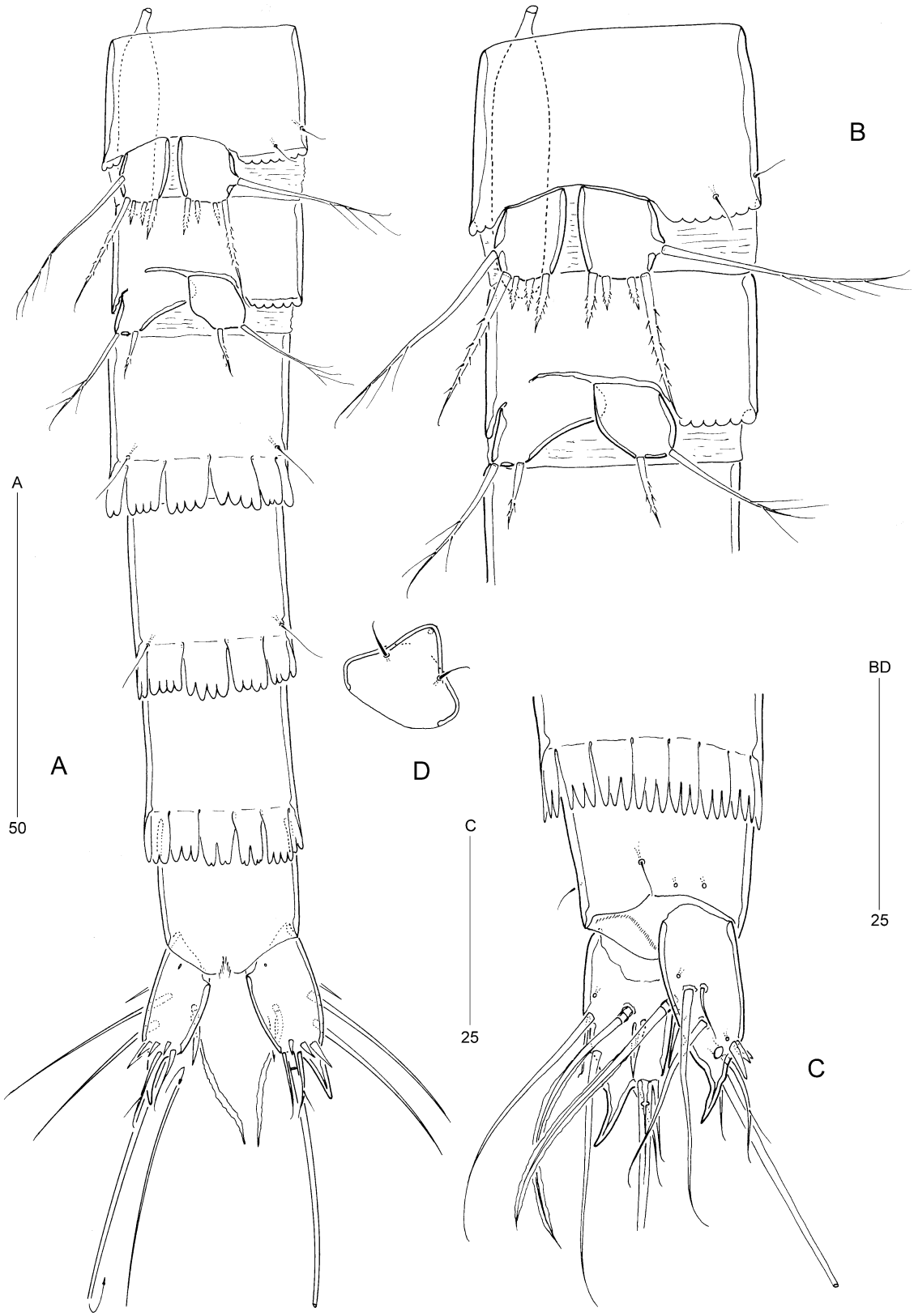

Figure 6. *Psammoleptastacus arenaridus* Pennak, 1942a (♂). A, urosome, ventral view. B, P5 and P6, ventral view. C, posterior portion of penultimate somite, anal somite, and caudal rami, dorsolateral view. D, rostrum.

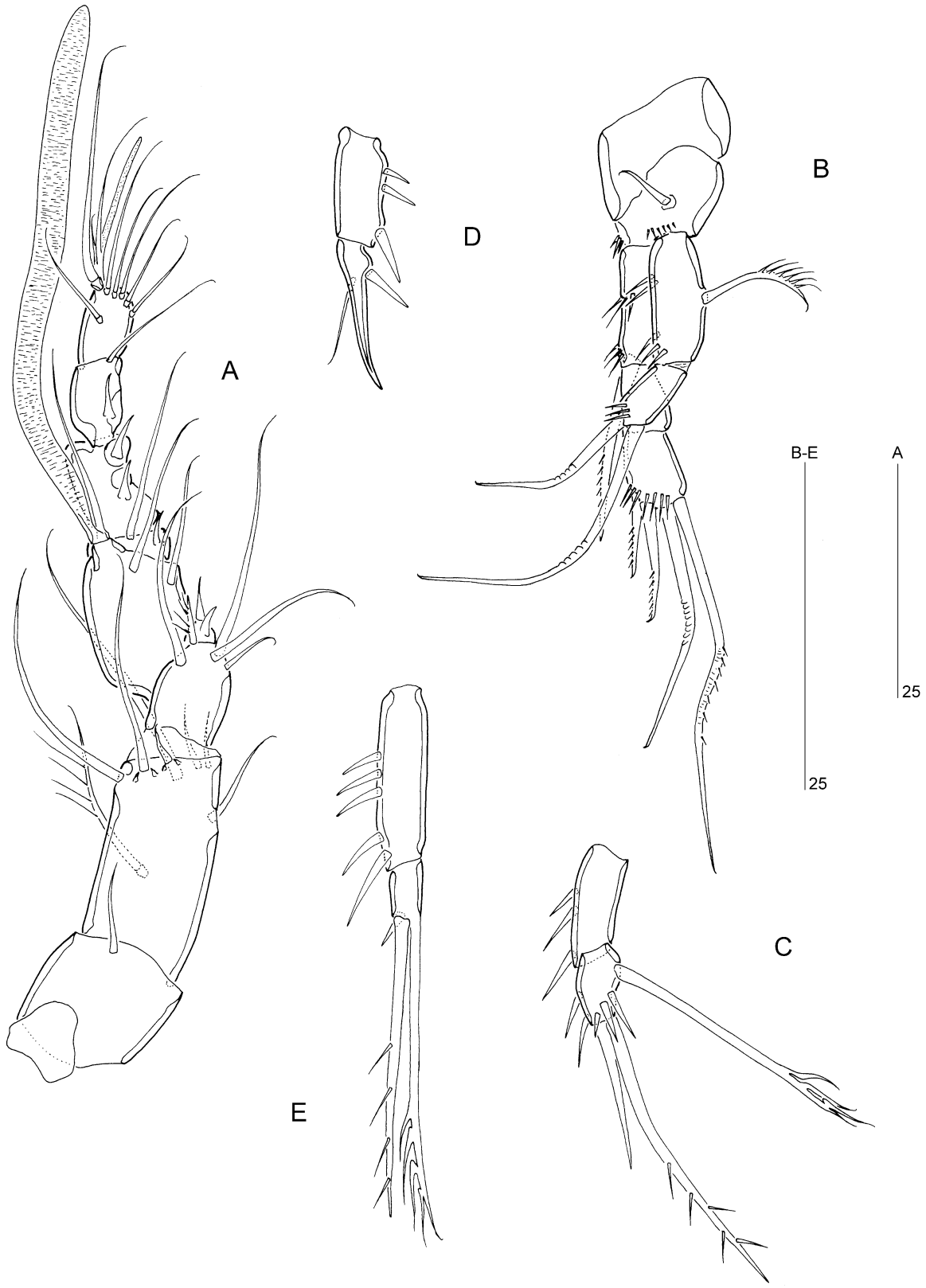

Figure 7. *Psammoleptastacus arenaridus* Pennak, 1942a (♂). A, antennule, ventral view. B, P1, anterior view. C, P2 endopod, anterior view. D, P3 endopod, anterior view. E, P4 endopod, anterior view.

margin; enp-2 about half the size of enp-1, with two geniculate setae and a few spinules.

P2 endopod (Fig. 7C): two-segmented; enp-1 with few spinules along outer margin; enp-2 short, with a long, apically serrate, backwardly directed seta near proximal inner corner, and a long bipinnate inner seta and a short bare outer spine around distal margin.

P3 endopod (Fig. 7D): two-segmented; enp-1 with few strong spinules along outer margin; enp-2 minute, with strong spinule at outer distal corner, short thin seta arising from inner distal corner (homologous with long inner distal seta of female), and naked curved apical spine, fused at base (homologous with outer distal spine of female).

P4 endopod (Fig. 7E): two-segmented; enp-1 with five strong spinules along outer margin; distal margin of enp-2 with long, basally fused, serrate seta and long, unipinnate outer seta.

P2–P4: spine and seta formula as for the genus.

P5 (Fig. 6B): forming subrectangular plate; outer basal seta sparsely plumose. Free distal margin: with three short bipinnate spines and one long bipinnate outer seta; inner spine longer than the other two.

Sixth legs (Fig. 6B): asymmetrical, with smallest P6 closing off functional gonopore; each with a short inner and a long plumose outer seta.

Remarks: Pennak's (1942a) illustrations of the male are restricted to the antennule, and no reference was made to the sexual dimorphism on the P3 endopod. His erroneous description of the caudal ramus, showing a basally swollen seta V and a triangular process at the distal outer corner, has no doubt been a source of confusion for subsequent identifications. Re-examination of a male paratype proved: (1) caudal ramus seta V to be normally developed, and the terminal spinous process to be much longer and more sharply pointed; and (2) P1 endopod to be markedly shorter than the exopod. Both aspects contradict Pennak's (1942a) description, but agree with Lindgren's (1976) observations based on North Carolina specimens. Lindgren also found that the proximal third of seta V was modified in approximately 60% of the population; individuals with unmodified setae were provisionally identified as *A. stygia*. Given this intraspecific variability, in conjunction with both 'populations' having the same distribution within the beach, we attribute all North Carolina records of *A. stygia* to *P. arenaridus*. These include Lindgren's (1976) intertidal record from west of the Iron Steamer Pier near Morehead City, and, although provisionally, Coull's (1971) subtidal record north of Cape Hatteras (at a depth of 100 m!). *Psammoleptastacus arenaridus* appears to be restricted to the north-eastern Atlantic seaboard of the USA, from the Woods Hole area in the north (Pennak, 1942a, b, 1952; Lindgren, 1976) to at least North Inlet, South Carolina (Coull & Dudley, 1985) in the south. Pennak (1942b) provides data on the horizontal distribution and relative abundance.

PSAMMOLEPTASTACUS STYGIUS (NOODT, 1955B) COMB. NOV.

Arenopontia stygia Noodt (1955b)

Arenopontia (*Arenopontia*) *stygia* Noodt (1955b): Wells (1967)

Original description: Noodt (1955b): pp. 101–102; Tafel 35 (figs 75–82) (♀ only).

Type locality: France, Landes, Mimizan-Plage; medium coarse sand.

Remarks: The type material of *A. stygia* (a single female) is no longer extant. Noodt's (1955b) dorsal view of the caudal ramus shows three setae inserting at about the same level; the short inner one (adjacent to seta VII) is not a setal element but the dorsolateral spur. In addition to the type locality (Delamare Deboutteville, Gerlach & Siewing, 1955; Noodt, 1955b, c; Delamare Deboutteville, 1960a), *P. stygius* has been recorded from the Bassin d'Arcachon, Gironde (Renaud-Debyser, 1963a, b) and the Portuguese coast (Francelos, south of Porto) (Galhano, 1970). Marinov's (1971) record from Bulgaria is attributable to *P. barani* sp. nov. (see below).

PSAMMOLEPTASTACUS BARANI SP. NOV.

Arenopontia stygia Noodt, 1955b *sensu* Marinov (1971)

Type locality: Turkey, Black Sea coast, Istanbul, Sahilköy (east of Bosporus); sandy beach.

Material examined: Holotype ♀ (dissected on eight slides) (BUZM). Paratypes are one ♀ and one ♂ in alcohol (NHM reg. nos. 2006. 1966–1967), and two ♂♂ dissected on two and seven slides, respectively (NHM reg. nos. 2006. 1968–1969); all collected at type locality; leg. S. Karaytuğ and S. Sak, 01 May 2001.

Description

Female: Total body length from tip of rostrum to posterior margin of caudal rami: 330–380 μm (mean = 361 μm; $N = 7$). Maximum width measured at P5-bearing somite. Body: slender and cylindrical, without clear distinction between prosome and urosome (Fig. 8A, B). Hyaline frills of thoracic somites weakly developed and crenulated; those of genital double-somite and free abdominal somites strongly developed, and consisting of rectangular digitate

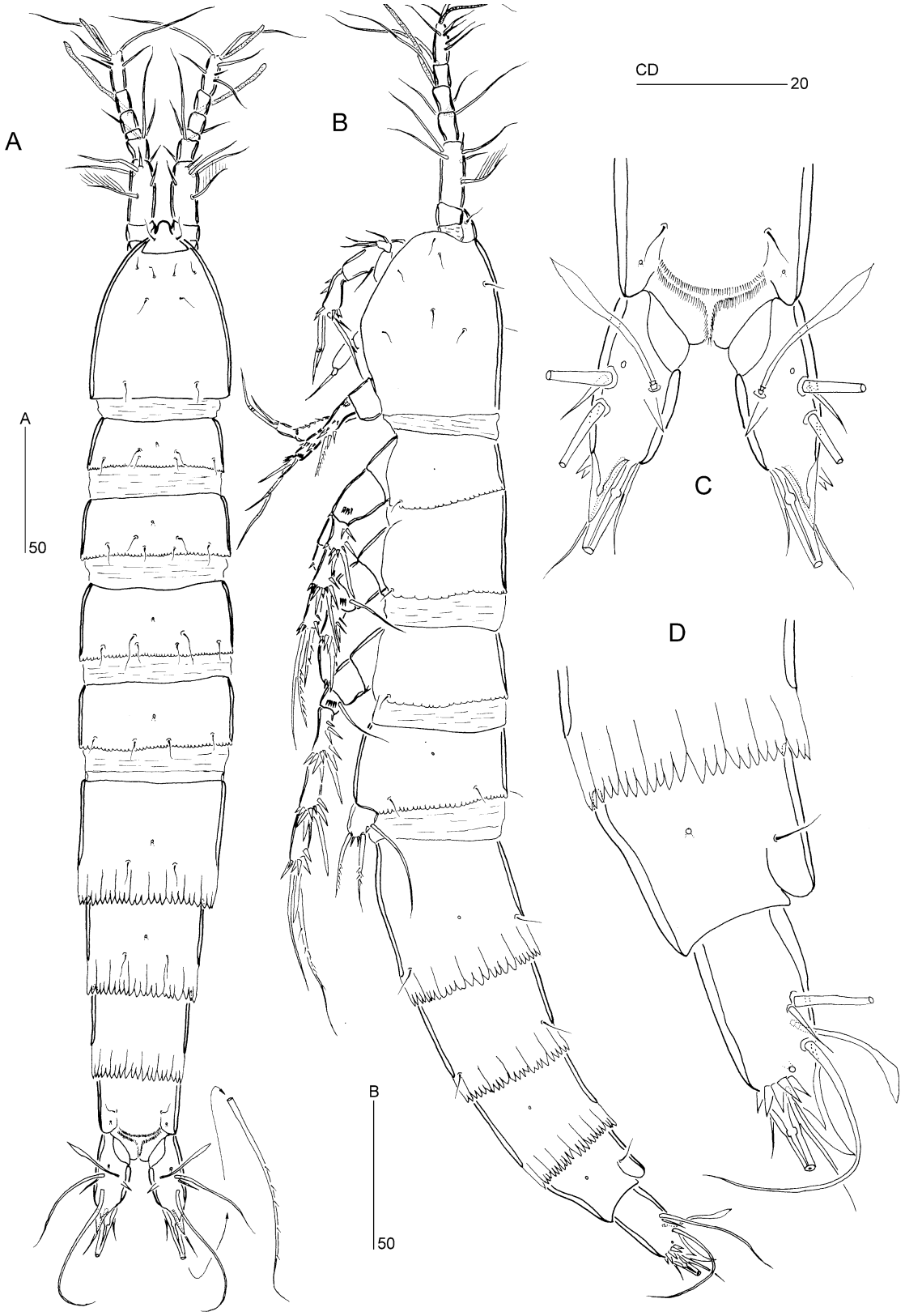

Figure 8. ***Psammoleptastacus barani*** **sp. nov.** (♀). A, habitus, dorsal view. B, habitus, lateral view. C, anal somite and caudal rami, dorsal view. D, posterior part of penultimate somite, anal somite, and left caudal ramus, lateral view.

lappets (Figs 8A, B, 9A, 8D). Genital double-somite (Fig. 9A): slightly longer than wide; without chitinous ribs marking original segmentation; with one middorsal, two lateral, and two ventral pores. Anal somite (Fig. 8C, D): with two dorsal and two lateral pores. Anal operculum: with minute spinules along free distal margin (Fig. 8C). Anus: positioned subterminally between caudal rami.

Caudal rami (Fig. 8C, D): approximately 2.75 longer than basal width, tapering posteriorly; with one pore dorsally, one near ventral proximal margin (Fig. 9A), and one laterally near outer spinules; outer distal corner produced into posteriorly directed recurved spinous process, accompanied by ventral spinular row at base; dorsomedial surface with posteriorly directed spinous process arising from base of seta VII. Armature: as in *P. arenaridus*, but with a more foliaceous seta VII.

