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Review of *Neoleptastacus* Nicholls, 1945 (Harpacticoida, Arenopontiidae), including an updated key to species and proposal of *Phreatipontia* gen. nov.

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SERDAR SAK, SÜPHAN KARAYTUĞ & RONY HUYS
**REVIEW OF *NEOLEPTASTACUS* NICHOLLS, 1945 (HARPACTICOIDA, ARENOPONTIIDAE),
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Table of Contents

Abstract	4
Introduction	4
Material and methods	5
Systematics	6
Family Arenopontiidae Martínez Arbizu & Moura, 1994	6
Genus <i>Neoleptastacus</i> Nicholls, 1945	6
Nomenclature and (re)descriptions	11
<i>Neoleptastacus spinicaudatus</i> Nicholls, 1945	11
<i>Neoleptastacus australis</i> (Chappuis, 1953)	12
<i>Neoleptastacus acanthus</i> (Chappuis, 1954)	12
<i>Neoleptastacus longiremis</i> (Chappuis, 1955)	20
<i>Neoleptastacus africanus</i> (Chappuis & Rouch, 1961)	21
<i>Neoleptastacus indicus</i> (Rao, 1967)	22
<i>Neoleptastacus ishikarianus</i> (Itô, 1968)	24
<i>Neoleptastacus gussoae</i> (Cottarelli, 1973a)	25
<i>Neoleptastacus trisetosus</i> (Mielke, 1982a)	26
<i>Neoleptastacus clasingi</i> (Mielke, 1985)	26
<i>Neoleptastacus pacificus</i> (Mielke, 1985)	27
<i>Neoleptastacus spicatus</i> (Mielke, 1985)	27
<i>Neoleptastacus angolensis</i> (Bodiou & Colomines, 1986) comb. nov.	28
<i>Neoleptastacus chaufrassei</i> (Bodiou & Colomines, 1986)	28
<i>Neoleptastacus ornamentus</i> (Mielke, 1987)	29
<i>Neoleptastacus reductaspina</i> (Mielke, 1987)	29
<i>Neoleptastacus huysi</i> (Karanovic, 2000)	30
<i>Neoleptastacus abbreviatus</i> sp. nov.	30
<i>Neoleptastacus chilensis</i> sp. nov.	31
<i>Neoleptastacus emendatus</i> sp. nov.	31
<i>Neoleptastacus panamensis</i> sp. nov.	36
<i>Neoleptastacus pseudishikarianus</i> sp. nov.	37
<i>Neoleptastacus rectus</i> sp. nov.	38
<i>Neoleptastacus supersetosus</i> sp. nov.	38
Species inquirendae	43
<i>Neoleptastacus secundus</i> Krishnaswamy, 1957	43
<i>Neoleptastacus accraensis</i> (Lang, 1965)	44
Taxa of doubtful identity	44
<i>Arenopontia</i> ? <i>gussoae</i> Cottarelli, 1973a <i>sensu</i> Mielke (1982b) [partim]	45
<i>Arenopontia</i> ? <i>gussoae</i> Cottarelli, 1973a <i>sensu</i> Mielke (1987) [2 nd form]	45
Species incertae sedis	46
<i>Arenopontia breviariculata</i> Mielke, 1975	46
Key to species	46
Genus <i>Phreatipontia</i> gen. nov.	47
<i>Phreatipontia phreatica</i> (Cottarelli, Bruno & Venanzetti, 1994) comb. nov.	48
<i>Phreatipontia speluncae</i> (Cottarelli, Bruno & Venanzetti, 1994) comb. nov.	54
Concluding remarks	61
Key to genera of Arenopontiidae	61
Acknowledgements	62
References	62

Abstract

A revision of the genus *Neoleptastacus* Nicholls, 1945 (Harpacticoida, Arenopontiidae) is presented, resulting in the recognition of 24 valid species. The genus is divided in five species groups based on shared morphological character states, *i.e.* the *acanthus*-, *australis*-, *speluncae*-, *trisetosus*- and *spinicaudatus*-groups with the *acanthus*-group being further fragmented in three subgroups (*acanthus*, *gussoae*, *ornamentus*). The two members of the *speluncae*-group, *Neoleptastacus phreatica* (Cottarelli, Bruno & Venanzetti, 1994) and *N. speluncae* (Cottarelli, Bruno & Venanzetti, 1994), are redescribed and transferred to a new genus, *Phreatipontia* **gen. nov.**, that appears to have a preference for low salinity habitats. The Mediterranean *N. acanthus* (Chappuis, 1954) is redescribed based on material from Türkiye and considered potentially conspecific with *N. huysi* (Karanovic, 2000). The male specimen illustrated in the original description of *N. longiremis* (Chappuis, 1955) is designated as the lectotype to define the nominal taxon objectively in the likely event that females and males assigned to this inadequately described species turn out to be non-conspecific. Detailed morphological comparison of species currently allocated to the *gussoae*-complex revealed three new cryptic taxa from Central and South America which are accorded specific rank (*N. abbreviatus* **sp. nov.**, *N. chilensis* **sp. nov.**, and *N. rectus* **sp. nov.**). The taxonomic status of *Arenopontia* (*Neoleptastacus*) *acantha accraensis* Lang, 1965 *sensu* Kunz (1971) is reassessed based on material from Angola and described as *N. emendatus* **sp. nov.** The Panamanian material previously identified as *N. trisetosus* (Mielke, 1982) is considered to represent a distinct species, *N. panamensis* **sp. nov.** while *N. pseudishikarianus* **sp. nov.** is proposed for the Chilean “population” of *N. ishikarianus* (Itô, 1968). *Neoleptastacus supersetosus* **sp. nov.** is described from Kuwait, representing the first arenopontiid record from the Arabian Peninsula. *Neoleptastacus secundus* Krishnaswamy, 1957 and *N. accraensis* (Lang, 1965) are treated as *species inquirendae* while *Arenopontia breviarticulata* Mielke, 1975 is removed from its provisional position in *Neoleptastacus* and placed as *species incertae sedis* in the Arenopontiidae. Distribution data are summarized for each species and the previously assumed amphi-Panamanian and amphi-Pacific distribution patterns of *N. gussoae* (Cottarelli, 1973) and *N. ishikarianus*, respectively, are rejected. Updated keys to the 24 valid species of *Neoleptastacus* and the six genera currently recognized in the family are provided.

Key words: identification keys, interstitial copepods, *Neoleptastacus abbreviatus* **sp. nov.**, *N. angolensis* **comb. nov.**, *N. chilensis* **sp. nov.**, *N. emendatus* **sp. nov.**, *N. panamensis* **sp. nov.**, *N. pseudishikarianus* **sp. nov.**, *N. rectus* **sp. nov.**, *N. supersetosus* **sp. nov.**, new combinations, new species, *Phreatipontia phreatica* **comb. nov.**, *P. speluncae* **comb. nov.**, species groups, taxonomic revision

Introduction

The Arenopontiidae, originally proposed as a subfamily in the Leptopontiidae (Martínez Arbizu & Moura 1994) but subsequently upgraded to family rank (Huys *et al.* 1996b; Wells 2007), is one of seven mesopsammic harpacticoid families that predominantly inhabit the interstitial realm of marine intertidal and subtidal substrata, the others being the Cylindropsyllidae, Latiremidae, Leptastacidae, Leptopontiidae, Paramesochridae and Psammopsyllidae. According to the most recent classification (Sak *et al.* 2008) the family currently accommodates five valid genera: *Arenopontia* Kunz, 1937; *Psammoleptastacus* Pennak, 1942; *Neoleptastacus* Nicholls, 1945; *Mesopontia* Sak, Huys & Karaytuğ, 2008; and *Onychopontia* Sak, Huys & Karaytuğ, 2008. The intricate taxonomic history of the Arenopontiidae involves nomenclatorial issues which were only recently settled (Sak *et al.* 2008). *Arenopontia*, *Psammoleptastacus* and *Neoleptastacus* were originally proposed as monotypic genera for *Arenopontia subterranea* Kunz, 1937 from Germany, *Psammoleptastacus arenaridus* Pennak, 1942 from the U.S.A. and *Neoleptastacus spinicaudatus* Nicholls, 1945 from Australia, respectively, and all three genera were initially placed in the Canthocamptidae which served as a catch-all taxon at the time (Kunz 1937; Pennak 1942; Nicholls 1945). Lang (1948), whose monograph was largely completed by 1938 but not published until a decade later due to World War II, did not consider Pennak’s or Nicholls’s work when he transferred *Arenopontia* to the subfamily Leptopontiinae in the Cylindropsyllidae. Both *Psammoleptastacus* and *Neoleptastacus* were almost simultaneously treated as junior subjective synonyms of *Arenopontia* by Noodt (1955a) and Chappuis (1954—erroneously cited the genus as *Paraleptastacus*, 1955) [not Kunz (1954) as claimed by Noodt (1955a: 85)], respectively. This course of action was followed by most authors except for Krishnaswamy (1957) who maintained both genera in the Cylindropsyllidae, placing *Neoleptastacus* in the subfamily Leptastacinae and *Psammoleptastacus* in the subfamily Leptopontiinae. Krishnaswamy (1957) added a second species, *N. secundus* Krishnaswamy, 1957, to *Neoleptastacus* and also transferred *Arenopontia australis* Chappuis, 1953, *A. acantha* Chappuis, 1954 and *A. longiremis* Chappuis, 1955 to the genus.

Wells (1967) advocated a subgeneric division of *Arenopontia* into the nominate subgenus *A.* (*Arenopontia*), and *A.* (*Neoleptastacus*), reflecting the divergence in P5 morphology [note that *A. intermedia* Rouch, 1962 was