Rostrum (Figs 8A, 10A): broadly subtriangular, tapering apically, with two delicate sensillae and one subapical ventral pore.

Antennule (Fig. 10A, B): six-segmented. Segment 1: with one seta near anterodistal margin. Segment 2: longest, about 3.5 times longer than wide. Segment 4: with long aesthetasc (30-μm long) fused at base with seta. Distal segment: with seven naked setae (one of which spatulate), and apical acrothek consisting of short aesthetasc (13-μm long) and two slender setae. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[7 + acrothek].

Antenna (Fig. 10C, D): coxa small, without ornamentation. Original segmentation of allobasis marked by partial transverse surface suture; with one spinular row along exopodal margin. Exopod: one-segmented, elongate, with long naked seta apically. Free endopod: with two spinular rows on anterior surface and finer spinules at outer distal corner; lateral armature consisting of two short spines; apical armature consisting of two spines and three geniculate setae, the longest of which with spinules around geniculation and fused basally to tiny accessory seta.

Mandible, maxillule, maxilla, and maxilliped: as in *A. nesaie*.

P1 (Fig. 11A): intercoxal sclerite long and rectangular. Praecoxa: subtriangular and naked. Coxa: without ornamentation. Basis: with spinular row near bases of endopod and exopod; anterior surface with a proximal pore and a small inner basal seta. Exopod: three-segmented; about 1.2 times longer than endopod; all segments with spinules along outer margin; exp-1 longest, with long unipinnate outer spine; exp-2 without outer element; exp-3 with two unipinnate outer spines and two geniculate apical setae. Endopod: two-segmented, not prehensile; enp-1 distinctly longer than exp-1, with a serrate seta at about two-thirds of the length of the inner margin, and several spinules along outer margin; enp-2 less than half the length of enp-1, with two geniculate setae (inner one about twice as long as outer).

P2–P4 (Fig. 11B–D): intercoxal sclerites naked. Praecoxae: small and naked. Coxae: rectangular and without ornamentation. Bases: smaller than coxae, with a spinular row near base of endopod (P3–P4); anterior surface with a proximal pore; outer basal seta absent (P2), plumose (P3), or naked (P4). Exopods: three-segmented; segments with spinular ornamentation, as illustrated; inner distal seta of exp-3 sparsely bipinnate, all other elements unipinnate; P3–P4 exp-3 with anterior pore. Endopods: two-segmented, with few spinules, as illustrated. P2 enp-2: with a long, apically serrate, backwardly directed seta. Distal margin of P3 enp-2: with naked outer spine and long bipinnate inner seta. P4 enp-1: slightly shorter than exp-1; distal margin of enp-2 with long, basally fused, serrate seta, and long, unipinnate outer seta. P2–P4: spine and seta formula as for the genus.

Fifth legs (Fig. 9A): closely set together but not touching in ventral midline. Baseoendopod and exopod fused, forming a semicircular plate; distal margin with two short bipinnate spines flanked by two long bipinnate setae; outer basal seta long and sparsely plumose.

Genital field (Fig. 10E): with genital apertures fused forming median common slit; closed off by fused P6 forming operculum, with one minute spinous process on either side; copulatory pore located midventrally, close to genital slit; seminal receptacles difficult to discern.

Male: Total body length from tip of rostrum to posterior margin of caudal rami: 290–335 μm (mean = 315 μm; $N = 6$). Body ornamentation (Figs 9B, 12A): essentially as in female. Sexual dimorphism: in antennule, genital segmentation, P3 endopod, P5, and P6. Spermatophore length: approximately 45 μm.

Antennule (Fig. 12C, D): nine-segmented, haplocer; geniculation between segments 7 and 8. Segment 2 longest, about 2.2 times as long as wide; segment 4 an incomplete sclerite with one modified (fused at base) and one tiny element; segment 5 with long aesthetasc (45-μm long) fused basally to very small seta; segments 6–8 with one seta and one basally fused spiniform element. Segment 9: with one spatulate seta. Setal formula: 1-[1], 2-[7 + 1 plumose], 3-[4 + 1 pinnate spine], 4-[1 + 1 modified], 5-[2 + (1 + ae)], 6-[1 + 1 modified], 7-[1 + 1 modified], 8-[1 + 1 modified], 9-[7 + acrothek]. Acrothek consisting of short aesthetasc (13-μm long) fused basally to two slender setae.

P3 endopod (Fig. 12B): two-segmented; enp-1 with few strong spinules along outer margin; enp-2

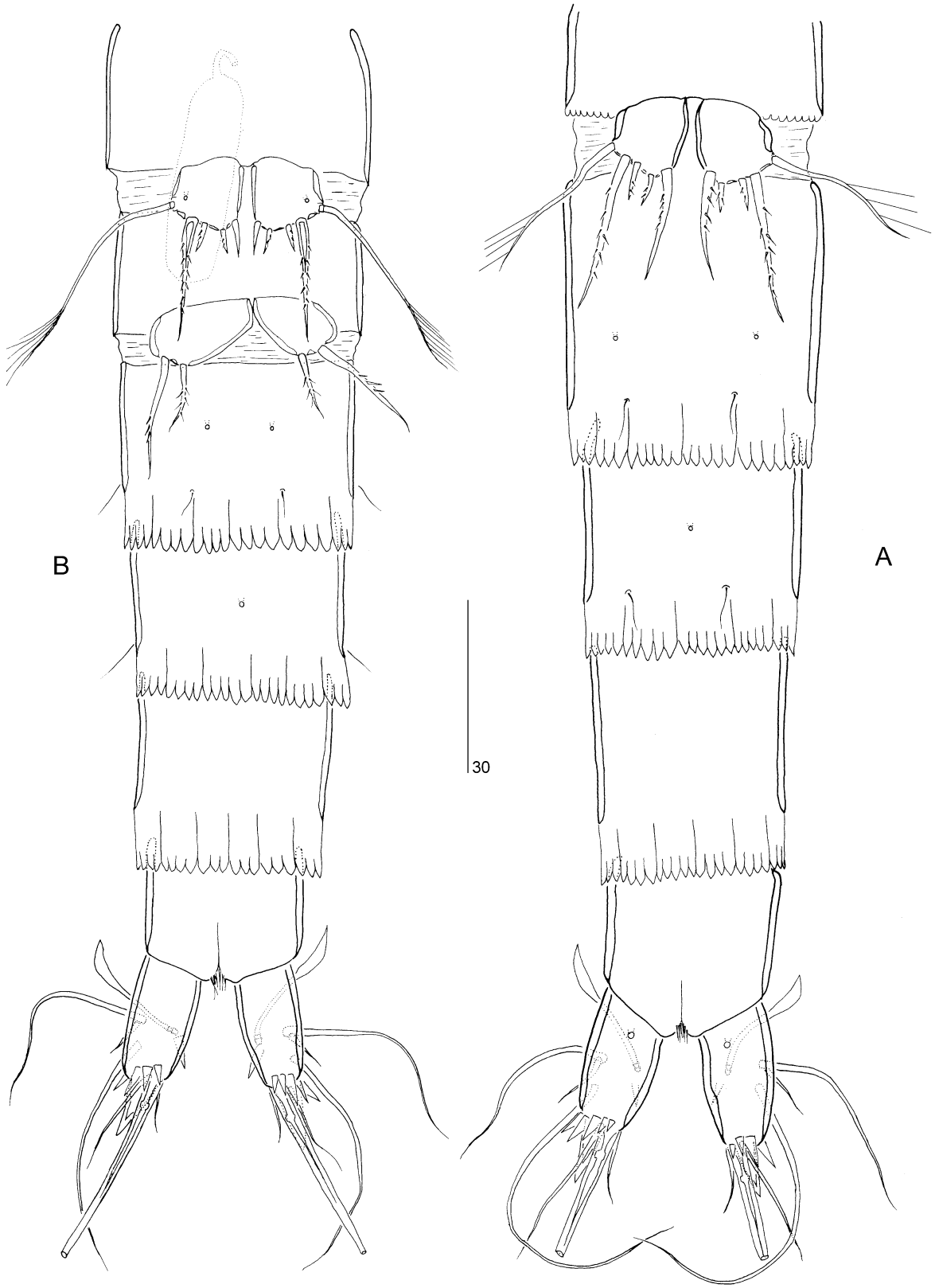

Figure 9. ***Psammoleptastacus barani*** **sp. nov.** A, urosome ♀, ventral view. B, urosome ♂, ventral view.

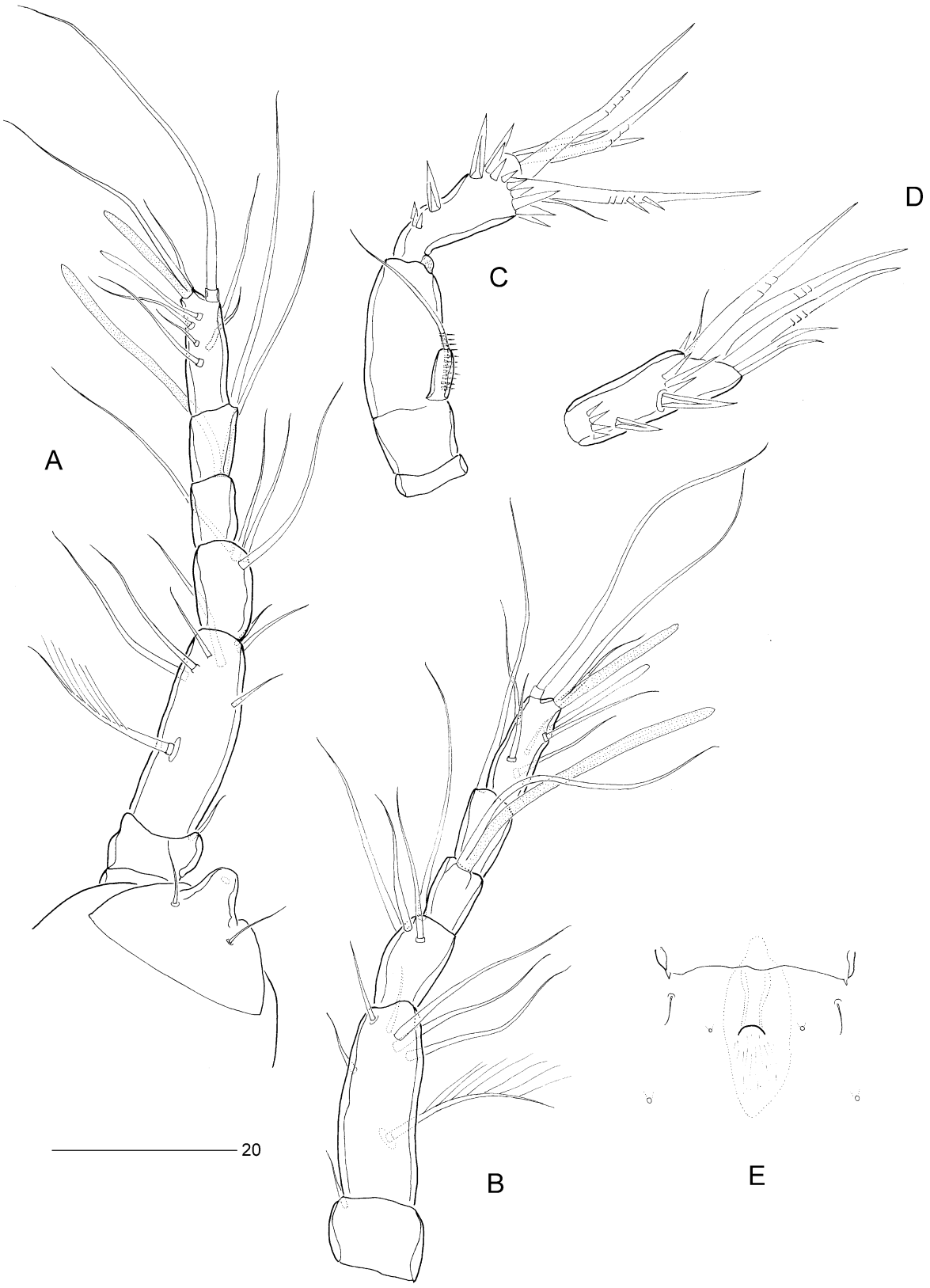

Figure 10. ***Psammoleptastacus barani*** **sp. nov.** (♀). A, rostrum and antennule, dorsal view. B, antennule, ventral view. C, antenna. D, free antennary endopod. E, genital field.

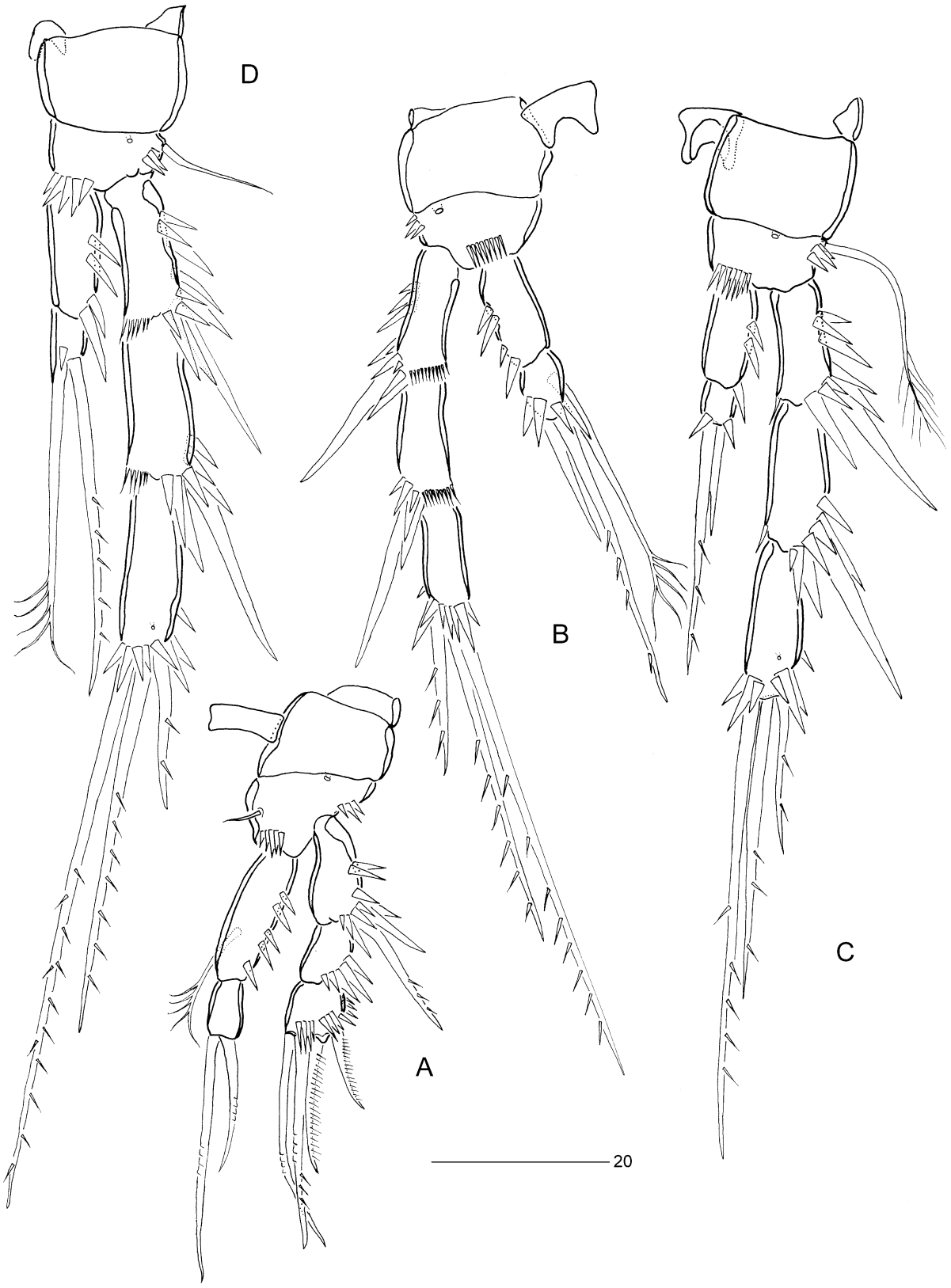

Figure 11. ***Psammoleptastacus barani*** **sp. nov.** (♀). A, P1, anterior view. B, P2, anterior view. C, P3, anterior view. D, P4, anterior view.

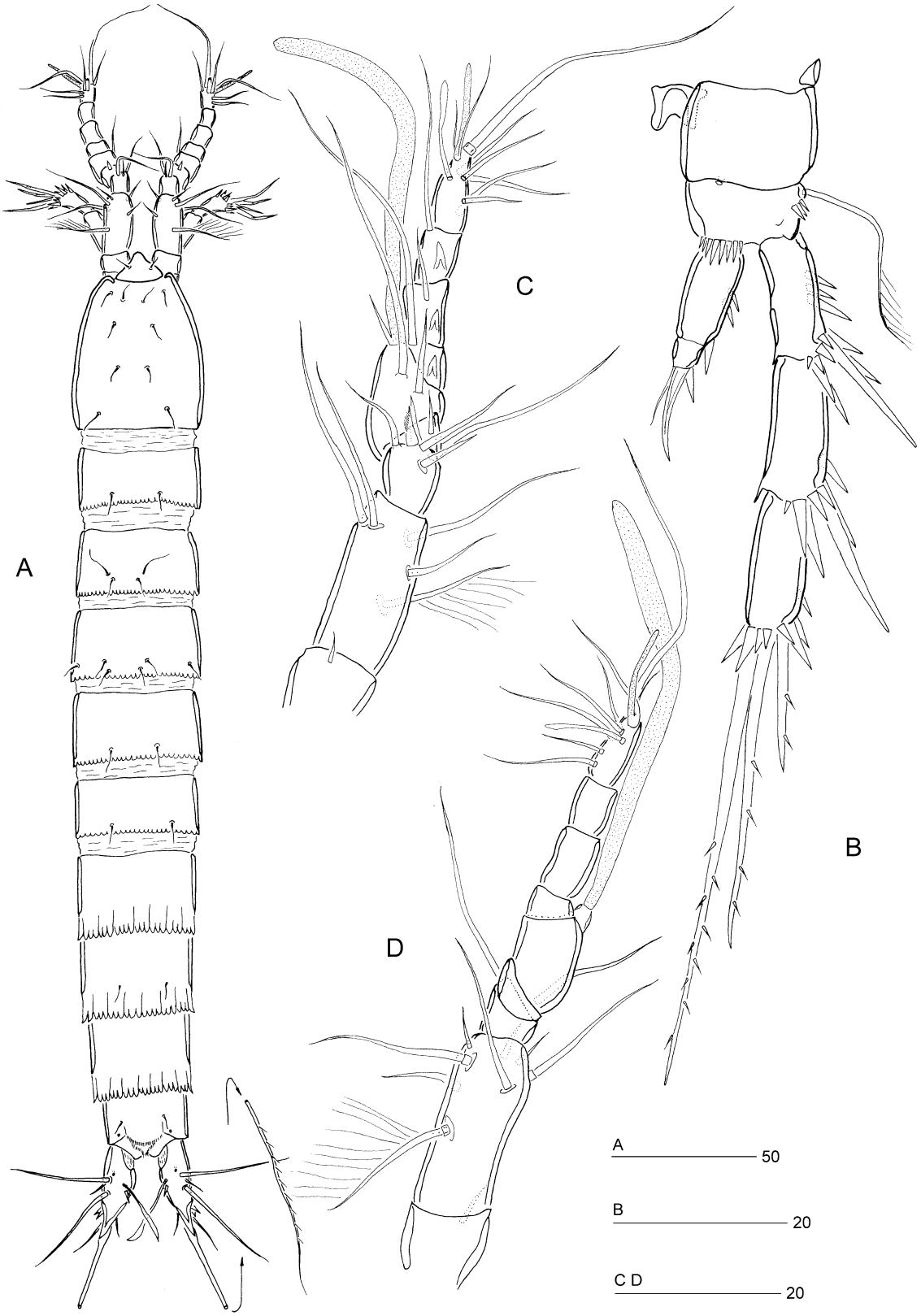

Figure 12. ***Psammoleptastacus barani*** **sp. nov.** (♂). A, habitus, dorsal view. B, P3, anterior view. C, antennule, ventral view. D, antennule, dorsal view.

Table 4. Diagnostic features of *Psammoleptastacus* species

	P. arenaridus	*P. stygius*	***P. barani* sp. nov.**
P1 exopod:endopod*	1.33	1.28	1.15
P3 enp-2 ♂ distal spine	fused	?	discrete
P4	exp-1 < enp-1	exp-1 < enp-1	exp-1 > enp-1
Caudal ramus length : basal width	2.75	3.85	2.75

*Length of rami calculated as sum of segment lengths.

minute, with strong spinule at outer distal corner, short fine seta arising from inner distal corner (homologous with long inner distal seta of female), and naked curved apical spine, discrete at base (homologous with outer distal spine of female).

P5 (Fig. 9B): with armature as in female, but with innermost element of distal margin much shorter and bare.

Sixth legs (Fig. 9B): asymmetrical, with smallest P6 closing off functional gonopore; each with two pinnate setae.

Etymology: The species is named after Prof. İbrahim Baran, Dokuz Eylül University, in recognition of his contributions to herpetology in Turkey.

Remarks: Psammoleptastacus barani sp. nov. differs from its two known congeners in the longer P1 endopod, and the length of P4 enp-2, which is shorter than, or at most as long as, the proximal exopod segment, instead of being distinctly longer. It is similar to *P. arenaridus* in the length of the caudal ramus, but deviates from it in the detailed morphology of the male P3 endopod. Marinov (1971) recorded a few specimens from the beaches of the Arkutino region (south of Sozopol) along the Bulgarian coast, which he attributed to *A. stygia*. He noted the difference in the relative length of the P1 endopod between his specimens and Noodt's (1955b) type population of *P. stygius*. The similarity in the relative length of the P1 endopod, P4 endopod, and caudal ramus, the P3 endopodal sexual dimorphism, and the female P5, leave little doubt that Marinov (1971) was dealing with *P. barani* sp. nov. The only discrepancy between both descriptions is found in the male P5, which has a much longer innermost seta in the Bulgarian material. Apostolov (1973) claimed that considerable variability was found in the P5 of his Black Sea *A. subterranea* (no localities specified), but it is conceivable that his drawings of the female P5 were based on two different species: his Figure 18-5 shows a P5 of the *Arenopontia* type, whereas his Figure 18-6 was almost certainly based on the species previously identified by Marinov (1971) as *A. stygia*. Note that the type locality of *P. barani* sp. nov. is in close proximity to the Bulgarian collecting sites.

ARENOPONTIA SUBTERRANEA KUNZ, 1937 *SENSU* RAO & GANAPATI (1969)

?*Arenopontia subterranea* Kunz (1937) *sensu* Rao (1967)

Original description: Rao & Ganapati (1969): pp. 268–269; figure 5.

Type locality: India, Andhra Pradesh, Vishakhapatnam, Waltair; sandy beach, medium sand.

Remarks: Rao & Ganapati (1969) stated that only minor variations occurred between their specimens from Waltair (India) and Kunz' 1937 type material of *A. subterranea*, listing examples such as the caudal ramus seta VII, which is not foliaceous, the inner seta on P1 exp-3, which is not modified, and the serrate nature of the inner setae on enp-2 of P2 and P4. However, their figure of the P1, showing a nonprehensile endopod and the absence of the penicillate seta on exp-3, unequivocally excludes the Indian specimens from the genus *Arenopontia*. The presence of two geniculate setae on P1 enp-2, in conjunction with the presence of the inner serrate seta on P2 enp-2, suggests a relationship with the genus *Psammoleptastacus*. Pending examination of new material, Rao & Ganapati's (1969) species is considered *species inquirenda* in the latter genus. Provided their figures of the fifth legs are correct, the presence of only four elements on this limb is thus far unique within the genus. The presence of two setae on the antennary exopod and the absence of the outer distal element on P2 enp-2 require confirmation. Rao's (1967) record of *A. subterranea* from Palm Beach, Waltair, conceivably refers to the same species.

Key to species

A straightforward dichotomous key is impossible to construct. Differences between species are subtle at best (Table 4), and any identification should be checked against the relevant descriptions.

GENUS *NEOLEPTASTACUS* NICHOLLS, 1945

The genus *Neoleptastacus* has had an intricate taxonomic history since its proposal by Nicholls (1945). It remained monotypic until Chappuis (1955), and not Kunz (1954), as claimed by Noodt (1955a), relegated it to a junior synonym of *Arenopontia*. This course of action was forecasted by Chappuis' (1954b) statement that Nicholls' new genus *Paraleptastacus* [*sic*] should be united with *Arenopontia*. Krishnaswamy (1957) argued against this inclusion, and maintained the validity of *Neoleptastacus* as a distinct genus; he also added a second species, *Neoleptastacus secundus*, from the Madras coast. Wells (1967) dismissed Krishnaswamy's (1957) decision, and retained *Neoleptastacus* as a subgenus of *Arenopontia*. Following some initial criticism by Mielke (1982a), the subgeneric classification was abolished by Martínez Arbizu & Moura (1994), and *Neoleptastacus* was synonymized with *Arenopontia*. Huys *et al*. (1996b) and Bodin (1997) reinstated both subgenera, but Wells (2007) preferred to amalgamate them, and consequently synonymized *Neoleptastacus* for the third time. The genus is resurrected here and redefined to accommodate: (1) all species that have previously been allocated to the subgenus *Neoleptastacus* (see Karanovic, 2000); (2) Mielke's (1985) Chilean species *A. clasingi*, *A. pacifica*, and *A. spicata*; and (3) the two species formerly included in the genus *Pararenopontia* [*Pararenopontia breviarticulata* (Mielke, 1975) and *Pararenopontia trisetosa* (Mielke, 1982a)]. A detailed review of the genus, including new species and an updated key, will be published elsewhere (Sak, Huys & Karaytuğ, in press b).

Diagnosis: Arenopontiidae. Urosomites: occasionally with conspicuous surface ornamentation (*Neoleptastacus clasingi*, *Neoleptastacus ornamentus*, and *Neoleptastacus reductaspina*). Anal somite: with (*acanthus* lineage) or without (all other lineages) paired dorsolateral spinous processes. Anal operculum: sometimes with median extension. Hyaline frills of abdominal somites with rectangular digitate or nondigitate lappets. Caudal ramus: usually with dorsolateral spur near medial margin. P1 exopod: two- or three-segmented; exp-1 with/without outer spine; exp-3 (or exp-2 when exopod two-segmented) with one or two spine(s) and two geniculate setae. P1 endopod: not prehensile, at least as long as exopod; enp-2 with two geniculate setae (*Neoleptastacus speluncae* and *Neoleptastacus phreaticus*) or outer spine plus inner geniculate seta (all other species). P2–P3 endopods: one- or two-segmented. P3 endopod: with outer distal element usually fused at base. P4 endopod: with well-developed outer distal element (except in *trisetosus* lineage). Armature formula as follows:

	Exopod	Endopod
P2	0.0.021	0.(0–1)(1–2)0 or 110
P3	0.0.021	0.0(1–2)0 or 010
P4	0.0.(0–1)21	0.020

P3 endopod ♂: not sexually dimorphic. P5 with outer basal seta and between one and three discrete elements; innermost element fused to segment forming spinous process (weakly delimited in *Neoleptastacus trisetosus*); length of process sometimes sexually dimorphic. P6 ♂ with one or two seta(e).

Type species: Neoleptastacus spinicaudatus Nicholls (1945) (by monotypy).

Other species: Arenopontia australis Chappuis, 1952 = *Neoleptastacus australis* (Chappuis, 1952) comb. nov.; *Arenopontia acantha* Chappuis, 1954b = *Neoleptastacus acanthus* (Chappuis, 1954b) comb. nov.; *Arenopontia longiremis* Chappuis, 1955 = *Neoleptastacus longiremis* (Chappuis, 1955) comb. nov.; *N. secundus* Krishnaswamy, 1957; *Arenopontia africana* Chappuis & Rouch, 1961 = *Neoleptastacus africanus* (Chappuis & Rouch, 1961) comb. nov.; *Arenopontia accraensis* Lang, 1965 = *Neoleptastacus accraensis* (Lang, 1965) comb. nov.; *Arenopontia indica* Rao, 1967 = *Neoleptastacus indicus* (Rao, 1967) comb. nov.; *Arenopontia ishikariana* Itô, 1968 = *Neoleptastacus ishikarianus* (Itô, 1968) comb. nov.; *A.* (*Neoleptastacus*) *africana* f. *angolensis* Kunz, 1971 = *Neoleptastacus angolensis* (Kunz, 1971) comb. nov.; *Arenopontia gussoae* Cottarelli, 1973 = *Neoleptastacus gussoae* (Cottarelli, 1973) comb. nov.; *Arenopontia trisetosa* Mielke, 1982a = *Neoleptastacus trisetosus* (Mielke, 1982a) comb. nov.; *Arenopontia clasingi* Mielke, 1985 = *Neoleptastacus clasingi* (Mielke, 1985) comb. nov.; *Arenopontia pacifica* Mielke, 1985 = *Neoleptastacus pacificus* (Mielke, 1985) comb. nov.; *Arenopontia spicata* Mielke, 1985 = *Neoleptastacus spicatus* (Mielke, 1985) comb. nov.; *Arenopontia chaufriassei* Bodiou & Colomines, 1986 = *Neoleptastacus chaufriassei* (Bodiou & Colomines, 1986) comb. nov.; *Arenopontia ornamenta* Mielke, 1987 = *Neoleptastacus ornamentus* (Mielke, 1987) comb. nov.; *Arenopontia reductaspina* Mielke, 1987 = *Neoleptastacus reductaspina* (Mielke, 1987) comb. nov.; *Arenopontia* (*Neoleptastacus*) *phreatica* Cottarelli *et al*., 1994 = *Neoleptastacus phreaticus* (Cottarelli *et al*., 1994) comb. nov.; *Arenopontia* (*Neoleptastacus*) *speluncae* Cottarelli *et al*., 1994 = *Neoleptastacus speluncae* (Cottarelli *et al*., 1994) comb. nov.; *Arenopontia* (*Neoleptastacus*) *huysi* Karanovic, 2000 = *Neoleptastacus huysi* (Karanovic, 2000) comb. nov.

Species inquirendae: Arenopontia ? *gussoae* Cottarelli, 1973 *sensu* Mielke (1982b); *Arenopontia* ? *ishikariana* Itô, 1968 *sensu* Mielke (1987).

Species incertae sedis: Arenopontia breviarticulata Mielke, 1975 (see below).

Neoleptastacus spinicaudatus Nicholls, 1945

Original description: Nicholls (1945): pp. 22–23; text-figure 3.

Type locality: Nicholls (1945) collected the species from two sandy beaches some 500 km apart on the coast of Western Australia; the first, Leighton Beach (in the region of Perth), was sampled in October 1939; samples from the second site, locally known as 'Back Beach' at Dongarra, were taken in March 1940. Nicholls did not specify a type locality; however, all NHM syntypes came from sand washings at the Dongarra site, which is regarded here as the *locus typicus*.

Material examined: Syntype series consisting of: (1) one ♀ dissected on one slide (NHM reg. no. 1947.10.3.8); (2) one ♂ dissected on one slide (NHM reg. no. 1947.10.3.9); and (3) one vial containing 25 ♀♀ and one ♂ in alcohol [besides a mixture of *Psammopsyllus operculatus* Nicholls, 1945 (one ♀ and one ♂), *Ectinosomoides longipes* Nicholls, 1945 (one ♀), and a new species of arenopontiid described below as *Onychopontia nichollsi* (ten ♀♀ and one ♂)]; leg. A.G. Nicholls on 25–26 March 1940.

Redescription

Female: Total body length from tip of rostrum to posterior margin of caudal rami: 274–295 μm (mean = 281 μm, $N = 15$). Maximum width: 33 μm (mean of 15 individuals = 32 μm), measured at posterior margin of cephalothorax. Body: slender and cylindrical, without clear distinction between prosome and urosome (Fig. 13A, B). Hyaline frills of thoracic somites weakly developed and crenulated; those of genital double-somite and free abdominal somites strongly developed and consisting of rectangular digitate lappets (Figs 13A, B, 14A, B, E). Genital double-somite (Figs 13A, B, 14A) as long as wide; without chitinous ribs marking original segmentation; with one middorsal, two lateral, and six ventral pores (Fig. 15F). Anal somite (Fig. 14A, C, E): with two ventral and two lateral pores; ventral posterior margin with medial spinule rows. Anal operculum: smooth (Fig. 14F). Anus positioned subterminally between caudal rami.

Caudal rami (Fig. 14C–F): approximately 2.2 times longer than maximum width (measured in dorsal view), tapering posteriorly; with one pore near ventral proximal margin (Fig. 14E), and two pores laterally near insertion site of seta II, and at base of distal spinous process (Fig. 14C); outer distal corner produced into posteriorly directed recurved spinous process; mediodorsal surface with small spur-like process at base of seta VII, accompanied by minute accessory process near inner margin (Fig. 14F). Armature consisting of seven setae: seta I, small; setae II and III, long and naked, the latter displaced dorsally; seta IV, short, sparsely pinnate, located between seta V and spinous process; seta V, long, and with fracture plane; seta VI small, naked, and located at inner distal corner; seta VII, not foliaceous and triarticulate at base.

Rostrum (Fig. 16B): small, broadly subtriangular, apical part lobate and offset, with two delicate sensillae and one midventral pore.

Antennule (Fig. 16A): long, six-segmented. Segment 1: with a tiny seta near anterodistal margin. Segment 2: longest, about 2.5 times longer than wide. Segment 4: with long aesthetasc (25-μm long), fused at base with seta. Distal segment: with seven naked setae (two of which are spatulate), and with apical acrothek consisting of short aesthetasc (10-μm long) and two slender setae. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[7 + acrothek].

Antenna (Fig. 17D): coxa, small and bare. Basis and proximal endopod segment incompletely separated by surface suture, without armature or ornamentation. Exopod: minute, one-segmented, with one long bare seta. Free endopod: with distal hyaline frill; abexopodal margin with two spinular rows and two bare, curved spines; apical margin with two geniculate setae, two bare spines and one composite element consisting of spinulose, geniculate seta and small, basally fused seta.

Labrum (Fig. 16C): sclerotized and wide; with blunt spinules bilaterally around distal margin.

Mandible (Fig. 17E): gnathobase elongate, about as long as palp; with several curved, minute teeth and one tiny recurved seta at dorsal corner. Palp consisting of elongate, unisetose basis and one-segmented endopod with one inner, two outer, and two apical setae.

Maxillule (Fig. 16D): praecoxal arthrite with one surface seta; distal margin with five spines and two setae. Coxal endite: cylindrical, with two recurved spines. Basis: elongate, with rami completely incorporated; basal armature consisting of three apical setae. Exopod and endopod: represented by one and three setae, respectively.