overlooked despite having been listed by Lang (1965)]. Although this subdivision received general approval (e.g. Kunz 1971; Mielke 1975; Lindgren 1976; Itô, 1978; Bodiou & Colomines 1986; Wells & Rao 1987; Bodin 1979, 1988; Cottarelli *et al.* 1994; Karanovic 2000), it was not universally adopted (e.g. Masry 1970; Cottarelli 1973a, 1975) and fell eventually into disuse when Mielke (1982a-b, 1985, 1987) described several species from Central and South America without assigning them to either subgenus. Mielke (1982a) in particular expressed scepticism about the value of the absence/presence of a spinous process on P5 as a subgeneric discriminant since some species (e.g. *Arenopontia trisetosa* Mielke, 1982a) displayed a condition that could be interpreted as intermediate between those expressed by *Arenopontia* and *Neoleptastacus*. A further element of confusion was introduced by Bodiou & Colomines (1986) who proposed the new genus *Pararenopontia* for two former *Arenopontia* species that displayed a 2-segmented P1 exopod, i.e. *A. breviarticulata* Mielke, 1975 and *A. trisetosa*. Martínez Arbizu & Moura (1994) subsumed both species as derived members under *Arenopontia* and, without providing any argumentation, claimed that a subgeneric division of *Arenopontia* is not justifiable on grounds of evident paraphyly of *A. (Arenopontia)* and potential polyphyly of *A. (Neoleptastacus)*. This course of action was not accepted by Huys *et al.* (1996a-b) who reinstated *Pararenopontia* Bodiou & Colomines, 1986 and Wells's (1967) subgeneric classification. Bodin (1997) treated *Pararenopontia* as a third subgenus and stated incorrectly that Martínez Arbizu & Moura (1994) were responsible for suggesting this new rank. Wells (2007), by abolishing the subgeneric classification altogether, sank *Neoleptastacus* as a junior subjective synonym for the third time and maintained *Pararenopontia* as a valid genus. Sak *et al.* (2008) reinstated both *Neoleptastacus* and *Psammoleptastacus* as valid genera, added two new genera (*Mesopontia* and *Onychopontia*), and relegated *Pararenopontia* to a junior subjective synonym of *Neoleptastacus*, its type species *P. breviarticulata* (Mielke, 1975) being treated *species incertae sedis* in the genus and *P. trisetosa* (Mielke, 1982a) as a member of the *Neoleptastacus trisetosus*-group.

Neoleptastacus is the most speciose genus of the family Arenopontiidae, currently accommodating 21 nominal species in addition to one *species incertae sedis* (*Arenopontia breviarticulata*) and three taxa of doubtful identity [*Arenopontia acantha* Chappuis, 1954 *sensu* Božić (1967); *Arenopontia ? gussoae* Cottarelli, 1973a *sensu* Mielke (1982b); *Arenopontia ? ishikariana* Itô, 1968 *sensu* Mielke (1987)]. Three species described by Mielke (1985), *Arenopontia clasingi*, *A. pacifica* and *A. spicata*, were not originally assigned to a subgenus by its author but were subsequently transferred to *Neoleptastacus* by Sak *et al.* (2008). The genus is widely distributed in both Northern and Southern Hemispheres with confirmed records from all oceanic basins. Except for the Mediterranean and Black Sea, it is notably absent from the northwestern Atlantic (note that the generic status of *Arenopontia breviarticulata*, described from the Isle of Sylt, remains to be confirmed). Here we set out to (1) review the current status, relationships and distribution records of each species with particular emphasis on the *N. gussoae*-complex; (2) reassess the taxonomic status of *Arenopontia (Neoleptastacus) acantha accraensis* Lang, 1965 *sensu* Kunz (1971) based on material from Angola; (3) redescribe both sexes of *N. acanthus* (Chappuis, 1954) in detail and describe a new *Neoleptastacus* species from Kuwait; (4) propose a new genus to accommodate two former *Neoleptastacus* species from phreatic habitats; and (5) provide identification keys to the 24 valid species of *Neoleptastacus* and the six currently recognized genera of the Arenopontiidae.

Material and methods

Samples from sandy beaches in Türkiye were collected using the Karaman-Chappuis method (Delamare Debutteville 1953b). 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. Scale bars in illustrations are in µm. The descriptive terminology is adopted from Huys *et al.* (1996b). Abbreviations used in the text, figures and table are: *ae*, aesthetasc; *P1–P6*, for swimming legs 1–6; *exp (enp)-1 (-2–3)* to denote the proximal (middle, distal) segment of a ramus; *CR*, for caudal ramus; *An Op*, for anal operculum; *L*, for length. The term ‘acrothek’ denotes the trifid setal structure typically found on the apical margin of the distal antennular segment (Huys & Iliffe 1998). Type material was deposited in the Natural History Museum, London (NHM) and the Balıkesir University Zoology Museum (BUZM).

Systematics

Family Arenopontiidae Martínez Arbizu & Moura, 1994

Genus *Neoleptastacus* Nicholls, 1945

Pararenopontia Bodiou & Colomines, 1986 (type species by original designation: *Arenopontia breviariculata* Mielke, 1975)

Diagnosis (adapted from Sak *et al.* 2008). Arenopontiidae. Urosomites occasionally with conspicuous surface ornamentation (*N. clasingi*, *ornamentus*, *reductaspina*). Anal somite with (*acanthus*-group) or without (all other species groups) paired dorsolateral spinous processes. Anal operculum sometimes with median extension. Hyaline frills of abdominal somites with rectangular digitate or non-digitate lappets. Caudal ramus usually with dorsolateral spur near medial margin. P1 exopod 2- or 3-segmented; exp-1 with/without outer spine; exp-3 (or exp-2 when exopod 2-segmented) with one–two spine(s) and two geniculate setae. P1 endopod not prehensile, at least as long as exopod; enp-2 with outer spine and inner geniculate seta at distal margin. P2–P3 endopods 1- or 2-segmented. P3 endopod with outer distal element (when present) usually fused at base. P4 enp-2 with well developed outer distal element (except in *trisetosus*-group). Armature formula as follows:

	Exopod	Endopod
P1	0.0.02(1–2) or 0.021	1.011
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 one–four discrete elements; innermost element fused to segment forming spinous process (weakly delimited in *N. trisetosus* and *N. panamensis* **sp. nov.**); length of process sometimes sexually dimorphic. P6 ♂ with one–two elements.