Maxilla (Fig. 17F): syncoxa with two cylindrical endites; proximal endite with three setae (one fused at base); distal endite with two setae (one fused at base). Allobasis: drawn out into long claw with one accessory seta. Endopod: one-segmented; with three setae. All elements are naked.

Maxilliped (Fig. 16E): syncoxa longer than wide, unarmed, with few spinules. Basis: elongate and

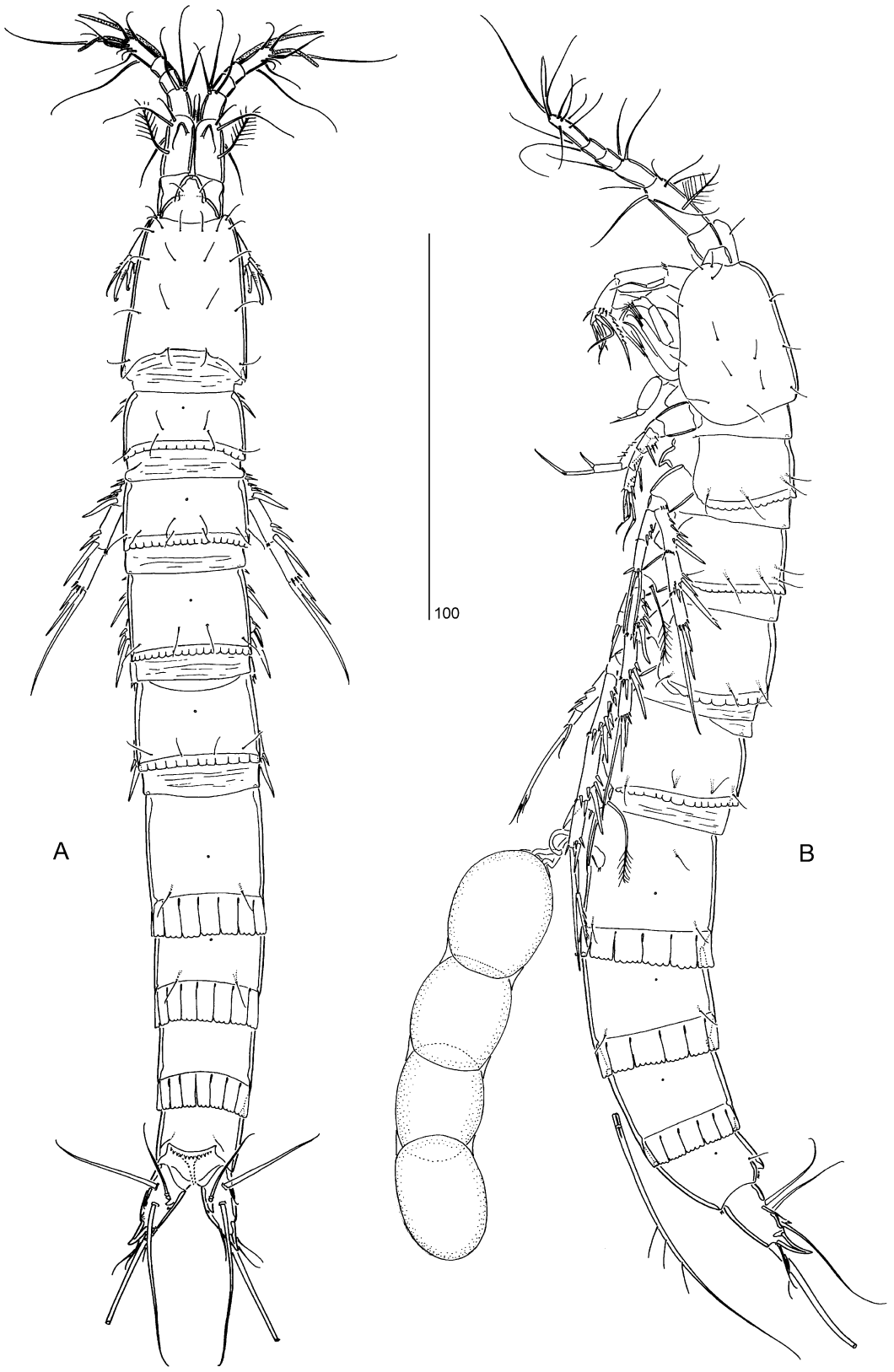

Figure 13. *Neoleptastacus spinicaudatus* Nicholls, 1945 (♀). A, habitus, dorsal view. B, habitus ovigerous specimen, lateral view.

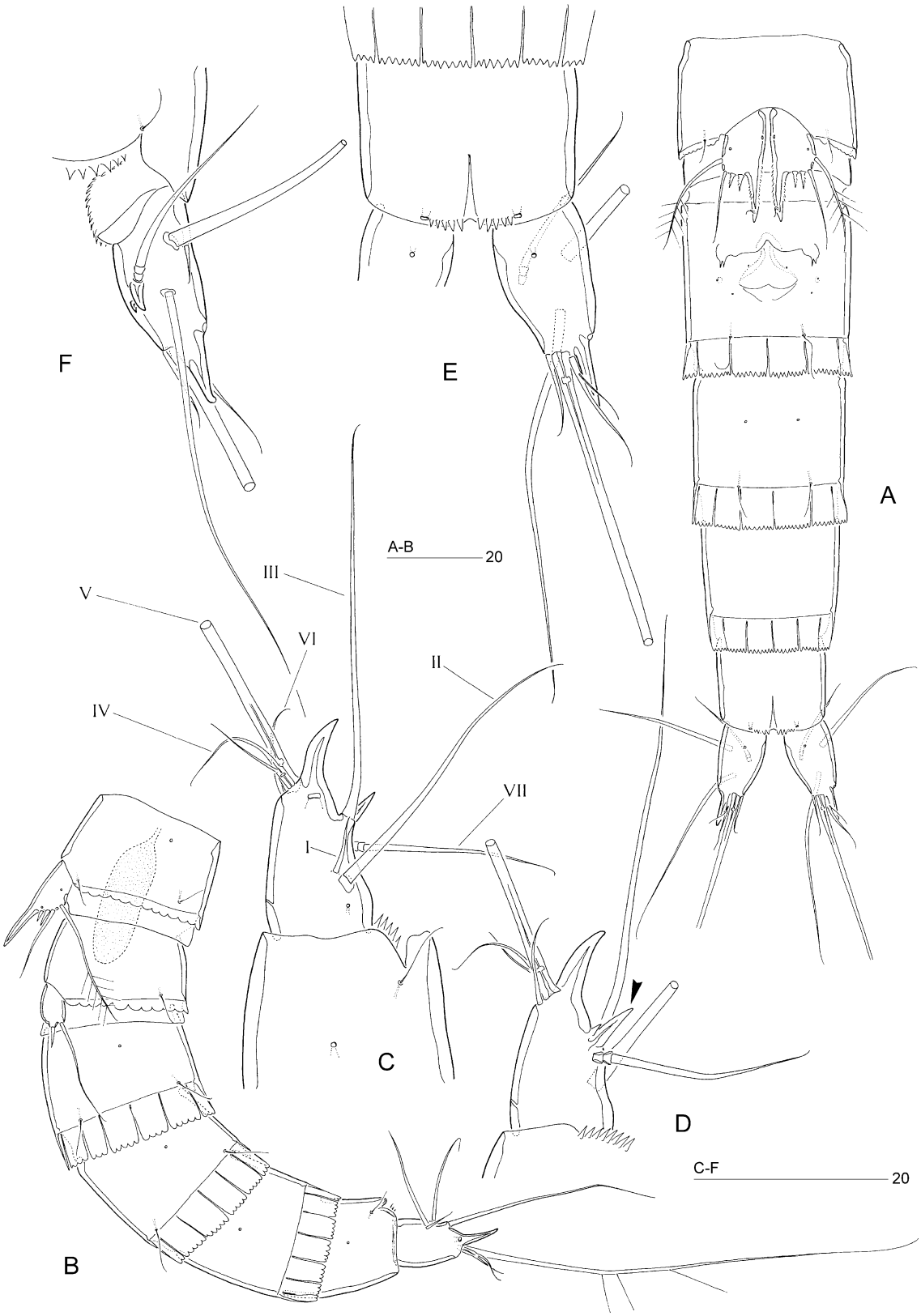

Figure 14. *Neoleptastacus spinicaudatus* Nicholls, 1945. A, urosome ♀, ventral view. B, urosome ♂, lateral view. C, anal somite and right caudal ramus ♀, outer lateral view. D, left caudal ramus ♀, inner lateral view (dorsal spur indicated by an arrow); E, anal somite and left caudal ramus ♀, ventral view. F, right caudal ramus ♀, dorsal view.

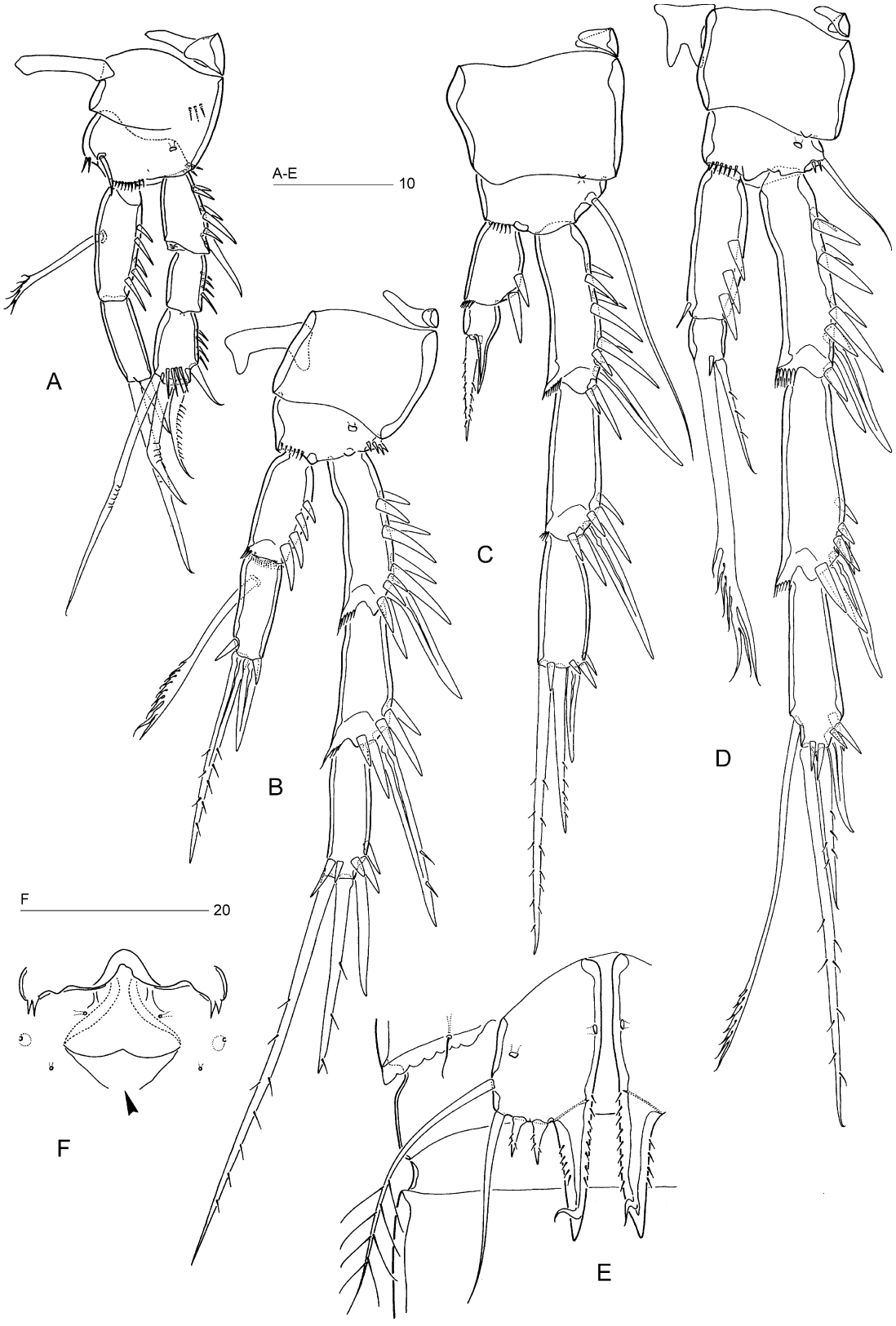

Figure 15. *Neoleptastacus spinicaudatus* Nicholls, 1945 (♀). A, P1, anterior view. B, P2, anterior view. C, P3, anterior view. D, P4, anterior view. E, P5, anterior view. F, genital field (copulatory pore indicated by arrow).

unarmed. Endopod: with small accessory seta and slightly curved claw, bearing strong, subterminal spinule.

P1 (Fig. 15A): intercoxal sclerite long and rectangular. Praecoxa: triangular and naked. Coxa: with few spinules on posterior surface. Basis: with spinules around base of endopod, and at inner and outer distal corners; anterior surface with a pore and a small inner seta. Exopod: three-segmented; exp-1 and exp-2 with spinules around outer margin; exp-1 longest, with short, bare outer spine; exp-2 without outer element; exp-3 with short, bare outer spine, a curved unipinnate spine, and two geniculate setae distally. Endopod: two-segmented, not prehensile, as long as exopod; enp-1 with a serrate inner seta at about halfway along the segment length, and coarse spinules along outer margin; enp-2 slightly shorter than enp-1, with a short bare outer spine and a geniculate inner seta.

P2–P4 (Fig. 15B–D): intercoxal sclerites naked. Praecoxae: very small and bare. Coxae: squarish and without ornamentation. Bases: smaller than coxae, with a spinular row near base of endopod, and a few spinules around outer corner in P2 and P4; anterior surface with a pore in P2 and P4; outer basal seta absent in P2, but present and bare in P3–P4. Exopods: three-segmented; segments with coarse spinular ornamentation, as illustrated; inner distal seta of exp-3 sparsely bipinnate, all other elements unipinnate or bare, except for inner seta of P4 exp-3 being serrate. Endopods: two-segmented; P2–P4 enp-1 about 1.1, 2.3, and 3.8 times longer than their respective distal segments, with coarse spinules along outer margin, and a few tiny spinules near inner distal corner. P2 enp-2: with a long, apically serrate, backwardly directed seta near proximal margin. P3 enp-2: with a short bipinnate spine apically and outer distal spine fused to segment forming bare spinous process. P4 enp-2: with large apically serrate seta, fused at base, and short unipinnate seta at outer distal corner. Spine and seta formula as follows:

	Exopod	Endopod
P2	0.0.021	0.120
P3	0.0.021	0.020
P4	0.0.121	0.020

Fifth legs (Fig. 15E): closely set together, but not touching in ventral midline. Baseoendopod and exopod fused, forming a rectangular plate; anterior surface with two pores. Inner distal corner: with strong spinous process (homologous to inner spine); process minutely bipinnate, with subapical flagella, and delimited at base on posterior surface. Distal margin with plumose outer basal seta, one naked seta, and two short, equally long, bipinnate spines.

Genital field positioned centrally on ventral surface of genital double-somite (Fig. 14A). Genital apertures (Fig. 15F) fused, forming median common slit; closed off by fused P6 forming operculum with two minute spinous processes on either side; copulatory pore large (arrowed in Fig. 15F), leading to short copulatory duct, and surrounded by three pairs of pores; seminal receptacles difficult to discern.

Male: Total body length from tip of rostrum to posterior margin of caudal rami: 272–277 μm ($N = 2$). Maximum width: 30–31 μm ($N = 2$), measured at cephalothorax. Body ornamentation (Fig. 14B): essentially as in female. Sexual dimorphism: in antennule, genital segmentation, P5 (weak), and P6. Spermatophore length: approximately 30 μm.

Antennule (Fig. 17A–C): nine-segmented, haplocer; geniculation between segments 7 and 8. Segment 1 with few spinules on anterior surface; segment 2 longest and about 1.9 times longer than wide; segment 4 an incomplete sclerite with one tiny element; segment 5 with two setae, plus long aesthetasc (43-μm long), fused basally to a slender seta; segment 6 with two short setae; segment 7 with two modified spines and a seta; segment 8 with three modified spines and posterior corner produced into lobate extension; distal segment with seven naked setae (two of which spatulate) and apical acrothek. Setal formula: 1-[1], 2-[6 + 1 plumose], 3-[4 + 2 pinnate spines], 4-[1], 5-[2 + (1 + ae)], 6-[2], 7-[1 + 2 modified], 8-[1 + 3 modified], 9-[7 + acrothek]. Acrothek consisting of short aesthetasc (15-μm long) fused basally to two slender setae.

P5 (Fig. 16F): with armature as in female; inner spinous process, without subapical flagella and leg slightly more slender than in female.

Sixth legs (Fig. 16F) asymmetrical, with smallest P6 closing off functional gonopore; each with a long, plumose, outer seta and a short, naked, inner spine.