Type species. *Neoleptastacus spinicaudatus* Nicholls, 1945 [by monotypy].

Other species. Twenty-three. See Table 1.

Species inquirenda. *Neoleptastacus secundus* Krishnaswamy, 1957; *N. accraensis* (Lang, 1965).

Taxa of doubtful identity. *Arenopontia acantha* Chappuis, 1954 *sensu* Božić (1967); *Arenopontia ? gussoae* Cottarelli, 1973a *sensu* Mielke (1982b) [partim]; *Arenopontia ? gussoae* Cottarelli, 1973a *sensu* Mielke (1987) [2nd form].

Gender. Masculine.

The genus shows considerable variation in swimming leg armature and segmentation, P5 morphology, abdominal ornamentation and caudal ramus structure. However, all species display a spinous apical process on the P5 which is derived from the fused innermost element (weakly delimited in *N. trisetosus* and *N. panamensis* **sp. nov.**). This apomorphic character state is unique in the Arenopontiidae and potentially serves as evidence in support of the monophyly of the genus. For practical reasons we have recognized several species groups within *Neoleptastacus*, some of which are monophyletic and may eventually be attributed separate generic status (Table 2). The majority of these groups are characterized by one or several autapomorphic character states with the notable exception of the *spinicaudatus*-group which contains the type species. For this reason, we have refrained from proposing new genera (except for the *spelunca*-group) as this would render *Neoleptastacus* a paraphyletic taxon.

(1) *acanthus*-group

Diagnosis. Anal somite with paired dorsolateral processes. Anal operculum weakly developed, without medial extension. P1 exp-1 with outer spine; exp-3 with four setae/spines (except *N. huysi*). P1 enp-2 with outer spine and inner geniculate seta distally. P2 exp-2 with outer spine of normal length (not extending far beyond distal margin of exp-3). Endopod P2–P3 2-segmented. P2 enp-2 with or without inner seta; with two distal spines. P3 enp-2 with 1–2 distal spines. P4 enp-2 with well developed outer seta.

TABLE 1. Valid species and *species inquirendae* (indicated by *) of *Neoleptastacus* Nicholls, 1945 and *Phreatipontia* **gen. nov.**

Current name	Original name and combination
<i>Neoleptastacus</i> Nicholls, 1945	
<i>Neoleptastacus spinicaudatus</i> Nicholls, 1945	
<i>Neoleptastacus australis</i> (Chappuis, 1953)	<i>Arenopontia australis</i> Chappuis, 1953
<i>Neoleptastacus acanthus</i> (Chappuis, 1954)	<i>Arenopontia acantha</i> Chappuis, 1954
<i>Neoleptastacus longiremis</i> (Chappuis, 1955)	<i>Arenopontia longiremis</i> Chappuis, 1955
<i>Neoleptastacus secundus</i> Krishnaswamy, 1957 *	
<i>Neoleptastacus africanus</i> (Chappuis & Rouch, 1961)	<i>Arenopontia africana</i> Chappuis & Rouch, 1961
<i>Neoleptastacus accraensis</i> (Lang, 1965) *	<i>Arenopontia accraensis</i> Lang, 1965
<i>Neoleptastacus indicus</i> (Rao, 1967)	<i>Arenopontia indica</i> Rao, 1967
<i>Neoleptastacus ishikarianus</i> (Itô, 1968)	<i>Arenopontia ishikariana</i> Itô, 1968
<i>Neoleptastacus gussoae</i> (Cottarelli, 1973a)	<i>Arenopontia gussoae</i> Cottarelli, 1973a
<i>Neoleptastacus trisetosus</i> (Mielke, 1982a)	<i>Arenopontia trisetosa</i> Mielke, 1982a
<i>Neoleptastacus clasingi</i> (Mielke, 1985)	<i>Arenopontia clasingi</i> Mielke, 1985
<i>Neoleptastacus pacificus</i> (Mielke, 1985)	<i>Arenopontia pacifica</i> Mielke, 1985
<i>Neoleptastacus spicatus</i> (Mielke, 1985)	<i>Arenopontia spicata</i> Mielke, 1985
<i>Neoleptastacus angolensis</i> (Bodiou & Colomines, 1986) comb. nov.	<i>Arenopontia (Neoleptastacus) africana</i> f. <i>angolensis</i> Kunz, 1971
<i>Neoleptastacus chaufriassei</i> (Bodiou & Colomines, 1986)	<i>Arenopontia (Neoleptastacus) chaufriassei</i> Bodiou & Colomines, 1986
<i>Neoleptastacus ornamentus</i> (Mielke, 1987)	<i>Arenopontia ornamenta</i> Mielke, 1987
<i>Neoleptastacus reductaspina</i> (Mielke, 1987)	<i>Arenopontia reductaspina</i> Mielke, 1987
<i>Neoleptastacus huysi</i> (Karanovic, 2000)	<i>Arenopontia (Neoleptastacus) huysi</i> Karanovic, 2000
<i>Neoleptastacus abbreviatus</i> sp. nov.	<i>Arenopontia ? gussoae</i> Cottarelli, 1973a <i>sensu</i> Mielke (1982b) [partim]
<i>Neoleptastacus chilensis</i> sp. nov.	<i>Arenopontia ? gussoae</i> Cottarelli, 1973a <i>sensu</i> Mielke (1987) [partim]
<i>Neoleptastacus emendatus</i> sp. nov.	<i>Arenopontia (Neoleptastacus) acantha accraensis</i> Lang, 1965 <i>sensu</i> Kunz (1971)
<i>Neoleptastacus panamensis</i> sp. nov.	<i>Arenopontia trisetosa</i> Mielke, 1982a <i>sensu</i> Mielke (1982b)
<i>Neoleptastacus pseudishikarianus</i> sp. nov.	<i>Arenopontia ? ishikariana</i> Itô, 1968 <i>sensu</i> Mielke (1987)
<i>Neoleptastacus rectus</i> sp. nov.	<i>Arenopontia ? gussoae</i> Cottarelli, 1973a <i>sensu</i> Mielke (1982b) [partim]
<i>Neoleptastacus supersetosus</i> sp. nov.	
<i>Phreatipontia</i> gen. nov.	
<i>Phreatipontia phreatica</i> (Cottarelli, Bruno & Venanzetti, 1994) comb. nov.	<i>Arenopontia (Neoleptastacus) phreatica</i> Cottarelli, Bruno & Venanzetti, 1994
<i>Phreatipontia speluncae</i> (Cottarelli, Bruno & Venanzetti, 1994) comb. nov.	<i>Arenopontia (Neoleptastacus) speluncae</i> Cottarelli, Bruno & Venanzetti, 1994