Remarks: Nicholls (1945) overlooked the inner seta on P4 exp-3, an error that perpetuated in various comparative analyses (Noodt, 1955b; Bodiou & Colomines, 1986) and species keys (Lang, 1965; Karanovic, 2000). Within the genus, *N. spinicaudatus* belongs to a lineage that is characterized by: (1) anal somite without paired dorsolateral processes; (2) anal operculum weakly developed, without rounded medial extension; (3) P1 exp-1 with outer spine, exp-3 with four setae/spines; (4) P1 enp-2 with outer spine and inner geniculate seta distally; (5) P2 exp-2 with outer spine of normal length (not extending far beyond distal margin of exp-3); (6) endopod P2–P3, two-segmented; (7) P2 enp-2 with inner seta and two distal spines; (8) P3 enp-2 with two distal spines

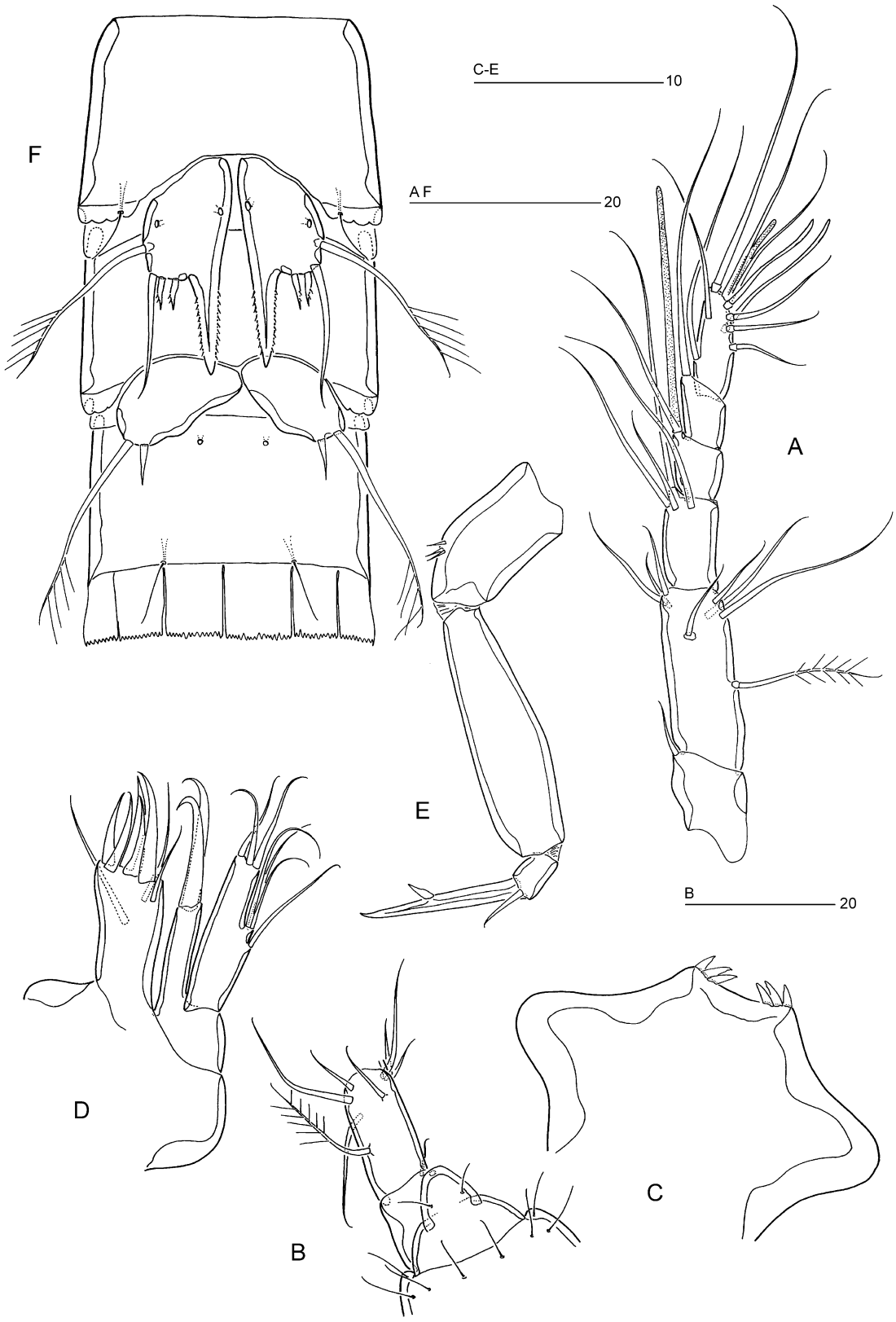

Figure 16. *Neoleptastacus spinicaudatus* Nicholls, 1945. A, antennule ♀, dorsal view. B, rostrum and proximal antennulary segments ♀, dorsal view. C, labrum ♀, anterior view. D, maxillule ♀, posterior view. E, maxilliped ♀. F, P5-bearing and genital somites (♂), ventral view.

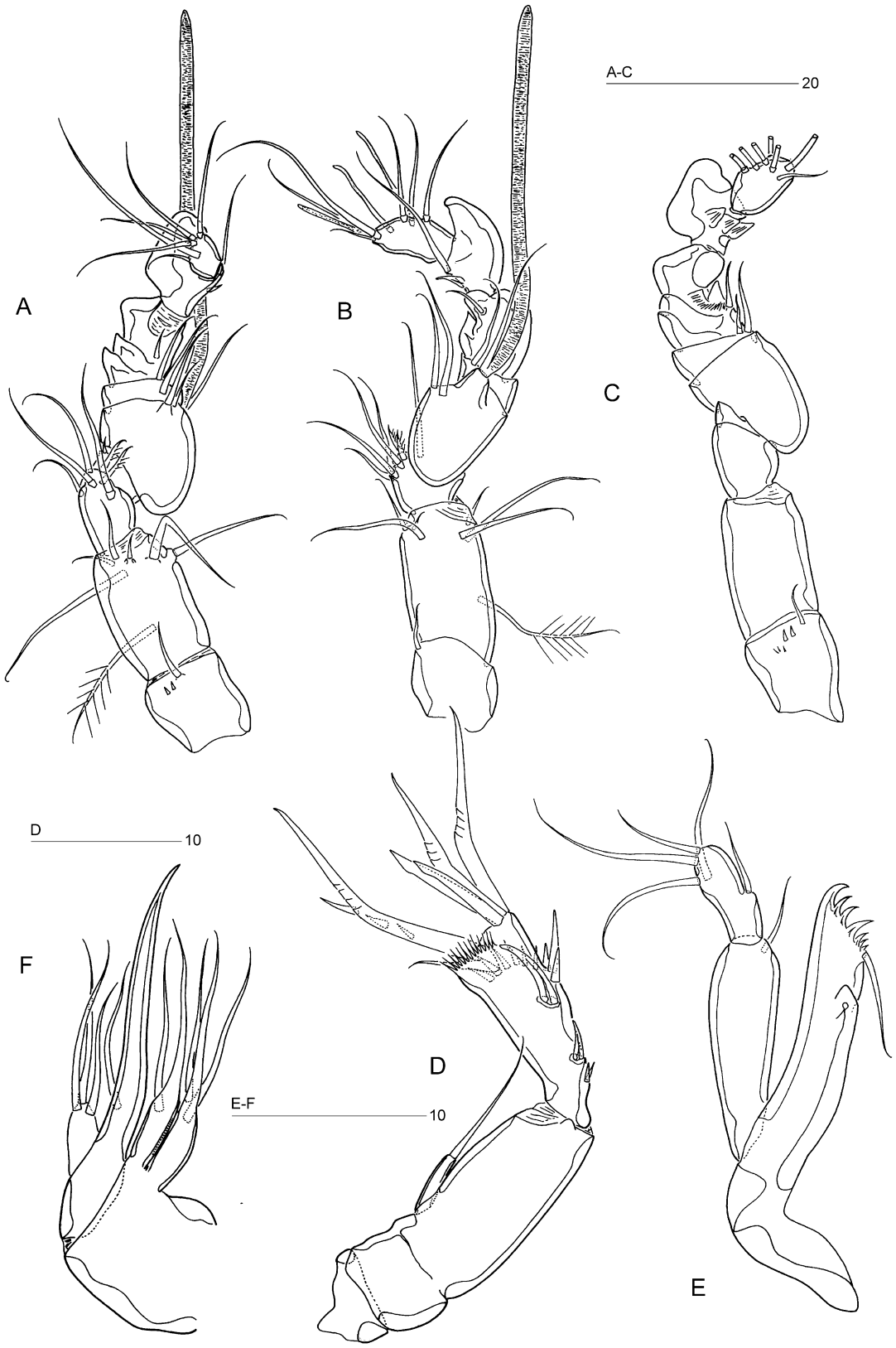

Figure 17. *Neoleptastacus spinicaudatus* Nicholls, 1945. A and C, antennule ♂, anterior view (at different angles, with armature largely omitted in C). B, antennule ♂, ventral view. D, antenna ♀. E, mandible ♀. F, maxilla ♀.

KEY TO SPECIES OF *SPINICAUDATUS* LINEAGE

1. P4 exp-3: without inner seta ..... *N. pacificus*.
   P4 exp-3: with inner seta ..... 2.
2. Urosome (except anal somite): with distinct surface ornamentation consisting of elongate rectangular plates ..... *N. clasingi*.
   Urosome: without conspicuous surface ornamentation ..... 3.
3. Caudal ramus: with dorsolateral spur near base of seta VII ..... 4.
   Caudal ramus: without dorsolateral spur near base of seta VII ..... *N. ishikarianus*.
4. Lappets of abdominal hyaline frills semi-incised obtusidigitate; inner seta of P2–P3 enp-2 longer than endopod; P5 3.0 times as long as wide, with naked spinous process ..... *N. spicatus*.
   Lappets of abdominal hyaline frills denticulate; inner seta of P2–P3 enp-2 shorter than endopod; P5 about 2.5 times as long as wide, with pinnate spinous process ..... *N. spinicaudatus*.

(outer one fused to segment); and (9) P4 enp-2 outer seta normally developed. In addition to the type species, this *spinicaudatus* lineage includes *N. ishikarianus*, *N. clasingi*, *N. pacificus* and *N. spicatus*, all of which assume a Pacific distribution. *Neoleptastacus spinicaudatus* is very similar to the Chilean *N. spicatus*, but differs from it in the form of the abdominal hyaline frills (lappets denticulate vs. semi-incised obtusidigitate in *N. spicatus*), the relative lengths of the inner distal seta on P2–P3 enp-2, and the shape and ornamentation of the spinous process on P5 (which is still delimited at base on the posterior surface).

The linear egg sac contains between two and four large eggs; occasionally six eggs are found, in which case they overlap. Nicholls (1945) also collected the species from Leighton Beach (in the region of Perth). Chappuis' (1958) record from Puget Sound almost certainly pertains to *Mesopontia dillonbeachia* (see below). Chappuis (1954b: 269) claimed to have found one female and one male in Annaba (= Bône), Algeria, which closely resembled *N. spinicaudatus*.

GENUS *PARARENOPONTIA* BODIOU & COLOMINES, 1986

Bodiou & Colomines (1986) established this genus to accommodate two unusual *Arenopontia* species with a two-segmented P1 exopod, *A. breviarticulata* Mielke (1975) (type species) and *A. trisetosa* Mielke (1982a); the third species (*Arenopontia biarticulata* Wells, 1967) displaying this character was placed in the genus *Notopontia* Bodiou in the Leptopontiidae. Both *Pararenopontia* species have very few characters in common, casting doubt on the monophyletic status of the genus. Martínez Arbizu & Moura (1994) considered *Pararenopontia* an amalgam of species sharing reduced leg segmentation, and synonymized it with *Arenopontia*; however, some authors have suggested that it should be maintained as a valid genus (Huys *et al.*, 1996a, b; Bruno *et al.*, 1998; Wells, 2007) or subgenus (Bodin, 1997).

Pararenopontia breviarticulata is known from a single male collected from the Isle of Sylt (Germany) (Mielke, 1975), and exhibits an interesting mosaic of both apomorphic (two-segmented P1 exopod; reduced P5) and plesiomorphic (armature of P2 endopod and P4 exopod) characters. There is, however, some circumstantial evidence that Mielke's (1975) description is deficient in some aspects. The P3 appears remarkably similar to the P4, including the presence of an inner seta on exp-3 (a feature not reported for any other arenopontiid) and two very long setae on enp-2 (not recorded elsewhere in the family), raising the suspicion that the author has not observed the real P3, but may instead have duplicated observations of P4. The male P5 is unique in possessing only three elements; it is not clear whether the inner spine (or spinous process) was overlooked, or whether the P5 is genuinely underdeveloped as a result of paedomorphosis. Evidence for the latter is found in the congruence between Mielke's illustration and the condition observed in copepodid IV of *N. indicus* (cf. Rao, 1967: fig. 3-22), at which stage the P1 exopod in arenopontiids is still two-segmented before adding a final segment at the next moult. Mielke (1975) described the anal operculum with two lateral 'Zacken' (prongs, teeth), which are conceivably the positional homologues of the paired lateral spinous processes on the anal somite in the *acanthus* group of *Neoleptastacus*. This group includes *N. acanthus*, *N. longiremis*, *N. secundus*, *N. indicus*, *N. gussoae*, *N. chaufriassei*, *N. ornamentus*, *N. reductaspina*, and *N. huysi*. In all these species, the P3 endopod has an inner distal seta; the outer distal spine is either short, and fused to the segment, or completely absent (*longiremis*, *gussoae*, *indicus*, and *reductaspina*), but never setiform, and is virtually as long as the outer distal seta [as illustrated by Mielke (1975) for *P. breviarticulata*]. The extreme disparity in the length of the outer basal seta between P3 and P4, and the very long outer spines on P2–P4 exp-2 are additional characters unique to this species. The armature formula of P1 enp-2 (one geniculate seta plus one outer distal spine) indicates

a relationship with the *Mesopontia–Arenopontia–Neoleptastacus* lineage, and the morphology of the anal somite suggests that *P. breviarticulata* is probably nested within the genus *Neoleptastacus*. Unfortunately, repeated requests to make the holotype available for re-examination failed, and its relationships necessarily remain unresolved. Pending the collection of topotype material, we propose to regard *Pararenopontia* as a junior subjective synonym of *Neoleptastacus*, and *A. breviarticulata* as a *species incertae sedis* in *Neoleptastacus*. Note that Bodin (1979) had already listed it under the subgenus *Neoleptastacus*.

Pararenopontia trisetosa is clearly closely related to *N. africanus* and *N. angolensis*, the only marked difference being the two-segmented P1 exopod in *P. trisetosa*. All three species differ from other members of *Neoleptastacus* by the lack of the outer spine on P1 exp-1, the presence of only one outer spine on the distal exopod segment of P1 (= exp-2 in *P. trisetosa*; exp-3 in *N. africanus* and *N. angolensis*), the one-segmented P2–P3 endopod, and the reduced setal formula on P2 endopod [110]. Based on these apomorphic character states, *P. trisetosa* is formally transferred to *Neoleptastacus* as *N. trisetosus* comb. nov.

GENUS *MESOPONTIA* GEN. NOV.

Lang (1965) noted that there is no close affinity between *A. dillonbeachia* and *A. subterranea*, but believed the former was '. . . most nearly related to the species *A. acantha* and *A. secunda*. . .', both of which currently belong to the *acanthus* lineage of *Neoleptastacus*. *Arenopontia dillonbeachia* shares with *Arenopontia* (as redefined herein) and *Neoleptastacus* the presence of an outer spine and an inner geniculate seta/claw on P1 enp-2, and the absence of sexual dimorphism on the P3 endopod; however, the morphology of the P5 indicates an intermediate position between both genera. In *Arenopontia*, the innermost element is setiform and defined at the base (as in *Psammoleptastacus* and *Onychopontia* gen. nov.); in *A. dillonbeachia* it is modified into a strong articulating spine, whereas in *Neoleptastacus* the inner corner of the P5 is modified into a spinous process. The pinnate nature of this process and the presence of a posterior surface suture in some species (e.g. *N. spinicaudatus*; Fig. 15E) indicate the *Neoleptastacus* condition originated from the incorporation of a spinous inner element (as expressed in *A. dillonbeachia*). The transitionary state of the P5 in conjunction with the nonprehensile P1 exclude *A. dillonbeachia* from both *Arenopontia* and *Neoleptastacus*, and consequently it is here designated as the type of a new genus. A unique feature for the genus is the bicuspidate dorsomedial process on the caudal ramus.

Diagnosis: Arenopontiidae. Urosomites: without conspicuous surface ornamentation. Anal somite: without paired dorsolateral spinous processes. Anal operculum: not modified. Hyaline frills of abdominal somites with narrow rectangular lappets. Caudal ramus: without dorsolateral spur, but with bicuspidate process near medial margin. P1 exopod: three-segmented, short; exp-1 longest, with outer spine; exp-3 with two spines and two geniculate setae. P1 endopod: not prehensile, about as long as exopod; enp-2 with outer spine and inner geniculate seta. P2–P3 endopods: two-segmented; inner serrate seta of P2 enp-2 present. P3 endopod: with outer distal element. P4 endopod: with outer distal element well developed. Armature formula as follows:

	Exopod	Endopod
P2	0.0.021	0.120
P3	0.0.021	0.020
P4	0.0.121	0.020

P3 endopod male: not sexually dimorphic, two-segmented. P5: with outer basal seta and four discrete elements in both sexes; innermost element a strong bipinnate spine. P6 male: with two setae.

Type and only species: Arenopontia dillonbeachia Lang, 1965 = *Mesopontia dillonbeachia* (Lang, 1965) comb. nov.

Etymology: The generic name is derived from the Greek *mesos* (μεσοσ meaning the middle), and the suffix *pontia* (ποντια, meaning the sea), commonly used in the formation of interstitial copepod names, and refers to the morphology of the P5, which exhibits a transitionary state between the *Arenopontia* condition (innermost element setiform) and the *Neoleptastacus* condition (inner spinous process).

MESOPONTIA DILLONBEACHIA (LANG, 1965) COMB. NOV.