Subgroups included. *acanthus*-subgroup, *gussoae*-subgroup, *ornamentus*-subgroup.

Remarks. Members of this group can readily be identified by the presence of paired dorsolateral spinous processes on the anal somite. The presence of these backwardly directed extensions, not found in any other species of the Arenopontiidae, is an apomorphic character state supporting the monophyletic status of this lineage.

Various authors (Itô 1978; Mielke 1982b, 1987; Wells & Rao 1987) have recognized a *gussoae*-subgroup of morphologically extremely similar species characterized by the presence of only one spine on P3 enp-2: *N. longiremis* (Chappuis, 1955), *N. indicus* (Rao, 1967), *N. gussoae* (Cottarelli, 1973a) and *N. sakagamii* (Itô, 1978). *Neoleptastacus accraensis* (Lang, 1965), which is generally believed to display this character (see below for a reinterpretation), has occasionally been cited as part of this species complex (Mielke 1982b, 1987). However, the absence of paired anal processes excludes this species from the *acanthus*-group. The 1-spine condition on the distal endopodal segment of P3 evolved convergently in the common ancestor of the *trisetosus*-group as well as in

N. australis (Chappuis, 1953) and *N. reductaspina* (Mielke, 1987) (Table 2). Wells & Rao (1987), inspired by the extensive variability observed in their material of *N. indicus*, proposed to sink *N. sakagamii* as a junior subjective synonym of the latter, but argued that that the caudal ramus and possibly P5 are sufficiently different to maintain *A. gussoae* as a distinct species. *Neoleptastacus secundus* should also be considered a member of the *acanthus*-group since Krishnaswamy (1957: 97) clearly stated that "...the anal segment bears two spines posteriorly" (hinted at in his illustration of the male habitus). Unfortunately, the P3 endopod was not figured and his statement that it resembles that of P2 (except for the absence of the inner seta on enp-1) has made most authors assume that P3 enp-2 bears two distal elements (Lang 1965; Bodiou & Colomines 1986; Karanovic 2000). Given its close similarity to *N. longiremis* (see below), which bears one element on this segment, this character must await confirmation. The species is here treated as a *species inquirenda* in the *gussoae*-subgroup. Reassessment of Mielke's (1982b, 1987) descriptions of "*Arenopontia* ? *gussoae*" resulted in the recognition of three additional members: *N. abbreviatus* **sp. nov.**, *N. chilensis* **sp. nov.** and *N. rectus* **sp. nov.** Finally, *Neoleptastacus emendatus* **sp. nov.**, proposed here (see below) for *Arenopontia* (*Neoleptastacus*) *acantha accraensis* Lang, 1965 *sensu* Kunz (1971), also belongs to this subgroup which contains species from the northern Atlantic, Indian Ocean, Japan and the Pacific seaboard of South America.

The *ornamentus*-subgroup currently includes two closely related Chilean species, *N. ornamentus* (Mielke, 1987) and *N. reductaspina* (Mielke, 1987), that display conspicuous surface ornamentation on the abdominal somites in the form of rectangular plates (areas of integumental reinforcement). Similar surface ornamentation has been reported for *N. clasingi* (Mielke, 1985) in the *spinicaudatus*-group. Both *N. ornamentus* and *N. reductaspina* share the unique absence of the inner seta on P2 enp-2 (Table 2), giving further credence to the monophyly of this subgroup.

Neoleptastacus acanthus (Chappuis, 1954), *N. chauffriassei* (Bodiou & Colomines, 1986) and *N. huysi* (Karanovic, 2000) exhibit the plesiomorphic 2-spine condition on P3 enp-2 and are united in the *acanthus*-subgroup. No synapomorphy has as yet been identified for this subgroup which includes species from the Mediterranean and the sub-antarctic Crozet Islands in the southern Indian Ocean.