Arenopontia dillonbeachia Lang, 1965

Arenopontia (*Arenopontia*) *dillonbeachia* Lang (1965): Wells (1967)

Arenopontia spinicaudata (Nicholls, 1945) *sensu* Chappuis (1958)

Original description: Lang (1965): pp. 419–422; figure 231 (♀ only).

Type locality: USA, California, Dillon Beach; about 3 m in depth, fine sand.

Material examined: SMNH: (1) one ♀ (syntype), from type locality; reg. no. 568 (Typ. Saml. 2210), leg. K. Lang, 30 August 1960; (2) five ♀♀ (syntypes), Cali-

fornia, Monterey Bay, off Hopkins Marine Laboratory, fine shell-sand, reg. no. 569 (Typ. Saml. 2211), leg. K. Lang, 12 September 1960.

Redescription

Female: Total body length from tip of rostrum to posterior margin of caudal rami: 337 μm. Maximum width: 41 μm, measured at posterior margin of cephalothorax. Body: slender and cylindrical, without clear distinction between prosome and urosome (Fig. 18A, B). Hyaline frills of thoracic somites weakly developed and crenulated; those of genital double-somite and free abdominal somites strongly developed, and consisting of narrow, rectangular, digitate lappets (Figs 18A–C, 19A). Genital double-somite (Fig. 19A): 1.2 times longer than wide; without chitinous ribs marking original segmentation; with two middorsal, two lateral, and two ventral pores. Anal somite (Figs 18C, D, 19A): with two lateral pores. Anal operculum: with minute spinules along free distal margin (Fig. 18C). Anus positioned subterminally between caudal rami.

Caudal rami (Figs 18C, D, 19A): approximately 2.7 times longer than maximum width (measured in dorsal view), tapering both proximally and distally; with a pore laterally; outer distal corner produced into posteriorly directed, recurved, spinous process; dorsal surface with bicuspidate process near inner margin (Fig. 18C). Armature consisting of seven setae: seta I, small; setae II and III, long and naked; seta IV, short, located between seta V and spinous process, naked; seta V, long and with fracture plane; seta VI, small, naked, and located at inner distal corner; seta VII, spatulate and triarticulate at base.

Rostrum (Fig. 19C): small, broadly subtriangular, apical part lobate and offset, with two delicate sensillae and a midventral pore near apex.

Antennule (Fig. 19B, C): long, six-segmented. Segment 2: longest, about 2.6 times longer than wide. Segment 4: with long aesthetasc (37-μm long) fused at base with seta. Distal segment: with seven naked setae (two of which are spatulate), and apical acrothek consisting of short aesthetasc (17-μm long) and two slender setae. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[8 + acrothek].

Antenna (Fig. 19D): coxa small, without ornamentation. Allobasis about 2.7 times as long as maximum width; original segmentation marked by partial transverse surface suture; with two spinular rows, as illustrated. Exopod: one-segmented; elongate, with a naked apical seta (about 3.0 times longer than exopod). Free endopod with two spinular rows on anterior surface, and finer spinules at outer distal corner; lateral armature consisting of two short spines; apical armature consisting of two spiniform elements and three geniculate setae, the longest of which with spinules around geniculation and fused basally to tiny accessory seta.

Mandible, maxillule, maxilla, and maxilliped, as in *N. spinicaudatus* (see Lang, 1965: Fig. 231d–g).

P1 (Fig. 20A): intercoxal sclerite, long with deeply concave ventral margin. Praecoxa: minute. Coxa: without ornamentation. Basis: with spinular row near base of endopod and at inner distal corner; anterior surface with small inner seta. Exopod: three-segmented; all segments with spinules around outer margin; exp-1 longest, with strong, unipinnate outer spine; exp-2 without outer element; exp-3 with short naked outer spine, a long curved unipinnate spine, and two geniculate setae distally. Endopod: two-segmented, not prehensile, about as long as exopod; enp-1 2.6 times longer than maximum width; with a serrate inner seta halfway along the segment length, and several spinules along outer margin; enp-2 about twice as long as wide, with a short, naked outer spine, and a long geniculate inner seta.

P2–P4 (Fig. 20B–D): intercoxal sclerites naked, with deeply concave ventral margin. Praecoxae: small and naked. Coxae: squarish and without ornamentation. Bases: smaller than coxae, with a spinular row near base of endopod (P3) or near outer distal corner (P2, P4); anterior surface with a pore in P3–P4; outer basal seta absent (P2), plumose (P3), or naked (P4). Exopods: three-segmented; segments with spinular ornamentation, as illustrated; inner distal seta of exp-3 sparsely bipinnate, all other elements unipinnate except for inner seta of P4 exp-3 being apically serrate; P4 exp-3 with anterior pore. Endopods: two-segmented; P2–P4 enp-1 about 1.3, 1.8, and 3.7 times longer than their respective distal segments, with few spinules, as illustrated. P2 enp-2: with a long, apically serrate, backwardly directed seta near proximal inner corner. P3 enp-2: with a long bipinnate inner seta, and a short bare outer spine apically. P4 enp-2: with long, apically serrate inner seta (fused at base), and long bipinnate seta at outer distal corner. Spine and seta formula: as for the genus.

Fifth legs (Fig. 19A) closely set together, but not touching in ventral midline. Baseoendopod and exopod: fused, forming a subrectangular plate; anterior surface with pore near outer proximal corner; distal margin with outer naked seta, two medial short setae, and strong bipinnate spine at inner corner; outer basal seta long and plumose.

Remarks: Lang (1965) remarked on the apparent similiarity in antennary exopod morphology between *A. dillonbeachia* and Pennak's (1942a) *P. arenaridus*; however, our re-examination and Itô's (1969) description failed to confirm the very long and slender shape of the exopod (as well as the completely separated

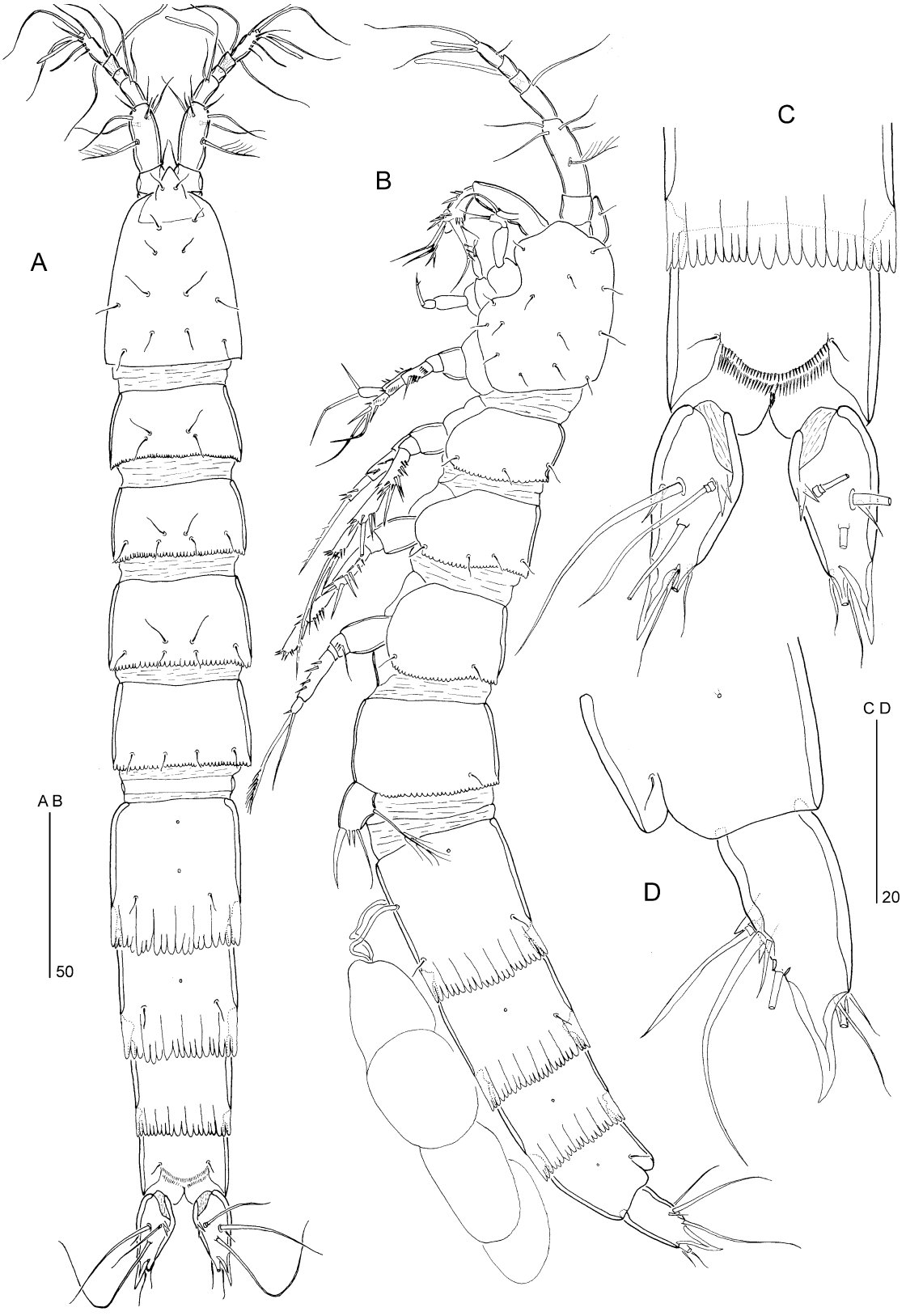

Figure 18. *Mesopontia dillonbeachia* (Lang, 1965) **comb. nov.** (♀). A, habitus, dorsal view. B, habitus ovigerous specimen, lateral view. C, posterior part of penultimate somite, anal somite, and caudal rami, dorsal view. D, anal somite and right caudal ramus, lateral view.

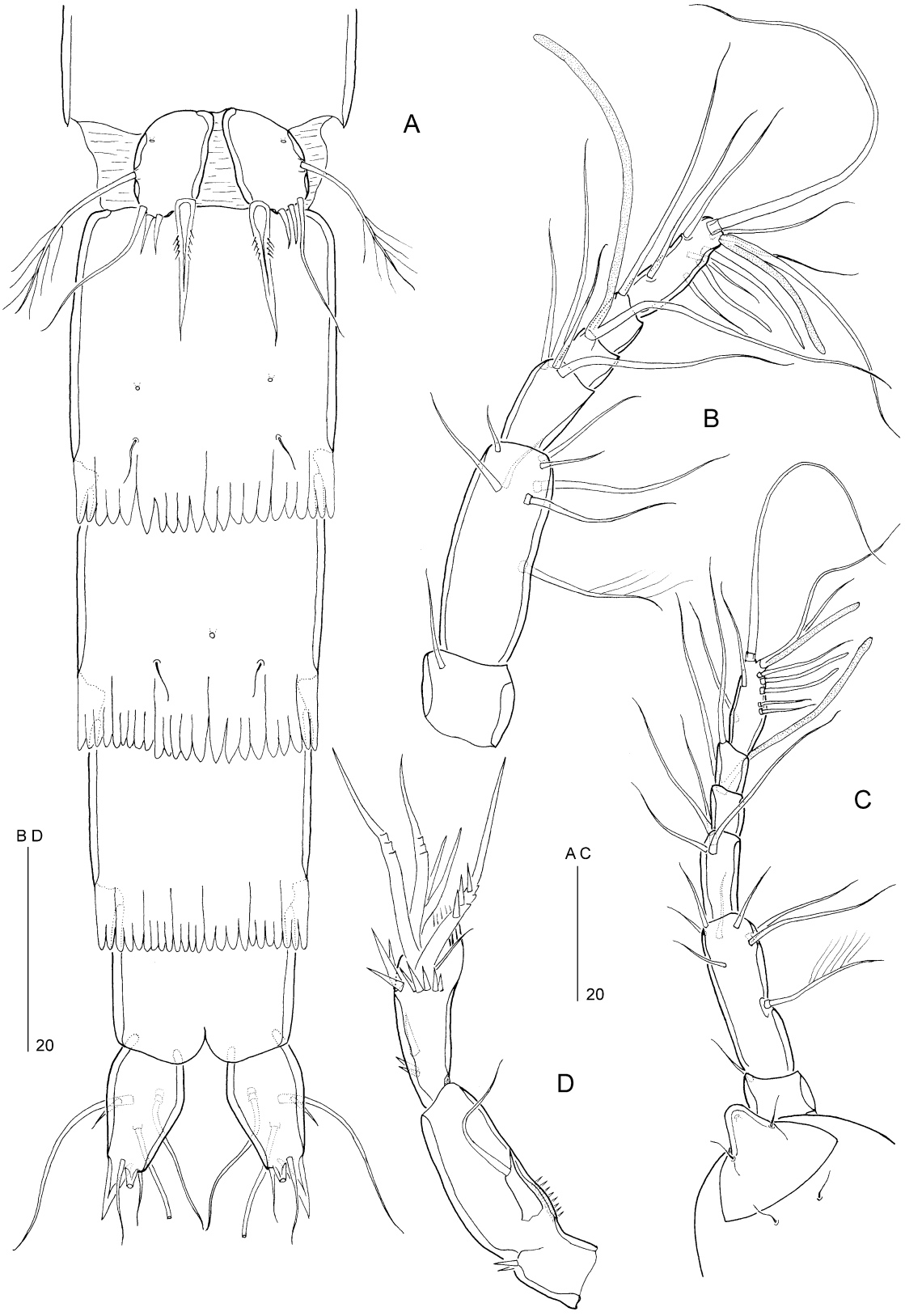

Figure 19. *Mesopontia dillonbeachia* (Lang, 1965) **comb. nov.** (♀). A, urosome, ventral view. B, antennule, ventral view. C, rostrum and antennule, dorsal view. D, antenna.

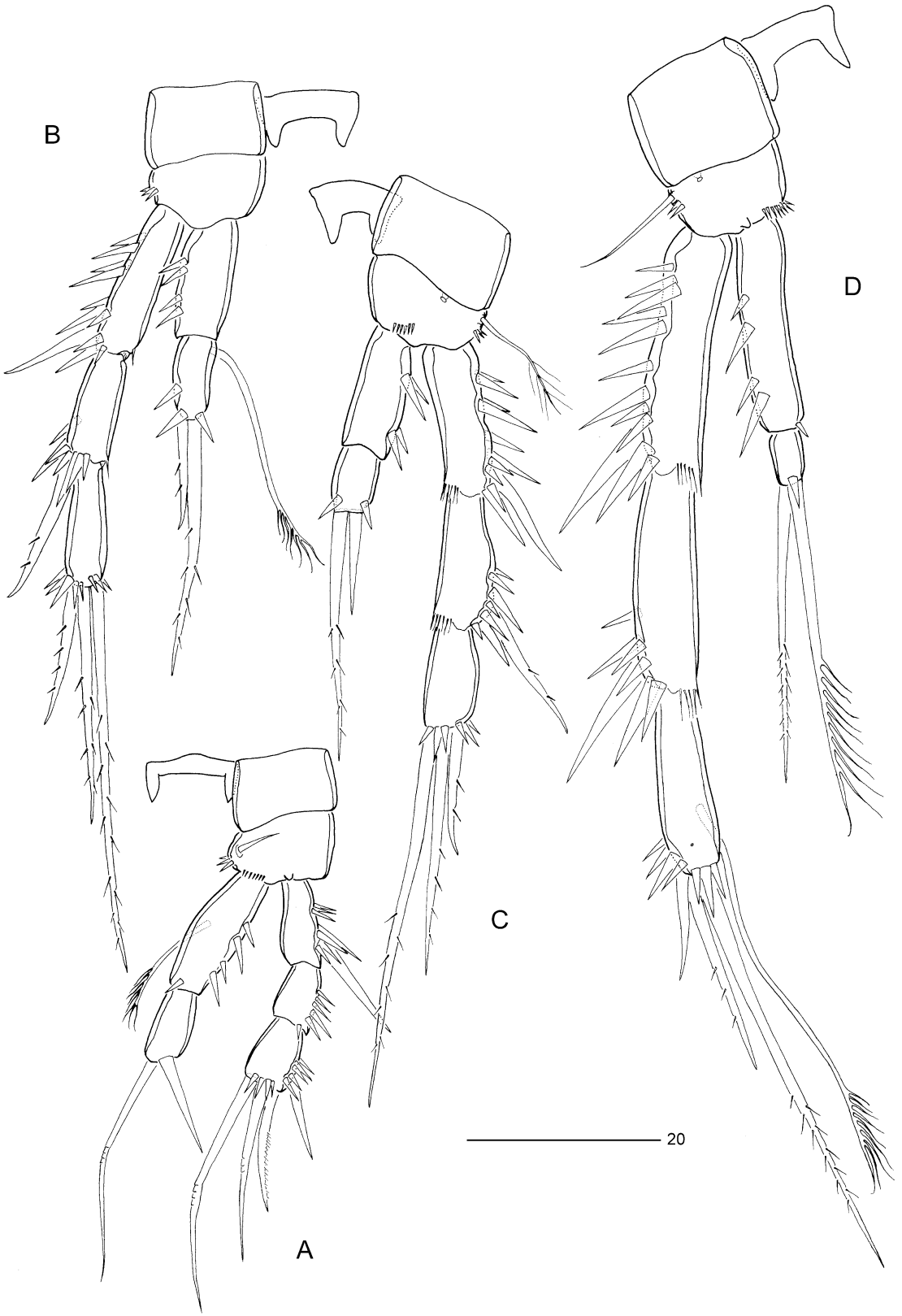

Figure 20. *Mesopontia dillonbeachia* (Lang, 1965) **comb. nov.** (♀). A, P1, anterior view. B, P2, anterior view. C, P3, anterior view. D, P4, anterior view.

basis). Both Lang (1965) and Itô (1969) overlooked the hyaline frills on the urosomites, and Lang erroneously illustrated an outer basal seta on P2. Itô provided the first and only description of the male, and illustrated the genital field of the female. Our redescription has shown that the few discrepancies between his specimens and the type material are to the result of small observational errors made by Lang (1965).

Chappuis' (1958) specimens of *A. spinicaudata* from Puget Sound cannot possibly belong to this species. His illustrations of the fifth legs, P2 endopod, female antennule, and caudal rami are in good agreement with Lang's description of *A. dillonbeachia.*

The currently known distribution includes records from Puget Sound, Washington (Chappuis, 1958), Dillon Beach and Monterey Bay, California (Lang, 1965), and Samani, Pacific coast of Hokkaido, Japan (Itô, 1969). The egg sac contains six eggs.

GENUS *ONYCHOPONTIA* GEN. NOV.

The close relationship between *A. orientalis* (Krishnaswamy, 1957), *A. intermedia* Rouch, 1962, and *A. peteraxi* Mielke, 1982a was first recognized by Mielke (1982a), who regarded the sexual dimorphism on the P3 endopod as a synapomorphy linking these species. The transformation of this ramus is more derived than the condition displayed in *Psammoleptastacus*, where the two-segmented state is retained in the male. Species of the latter genus have a well-developed P1 exopod and an inner serrate seta on P2 enp-2. In *A. orientalis*, *A. intermedia*, and *A. peteraxi*, the P1 exopod is more condensed and the serrate seta on P2 enp-2 is lost. These three species are here collectively transferred to a new genus, *Onychopontia*, together with a new species from Australia found among the type material of *N. spinicaudatus*. Additional autapomorphies for *Onychopontia* are the modification of the two outer elements on P1 exp-3 into naked setae and the strong reduction of the outer geniculate seta; in all other genera the outer elements are spiniform and pinnate, and the outer geniculate seta is well developed. Lang's (1965) claim that *P. orientalis* belongs to *Arenocaris* is obviously a slip of the pen, which was inadvertently adopted by Bodin (1967). The current known distribution of the genus is highly disjunct, with species recorded from Brazil, India, Australia, Galápagos, Panamá, Chile, and Venezuela.

Diagnosis: Arenopontiidae. Urosomites: without conspicuous surface ornamentation. Anal somite: without paired dorsolateral spinous processes. Anal operculum: not modified. Hyaline frills of abdominal somites with narrow rectangular lappets. Caudal ramus: without dorsolateral spur near medial margin. P1 exopod: three-segmented, short; exp-1 longest, with outer spine; exp-3 with two spines and two geniculate setae. P1 endopod: not prehensile, longer than exopod; enp-2 with two geniculate setae. P2–P3 endopods: two-segmented; inner serrate seta of P2 enp-2 absent. P3 endopod: without outer distal element (but see variability in *Onychopontia peteraxi*). P4 endopod: with outer distal element well developed or reduced. Armature formula as follows:

	Exopod	Endopod	
P2	0.0.021	0.020	[or 0.010*]
P3	0.0.021	0.010	[or 0.020*†]
P4	0.0.021	0.020	

P3 endopod male: sexually dimorphic, one-segmented, with distal curved spine. P5: with outer basal seta and either three or four discrete elements in female; with outer basal seta and three elements in male, innermost one distinctly smaller than in female, and sometimes fused at base. P6 male: with two setae.

Type species: Onychopontia nichollsi sp. nov.

Other species: Psammoleptastacus orientalis Krishnaswamy, 1957 = *Onychopontia orientalis* (Krishnaswamy, 1957) comb. nov.; *A. intermedia* Rouch, 1962 = *Onychopontia intermedia* (Rouch, 1962) comb. nov.; *A. peteraxi* Mielke, 1982 = *Onychopontia peteraxi* (Mielke, 1982) comb. nov.

Etymology: The generic name is derived from the Greek *onyx* (ονυξ; genitive *onychos*), meaning nail, or claw, and the suffix *pontia* (ποντια, the sea), commonly used in the formation of interstitial copepod names, and refers to the morphology of the modified P3 endopod in the male.

ONYCHOPONTIA ORIENTALIS (KRISHNASWAMY, 1957) COMB. NOV.

Psammoleptastacus orientalis Krishnaswamy, 1957

Arenocaris orientalis (Krishnaswamy, 1957) Lang (1965) (*lapsus calami*)

Arenopontia (*Arenopontia*) *orientalis* (Krishnaswamy, 1957): Wells (1967)

Original description: Krishnaswamy (1957): pp. 101–103; text-figure 23.

Type locality: India, Tamil Nadu, Madras; sandy beach [cf. Krishnaswamy (1957: 144–151) for sand texture characteristics].

*Variability noted in some populations of *Onychopontia peteraxi*; †there is some confusion about the correct number of elements in *Onychopontia orientalis* and *Onychopontia intermedia*.

Remarks. The type material no longer exists. Krishnaswamy (1957) observed sexual dimorphism on the P3 endopod, but the relevant illustration was mislabelled as 'end P♂?'. His claims of five elements on P1 exp-3 and an outer spine on exp-2 are undoubtedly wrong, and the outer basal seta on ♂ P5 was probably overlooked. Also, Krishnaswamy (1957) did not illustrate the P3, but stated that it '. . . resembles the second one, except for the increase in the number of spines and the presence of longer setae in the endopod', implying that there are probably two setae on enp-2 (as shown in his setal formula).

Onychopontia orientalis appears to prefer the drier zones on the beach, and reaches maximum densities around the high-tide level; known only from the type locality.

ONYCHOPONTIA INTERMEDIA (ROUCH, 1962) COMB. NOV.

Arenopontia intermedia Rouch, 1962

Arenopontia (*Arenopontia*) *intermedia* Rouch, 1962: Bodin (1979)

Original description: Rouch (1962): pp. 277–278; figures 158–166 (♂ unknown).

Type locality: Brazil, Pernambuco State, Recife, Olinda; sandy beach.

Remarks: Mielke (1985, 1987) commented on the similarity in body sculpturing between *O. intermedia* and some species of *Neoleptastacus* (*N. clasingi*, *N. ornamentus*, and *N. reductaspina*); however, this was based on an erroneous interpretation of Rouch's (1962) text and figures. In the *Neoleptastacus* species the abdominal somites display rectangular integumental plates both ventrally and dorsally. Rouch's statement that each somite boundary has '. . . une série de cannelures longitudinales en forme de pallissade' clearly refers to the deeply incised hyaline frill (as suggested by his figs 162, 163, 166). Mielke (1982a) remarked on the discrepancy in the number of spines on P3 enp-2 between Rouch's (1962) text and his illustration (fig. 160). *Onychopontia intermedia* is known only from the type locality. The type material is no longer available for examination.

ONYCHOPONTIA PETERAXI (Mielke, 1982a) COMB. NOV.

Arenopontia peteraxi Mielke, 1982a

Arenopontia (*Arenopontia*) *peteraxi* Mielke (1982a): Bodin (1988)

Original description: Mielke (1982a): pp. 36–42; Abb. 22–24, 28 (distribution map).

Type locality: Ecuador, Galápagos, Jervis, north coast; sandy beach.

Remarks: The species has also been reported from three other islands of the Galápagos archipelago (Isabela, James, and Marchena) (Mielke, 1982a), three localities along the Pacific seaboard of Panamá (Isla Taboga, Playa Nueva Gorgona, and Playa Lagomar) (Mielke, 1982b), Arica in northern Chile (Mielke, 1987), and Isla Margarita in Venezuela (Martínez Arbizu & Moura, 1994). Variability in the number of elements (either one or two) on P2 enp-2 and P3 enp-2 was recorded in the Panamá and Galápagos populations, respectively. Additional variability can be noted in the length of the caudal ramus spinous process, and the robustness of the spinules on the anal operculum. Mielke (1982b) also reported one individual with an outer spine on P1 exp-2 (atavism!); some Galápagos specimens were found *in copula*. Mielke's (1982a) claim that there is a short outer basal seta on P1 is probably false.

ONYCHOPONTIA NICHOLLSI SP. NOV.

Type locality: Australia, Western Australia, 'Back Beach' at Dongarra; washed from sand taken from below 15 cm of the surface.

Material examined: Type material found among syntype series of *N. spinicaudatus* (see above). Holotype ♀: dissected on six slides (NHM reg. no. 1994.4807). Paratypes: eight ♀♀ and one ♂ in alcohol (NHM reg. nos 1994.4808–4816; antennule of ♂ paratype mounted on separate slide). Collected by A.G. Nicholls on 25–26 March 1940.

Description

Female: Total body length from tip of rostrum to posterior margin of caudal rami: 210–245 μm (mean = 225 μm, $N = 9$). Body: slender and cylindrical, without clear distinction between prosome and urosome (Fig. 21A, B). Hyaline frills of thoracic somites weakly developed and crenulated; those of genital double-somite and free abdominal somites strongly developed, and consisting of narrow, rectangular digitate lappets (Fig. 21A–D). Genital double-somite (Fig. 21A–C): as long as wide; without chitinous ribs marking original segmentation; with one middorsal, two lateral, and two ventral pores. Anal somite (Fig. 21A, B, D): with two dorsal and two

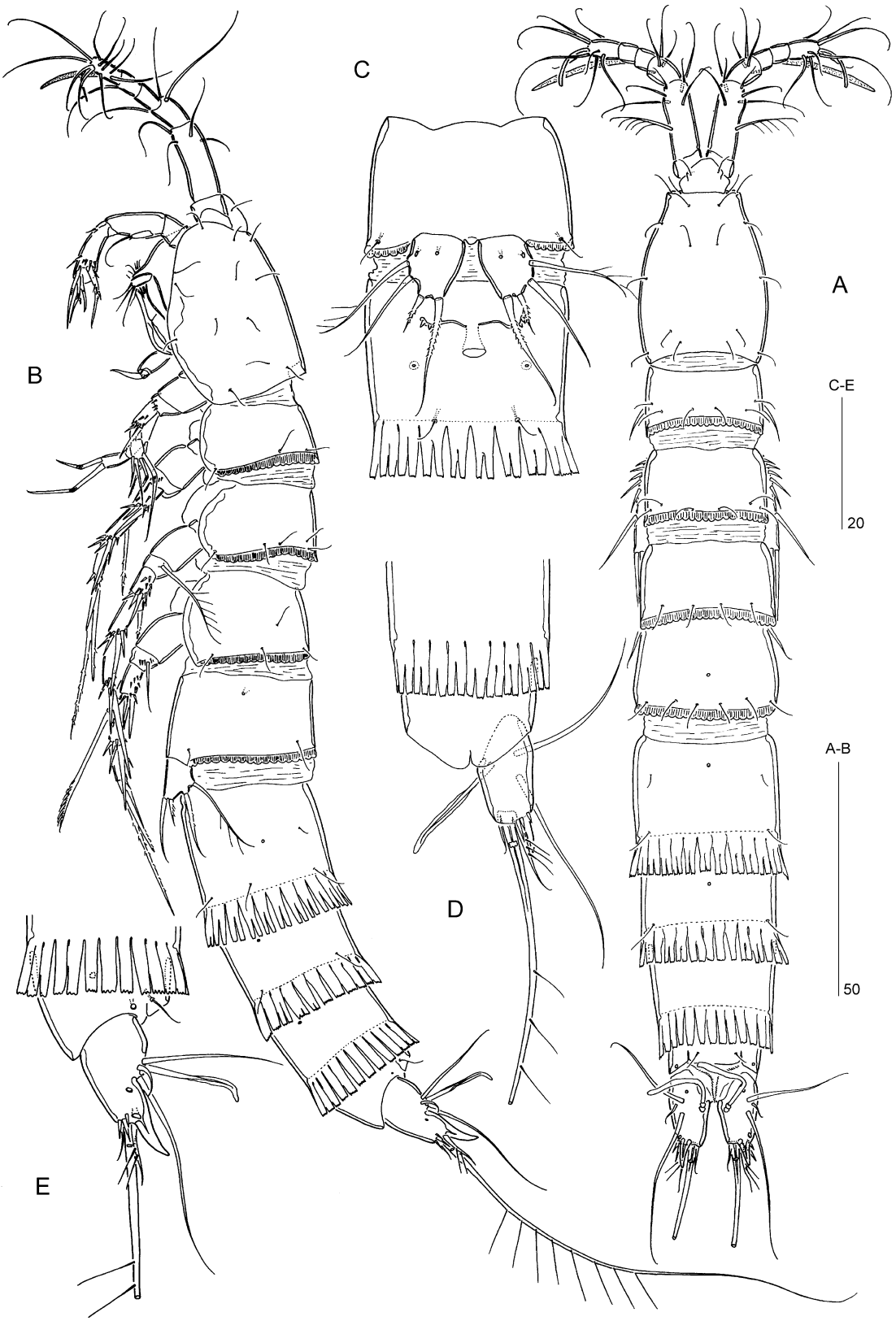

Figure 21. ***Onychopontia nichollsi*** **gen. nov. sp. nov.** (♀). A, habitus, dorsal view. B, habitus, lateral view. C, P5-bearing somite and genital double-somite, ventral view. D, posterior half of penultimate somite, anal somite, and left caudal ramus, ventral view. E, left caudal ramus, lateral view.

lateral pores. Anal operculum: naked. Anus positioned subterminally between caudal rami.

Caudal rami (Figs 21D, E, 22F): approximately 2.3 times longer than wide (measured in dorsal view), tapering posteriorly; with a pore dorsally (Fig. 22F) and two pores laterally (Fig. 21E); outer distal corner produced into posteriorly directed recurved spinous process, accompanied by outer spinular row at base (Fig. 21E); dorsal surface without process or spinular row near inner margin. Armature consisting of seven setae: seta I, small; setae II and III, long and naked; seta IV, short, sparsely pinnate, located between seta V and spinous process, and fused basally to seta V; seta V, long, sparsely plumose, and with fracture plane; seta VI, small, naked, and located at inner distal corner; seta VII, foliaceous and triarticulate at base.

Rostrum (Fig. 21A): small, broadly subtriangular, tapering distally, with two delicate sensillae.

Antennule (Fig. 22A): long, six-segmented. Segment 1: with a tiny seta near the anterodistal margin. Segment 2: longest, about 2.8 times longer than wide. Segment 4: with long aesthetasc (22-μm long) fused at base with seta. Distal segment: with seven naked setae (one of which spatulate), and apical acrothek consisting of short aesthetasc (13-μm long) and two slender setae. Armature formula: 1-[1], 2-[6 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[7 + acrothek].

Antenna (Fig. 22B): coxa small, without ornamentation. Allobasis: about 2.4 times as long as maximum width; original segmentation marked by partial transverse surface suture; without spinular ornamentation. Exopod: one-segmented, elongate, with a naked apical seta (slightly longer than exopod). Free endopod with two spinular rows on anterior surface; lateral armature consisting of two short spines; apical armature consisting of two spines and three geniculate setae, strongest of which with spinules around geniculation and fused basally to tiny accessory seta.

Mandibular palp: two-segmented (Fig. 22C, D); basis elongate with one lateral seta; endopod with one inner, one outer, and three apical setae (two fused at base); all armature elements naked. Gnathobase: with few sharp teeth distally and one naked seta at dorsal corner.

Maxillule and maxilla: as in *O. peteraxi*.

Maxilliped (Fig. 22E): syncoxa, small and unarmed. Basis: elongate and unarmed. Endopod: with small accessory seta and slightly curved claw bearing subterminal spinule.

P1 (Fig. 23A): intercoxal sclerite, long and narrow. Praecoxa: triangular and naked. Coxa: without ornamentation. Basis: with spinular row near base of endopod; anterior surface with a small inner seta. Exopod: three-segmented, condensed; exp-1 and exp-2 with spinules around outer margin; exp-1 longest, with strong, naked outer spine; exp-2 without outer element; exp-3 with two naked setae, one short, and one long geniculate seta. Endopod: two-segmented, longer than exopod, not prehensile; enp-1 2.2 times longer than wide, with a short serrate inner seta at about halfway along the segment length, and with few spinules along outer margin; enp-2 longer than wide, with a short outer and a long inner geniculate seta.

P2–P4 (Fig. 23B–D): intercoxal sclerites naked. Praecoxae: small and naked. Coxae: without ornamentation. Bases: generally smaller than coxae, with a spinular row near the base of the endopod and with few spinules along the outer margin; anterior surface with a pore in P4; outer basal seta absent (P2), plumose (P3), or naked (P4). Exopods: three-segmented; segments with spinular ornamentation, as illustrated; inner distal seta of exp-3 sparsely bipinnate, all other elements unipinnate; P3–P4 exp-3 with anterior pore. Endopods: two-segmented, enp-2 very small; P2–P4 enp-1 about 3.5, 3.4, and 3.8 times longer than their respective distal segments, with few spinules along outer margin, as illustrated. P2 enp-2: without inner seta. P2–P3 enp-2: with a sparsely bipinnate apical seta. P4 enp-2: with large, apically serrate seta, fused at base, and minute seta at outer distal corner. Spine and seta formula as follows:

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.021	0.010
P4	0.0.021	0.020

Fifth legs (Figs 21C, 23E): closely set together, but not touching in ventral midline. Baseoendopod and exopod: fused, forming a squarish plate; anterior surface with two pores; distal margin with two pinnate setae (inner one twice the length of the outer one) and long, naked outer seta; outer basal seta, long and plumose.