(2) *spinicaudatus*-group

Diagnosis. Anal somite without paired dorsolateral processes. Anal operculum weakly developed, without rounded medial extension (except for *A. pseudishikarianus* **sp. nov.**). P1 exp-1 with outer spine; exp-3 with four setae/spines. P1 enp-2 with outer spine and inner geniculate seta distally. P2 exp-2 with outer spine of normal length (not extending far beyond distal margin of exp-3). Endopod P2–P3 2-segmented; P2 enp-2 with inner seta and two distal spines; P3 enp-2 with two distal spines (outer one fused to segment). P4 enp-2 with normally developed outer seta.

Species included. *N. spinicaudatus* Nicholls, 1945, *N. ishikarianus* (Itô, 1968), *N. clasingi* (Mielke, 1985), *N. pacificus* (Mielke, 1985), *N. spicatus* (Mielke, 1985) and *N. pseudishikarianus* **sp. nov.**

The *spinicaudatus*-group accommodates six morphologically very similar species, all of which are currently restricted to the Pacific Ocean. All species display the plesiomorphic armature on P1–P4, except for *N. pacificus* which lacks the inner seta on P4 exp-3 (Table 2). In the absence of any morphology-based apomorphies that could support the common origin of these species, assessment of the potential monophyly of this species group will have to await the arrival of molecular sequence data. Sak *et al.* (2008) provided a key to the members of the *spinicaudatus*-group (except *N. pseudishikarianus* **sp. nov.**).

Chappuis & Rouch's (1961) description of *Neoleptastacus accraensis* (Lang, 1965) is inadequate and incomplete. Based on a reinterpretation of the armature pattern of the P3 endopod (see below) the species is treated here as a *species inquirenda* in the *spinicaudatus*-group.

(3) *australis*-group

Diagnosis. Anal somite without paired dorsolateral processes. Anal operculum weakly developed, without rounded medial extension. P1 exp-1 with outer spine; exp-3 with four setae/spines. P1 enp-2 with outer spine and inner geniculate seta distally. P2 exp-2 with outer spine of normal length (not extending far beyond distal margin of exp-3). P2 endopod 2-segmented; enp-2 with inner seta and two distal spines. P3 endopod 1-segmented; with one distal spine. P4 enp-2 with normally developed outer seta.

Species included. *N. australis* (Chappuis, 1953).

This species group includes one incompletely described African species which does not fit comfortably in either the *spinicaudatus*- or *trisetosus*-groups defined herein. The reduced armature on the P3 endopod (one apical element on the distal segment) is not exclusive to *N. australis* (Table 2). More information is required before any statement can be made about its relationships, particularly whether it may be nested as an advanced member in the *spinicaudatus*-group.

(4) *trisetosus*-group

Diagnosis. Anal somite without paired dorsolateral processes. Anal operculum well developed, often produced into a rounded medial extension (not illustrated for *N. trisetosa*). P1 exp-1 without outer spine (exopod sometimes 2-segmented); exp-3 with three setae/spines. P1 enp-2 with outer spine and inner geniculate seta distally. P2 exp-2 with very long outer setiform element (extending far beyond distal margin of exp-3). Endopod P2–P3 1-segmented. P2 endopod with inner seta and one distal spine. P3 endopod with one distal spine. P4 enp-2 outer seta reduced.

Species included. *N. africanus* (Chappuis & Rouch, 1961), *N. trisetosus* (Mielke, 1982a), *N. angolensis* (Bodiou & Colomines, 1986) **comb. nov.**, *N. panamensis* **sp. nov.**, *N. supersetosus* **sp. nov.**

The common origin of the species included in this group is strongly supported by five apomorphic character states: (1) absence of outer spine on P1 exp-1, (2) presence of only three elements on the distal segment of P1 exopod, (3) 1-segmented P2–P3 endopods with reduced armature (110 and 010, respectively), (4) P2 exp-2 with very long outer setiform element, extending far beyond distal margin of exp-3, and (5) anal operculum well developed, often produced into a rounded median extension (unconfirmed for *N. trisetosus* and *N. panamensis* **sp. nov.**). *Neoleptastacus africanus* and *N. angolensis* **comb. nov.** share the plesiomorphic 3-segmented P1 exopod, a distinctly elongate P4 exopod and possibly reduced armature on the P5. *Neoleptastacus trisetosus*, *N. panamensis* **sp. nov.** and *N. supersetosus* **sp. nov.** exhibit the apomorphic 2-segmented condition of the P1 exopod. The group has a wide distribution with records from the Galápagos archipelago (Ecuador), Panama, Kuwait and the Atlantic seaboard of Africa.

(5) *speluncae*-group

Diagnosis. Anal somite without paired dorsolateral processes. Anal operculum weakly developed, without rounded medial extension. P1 exp-1 with outer spine; exp-3 with 4 setae/spines. P1 enp-2 with two geniculate setae distally. P2 exp-2 with outer spine of normal length (not extending far beyond distal margin of exp-3). Endopod P2–P3 2-segmented; P2 enp-2 with inner seta but only one distal spine. P3 enp-2 with one distal spine. P4 enp-2 outer seta relatively short.

Species included. *N. phreaticus* (Cottarelli, Bruno & Venanzetti, 1994), *N. speluncae* (Cottarelli, Bruno & Venanzetti, 1994).