Genital field positioned near anterior margin of genital double-somite (Fig. 21C). Genital apertures fused, forming median common slit; closed off by fused P6 forming operculum, with two minute spinous processes on either side; copulatory pore located midventrally, close to genital slit, and flanked by paired secretory pores; seminal receptacles difficult to discern.

Male: Total body length from tip of rostrum to posterior margin of caudal rami: 295 μm. Body ornamentation (Fig. 24A, B): essentially as in female. Sexual dimorphism: in antennule, genital segmentation, P3 endopod, P5, and P6. Spermatophore length: approximately 18 μm.

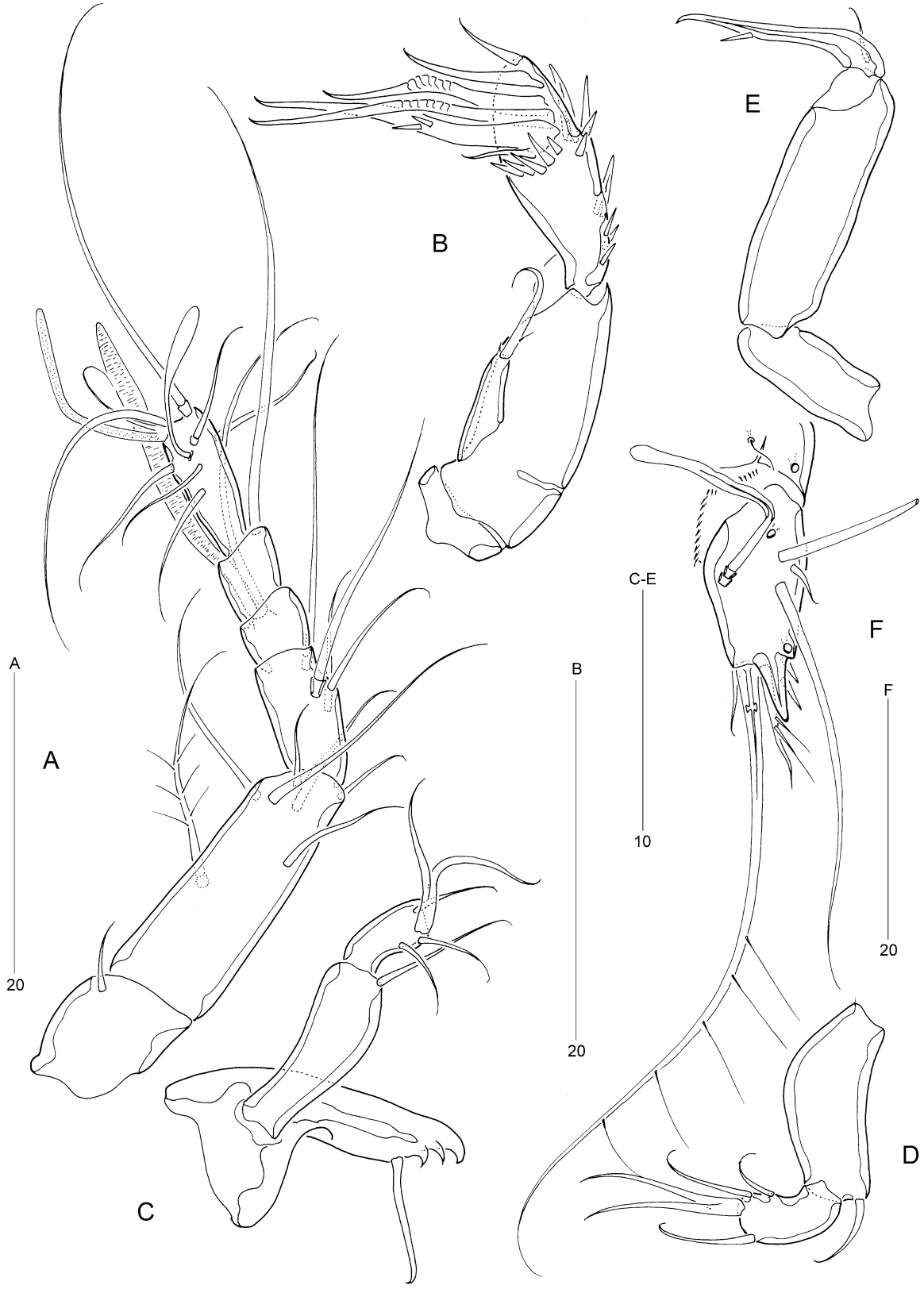

Figure 22. ***Onychopontia nichollsi*** **gen. nov. sp. nov.** (♀). A, antennule, dorsal view. B, antenna. C, mandible. D, mandibular palp. E, maxilliped. F, right caudal ramus, dorsal view.

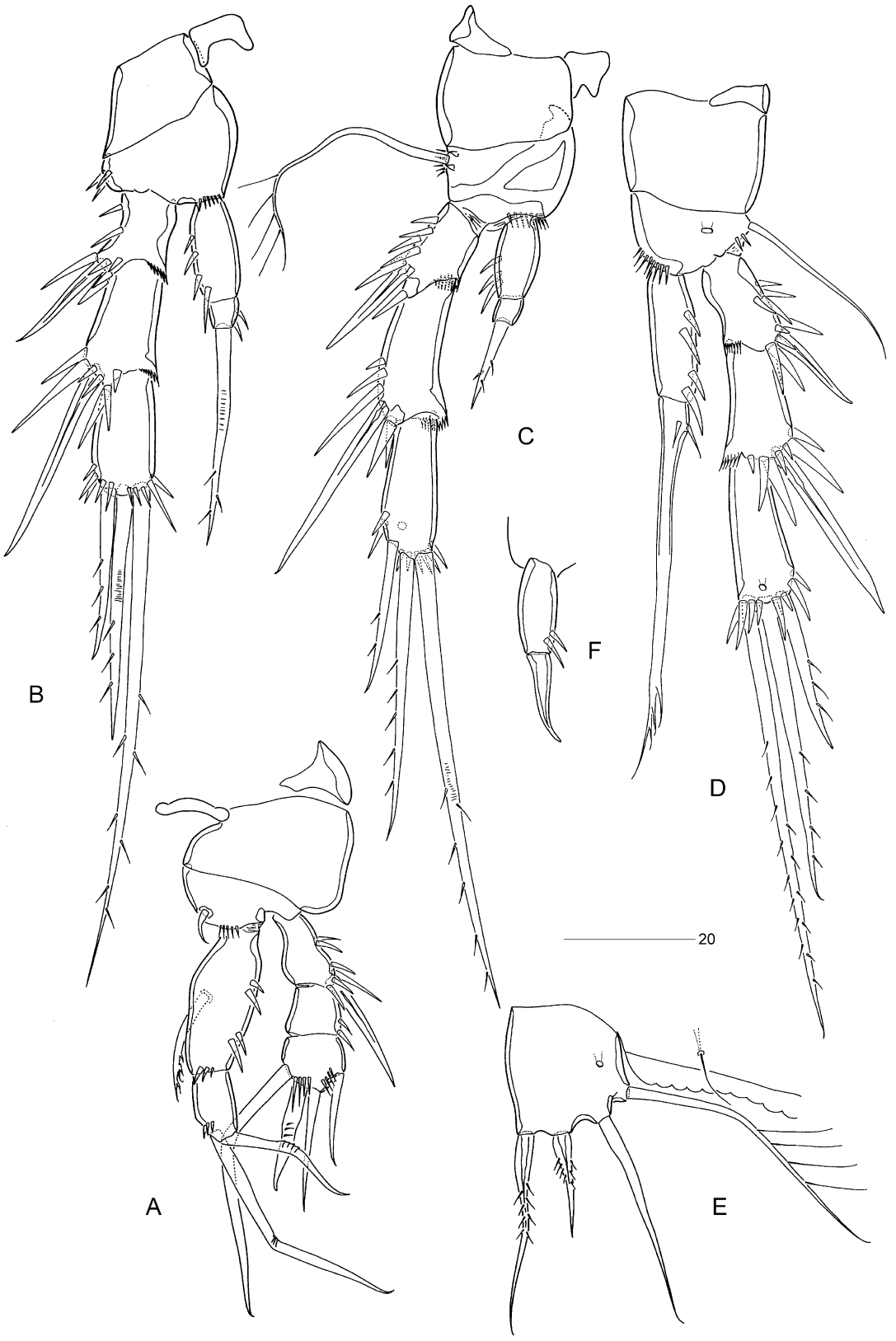

Figure 23. ***Onychopontia nichollsi*** **gen. nov. sp. nov.** A, P1 ♀, anterior view. B, P2 ♀, anterior view. C, P3 ♀, posterior view. D, P4 ♀, anterior view. E, P5 ♀, anterior view. F, P3 endopod ♂, anterior view.

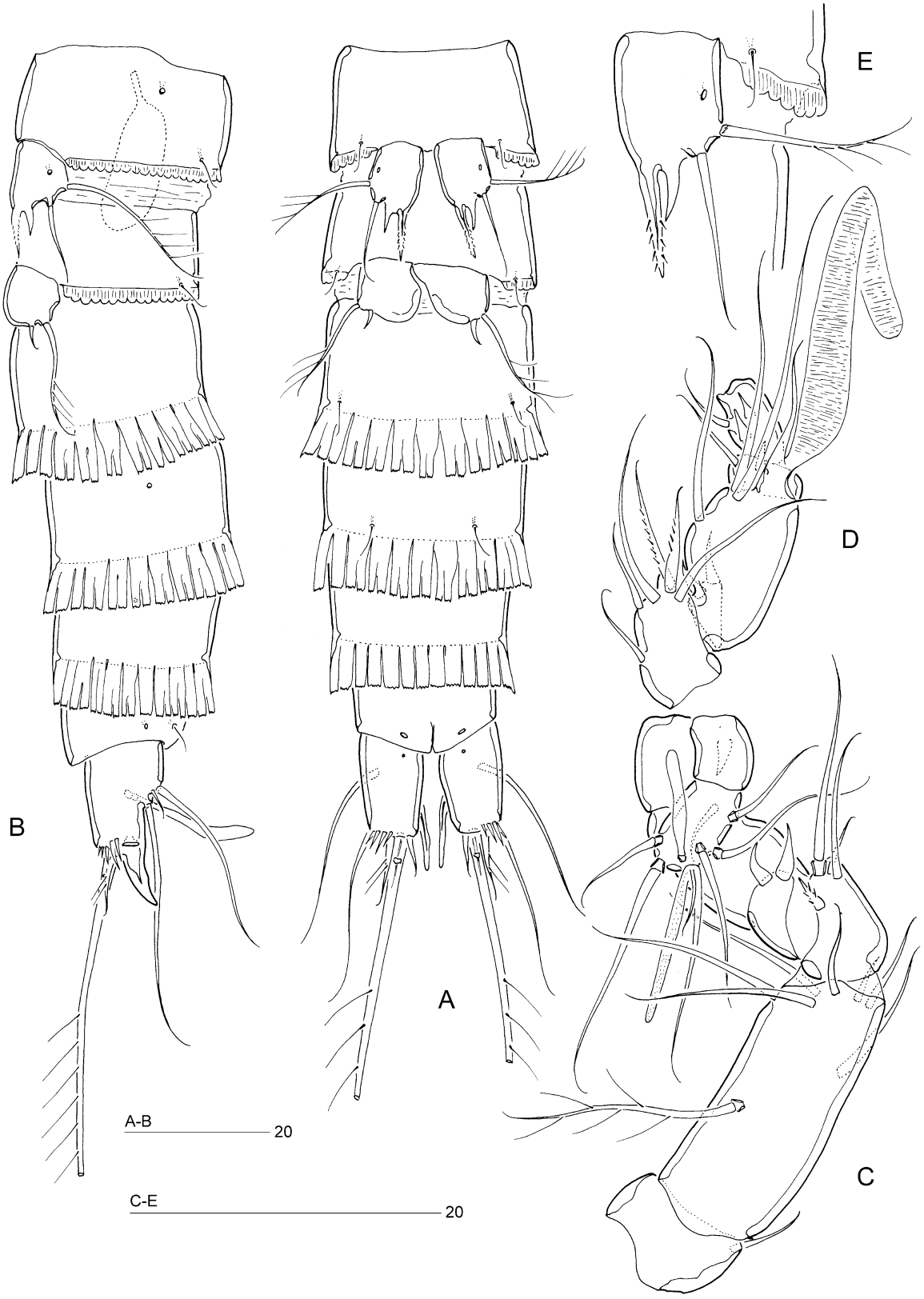

Figure 24. ***Onychopontia nichollsi*** **gen. nov. sp. nov.** (♂). A, urosome, ventral view. B, urosome, lateral view. C, antennule, dorsal view. D, antennulary segments 3–7, anterior view. E, P5, anterior view.

KEY TO SPECIES

Although some variability has been noted for *O. peteraxi*, we consider 0.020 and 0.010 as the normal formulae for P2–P3 endopods, respectively (as found in the Chilean population; Mielke, 1987).

1. P4 enp-2: with two well-developed setae ..... 2.
   P4 enp-2: with vestigial outer seta ..... 3.
2. P2 enp-2: with inner spine over twice the length of the outer spine; P5 female with five setae ..... *O. intermedia*.
   P2 enp-2: with both elements equally long; P5 female with four setae ..... *O. orientalis.*
3. P5 male: with innermost element setiform and defined at base ..... *O. peteraxi.**
   P5 male: with innermost element spiniform and fused to segment ..... ***O. nichollsi* sp. nov.***

*Females of these species can be separated by the relative length of P2–P4 exp-1, being much shorter in *O. nichollsi*.

KEY TO GENERA

1. P1 endopod: prehensile; innermost element of P1 exp-3 penicillate ..... *Arenopontia*.
   P1 endopod: not prehensile; innermost element of P1 exp-3 geniculate ..... 2.
2. P5 of both sexes: with innermost element forming distinct spinous process ..... *Neoleptastacus*.
   P5 of both sexes: with innermost element not modified (occasionally fused at base) ..... 3.
3. P1 enp-2: with one geniculate seta and one spine; P3 endopod not modified in male ..... ***Mesopontia* gen. nov.**
   P1 enp-2: with two geniculate setae; P3 endopod sexually dimorphic ..... 4.
4. P2 enp-2: with inner serrate seta; P3 endopod male two-segmented ..... *Psammoleptastacus*.
   P2 enp-2: without inner serrate seta; P3 endopod male one-segmented ..... ***Onychopontia* gen. nov.**

Antennule (Fig. 24C, D): nine-segmented, haplocer; geniculation between segments 7 and 8. Segment 2 longest, and about 2.2 times longer than wide; segment 4 an incomplete sclerite with two short spiniform elements; segment 5 with three setae plus long aesthetasc (29-μm long), fused basally to a small seta; segment 6 with a fused spine and long distal seta; segment 7 with two modified, fused spines and a seta; segment 8 with a modified fused spine; distal segment with seven naked setae (one of which spatulate) and apical acrothek. Setal formula: 1-[1], 2-[7 + 1 plumose], 3-[4 + 1 spine], 4-[2 modified], 5-[3 + (1 + ae)], 6-[1 + 1 modified], 7-[1 + 2 modified], 8-[1 modified], 9-[7 + acrothek]. Acrothek consisting of short aesthetasc (10-μm long) fused basally to two slender setae.

P3 endopod (Fig. 23F): a small segment with two spinules on anterior surface, and with a curved claw-like spine apically.

P5 (Fig. 24E): longer than wide; with same number of armature elements as in female, but with middle and inner elements of distal margin fused to segment; inner one being replaced by a short bipinnate spine, and middle one naked and comparatively shorter than in female.

Sixth legs (Fig. 24A): slightly asymmetrical, with smallest P6 closing off functional gonopore; each with a short inner spine and a long, naked outer seta.

Remarks: Onychopontia nichollsi sp. nov. is closely related to *O. peteraxi*, with which it shares the vestigial outer seta on P4 enp-2. It differs in the antennule (longer, in particular in segment 2), P1 (outer geniculate seta shorter), and male P5 (plate more rectangular; middle and inner elements fused at base). The species is known only from the type locality where it coexists with *N. spinicaudatus*.

ADDITIONAL REMARKS

There has been some controversy over the taxonomic significance of the foliaceous seta VII, and the absence/presence of this character has often led to confusion as to the true specific identity of certain populations (e.g. Şerban, 1959; Apostolov, 1973; Lindgren, 1976). In some species, including *A. subterranea*, the transparent leaf-like flanges of this seta are very well developed, and are easy to observe under low magnification; however, it is clear that some authors have overlooked them in their descriptions (e.g. Masry, 1970; *A. problematica*). Recent high-quality descriptions (Mielke, 1982a, b, 1985, 1987) have demonstrated that this character is widespread in the family. Our observations showed that it is expressed (but often only weakly) in all genera, indicating that it is a potential autapomorphy for the family.

Arenopontiids appear to have a propensity for developing modified setation elements. Our study

revealed that at least some members of every genus exhibit one or (usually) two spatulate setae on the posterior margin of the distal antennulary segment in both sexes. This character, which is probably another arenopontiid diagnostic, has thus far remained unnoticed in descriptions, except for Mielke's (1982a) excellent illustrations of *N. trisetosus* (as *A. trisetosa*).

ACKNOWLEDGEMENTS

Results included in this paper partly originated from a PhD thesis by the senior author. Funding by TÜBITAK [project no TBAG–1962(100T120)] and the Balıkesir University Research Fund (project no BAP 2003/21) is gratefully acknowledged by SS and SK. Thanks are also due to Dr Karin Sindemark (Swedish Museum of Natural History, Stockholm) for arranging the loan of *Mesopontia dillonbeachia*.

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