Members of this group are restricted to the Mediterranean and the Black Sea where they typically inhabit reduced salinity environments that are exposed to freshwater inflow. They also diverge morphologically from all species currently included in *Neoleptastacus* by the armature of the P1 endopod, displaying two geniculate setae on the distal segment instead of an outer spine and an inner geniculate seta. Another shared character is the reduced armature on P2–P3 enp-2, showing only one apical element (0.110 and 0.010, respectively). The *speluncae*-group cannot be accommodated in *Neoleptastacus* and is here attributed generic rank (see below—*Phreatipontia* **gen. nov.**).

TABLE 2. Species groups in *Neoleptastacus* Nicholls, 1945 *sensu lato*. [AP = paired spinous processes on anal somite; G+G = two geniculate setae; G+S = outer spine + inner geniculate seta; P5 = number of marginal elements (excluding outer basal seta) in both sexes (when known); p = spinous process; + = present; – = absent; ? = missing data].

	AP	P1 exp	P1 exp- 1 spine	P1 enp-2	P2 enp	P3 enp	P4 exp	P4 enp	P5
acanthus-group									
I. <i>acanthus</i> -subgroup									
<i>acanthus</i>	+	0.0.022	+	G+S	0.120	0.020	0.0.121	0.020	3
<i>chaufriassei</i>	+	0.0.022	+	G+S	0.120	0.020	0.0.121	0.020	1+p
<i>huysi</i>	+	0.0.021	+	G+S	0.120	0.020	0.0.121	0.020	3
II. <i>gussoae</i> -subgroup									
<i>abbreviatus</i> sp. nov.	+	0.0.022	+	G+S	0.120	0.010	0.0.121	0.020	3
<i>chilensis</i> sp. nov.	+	0.0.022	+	G+S	0.120	0.010	0.0.121	0.020	3
<i>emendatus</i> sp. nov.	+	0.0.022	+	G+S	0.120	0.010	0.0.121	0.020	3
<i>gussoae</i>	+	0.0.022	+	G+S	0.120	0.010	0.0.121	0.020	3
<i>indicus</i>	+	0.0.022	+	G+S	0.120	0.010	0.0.121	0.020	3
<i>longiremis</i>	+	0.0.022	+	G+S	0.120	0.010	0.0.121	0.020	3
<i>rectus</i> sp. nov.	+	0.0.022	+	G+S	0.120	0.010	0.0.121	0.020	3
<i>secundus</i>	+	0.0.022	+	G+S	0.120	0.0?0 ^a	0.0.121	0.020	3
III. <i>ornamentus</i> -subgroup									
<i>ornamentus</i>	+	0.0.022	+	G+S	0.020	0.020	0.0.121	0.020	3
<i>reductaspina</i>	+	0.0.022	+	G+S	0.020	0.010	0.0.121	0.020	2
australis-group									
<i>australis</i>	–	0.0.022	+	G+S	0.120	010	0.0.021 ^b	0.020	3
spinicaudatus-group									
<i>accraensis</i>	–	0.0.022	+	G+S	0.120	0.020 ^d	0.0.??? ^c	0.0?0 ^c	3
<i>clasingi</i>	–	0.0.022	+	G+S	0.120	0.020	0.0.121	0.020	3
<i>ishikarianus</i>	–	0.0.022	+	G+S	0.120	0.020	0.0.121	0.020	3
<i>pacificus</i>	– ^e	0.0.022	+	G+S	0.120	0.020	0.0.021	0.020	3
<i>pseudishikarianus</i> sp. nov.	–	0.0.022	+	G+S	0.120	0.020	0.0.121	0.020	3
<i>spicatus</i>	–	0.0.022	+	G+S	0.120	0.020	0.0.121	0.020	3
<i>spinicaudatus</i>	–	0.0.022	+	G+S	0.120	0.020	0.0.121	0.020	3
trisetosus-group									
<i>africanus</i>	–	0.0.021	– ^f	G+S	110	010	0.0.121	0.020	1
<i>angolensis</i> comb. nov.	–	0.0.021	–	G+S	110	010	0.0.121	0.020	2
<i>panamensis</i> sp. nov.	–	0.021	–	G+S	110	010	0.0.121	0.020	4 ^g
<i>supersetosus</i> sp. nov.	–	0.021	–	G+S	110	010	0.0.121	0.020	4 ^h
<i>trisetosus</i>	–	0.021	–	G+S	110	010	0.0.121	0.020	4 ^g
speluncae-group (= <i>Phreatipontia</i> gen. nov.)									
<i>phreaticus</i> comb. nov.	–	0.0.022	+	G+G	0.110 ⁱ	0.010	0.0.121	0.020 ^j	3
<i>speluncae</i> comb. nov.	–	0.0.022	+	G+G	0.110	0.010	0.0.121	0.020	3

^a Krishna

swamy (1957) states that P3 resembles P2 but does not figure it.

^b Chappuis (1953) states that exopodal setal formula is as in *A. subterranea* Kunz, 1937 but does not illustrate the P4 exopod.

^c Based on reinterpretation presented herein. Previous authorities (Lang 1965; Bodiou & Colomines 1986; Karanovic 2000; Wells 2007) cited/interpreted the armature formula as 0.010.

^d Chappuis & Rouch (1961) do not provide information about P3 exopod or P4 but Lang (1965), Bodiou & Colomines (1986) and Wells (2007) considered their armature patterns to be identical with those of *N. longiremis* without giving evidence underpinning their assumption.

^e replaced by 2–3 spinules.

^f The small outer element figured by Chappuis & Rouch (1961) on P1 exp-1 is here interpreted as a spinule.

^g The fourth (innermost) marginal element is delimited at the base, representing the homologue of the spinous process in other members of *Neoleptastacus*.

^h Four articulating elements in addition to the inner spinous process.

ⁱ Cottarelli *et al.* (1994) erroneously show the inner seta originating from enp-1.

^j According to Cottarelli *et al.* (1994) the outer distal element of enp-2 is absent but this is contradicted by our re-examination (Fig. 14D).

Nomenclature and (re)descriptions

Neoleptastacus spinicaudatus Nicholls, 1945

Paraleptastacus spinicaudatus Nicholls, 1945: *lapsus calami* by Chappuis (1954: 269)

Arenopontia spinicaudata (Nicholls, 1945) Chappuis (1955: 56)

Arenopontia (Neoleptastacus) spinicaudata (Nicholls, 1945): Wells (1967: 324)

Neoleptastacus longipes Nicholls, 1945: *lapsus calami* by Karanovic (2008: 5, 331)

Original description. Nicholls (1945): 22–23; Text fig. 3.

Additional description. Sak *et al.* (2008): 435–441; Figs 13–17.

Type locality. Australia, Western Australia. Nicholls (1945) did not specify a type locality but collected the species from two sandy beaches some 500 km apart. The first, Leighton Beach (in the vicinity of Perth), was sampled in October 1939 while samples from the second site, locally known as ‘Back Beach’ at Dongarra, were collected in March 1940. All syntypes deposited at the Natural History Museum in London originated from Back Beach which was designated as the type locality by Sak *et al.* (2008).

Body length. 280–300 µm (both sexes) [Nicholls 1945].

Remarks. Sak *et al.* (2008) re-examined the type material and redescribed both sexes in detail. Nicholls’s (1945) original description is adequate by contemporary standards except for the reported absence of the inner seta on P4 exp-3, an error that was perpetuated in some morphological comparisons (Noodt 1955b; Bodiou & Colomines 1996) and identification keys (Lang 1965; Karanovic 2000; Wells 2007). Within the *spinicaudatus*-group, *N. spinicaudatus* is morphologically closest to *N. spicatus*, both of which exhibit a dorsolateral spur near the base of caudal ramus seta VII. The type species can be differentiated from *N. spicatus* by the shape of the abdominal hyaline frills (lappets denticulate *vs* semi-incised obtusidigitate), the proportional size of the inner distal seta on P2–P3 enp-2 (shorter *vs* longer than endopod) and the morphometric dimensions of the P5 (2.5 times as long as wide *vs* 3.0 times). The apical spinous process on the P5 of both sexes is minutely bipinnate in *N. spinicaudatus* (and still delimited at its base on the posterior surface in the ♀) while it is lacking such ornamentation in *N. spicatus* (and completely fused to the segment in the ♀). The linear egg-sac typically contains 2–4 large eggs; occasionally six eggs are found in which case they overlap (Nicholls 1945).

The species is so far known only from two sandy beaches in Western Australia (Nicholls 1945). Chappuis (1954: 269) claimed to have found one female and one male in Annaba (= Bône) in northeastern Algeria which closely resemble *N. spinicaudatus* but did not present any illustrations to substantiate his record. In a later report, Chappuis (1958: 414, Figs 2–5) provided illustrations of the female antennule, P2 endopod, P5 and caudal ramus of specimens he collected in Puget Sound, Washington State. Despite differences in the P5, length of P3–P4 endopods and caudal rami, Chappuis (1958) assigned his material to *N. spinicaudatus*, stating that such morphological minutiae do not warrant the proposal of a distinct subspecies. As pointed out by Sak *et al.* (2008), the morphology of the fifth legs suggests that Chappuis (1958) was almost certainly dealing with *Mesopontia dillonbeachia* (Lang, 1965). Karanovic (2008) erroneously cited the species as *Neoleptastacus longipes* Nicholls, 1945.

Neoleptastacus australis (Chappuis, 1953)

Arenopontia australis Chappuis, 1953

Arenopontia (*Neoleptastacus*) *australis* Chappuis, 1953: Wells (1967: 324)

Neoleptastacus australis (Chappuis, 1953) Sak *et al.* (2008: 412)

Original description. Chappuis (1953): 148–150; Fig. 2.

Type locality. Madagascar, Faux Cap (south coast); sandy beach.

Body length. 380 μm (♀).

Remarks. Chappuis (1953) stated that the antennary exopod bears either one or two setae but this must be an error. He also illustrated a short inner spine on P1 exp-2 and P4 enp-1 and a short outer seta on P2 enp-1. In reality these structures are ornamentation elements and their taxonomic value was rightly dismissed by Noodt (1955b). It must also be noted that the entire P4 endopod was accidentally rotated in Chappuis's mount as indicated by the position of the shorter distal element (being positioned on the inner corner instead of the outer one). His drawing of the female P2 endopod appears to be based on a similar observational error (the correct setation pattern is shown for the male) and the distal portion of the P1 endopod also seems to be rotated, showing the short apical element at the inner instead of the outer corner of enp-2. Although Chappuis (1953) illustrated both rami only for P2, he stated explicitly that the exopods of P2–P4 display the same formula as in *Arenopontia subterranea* Kunz, 1937. The inferred absence of the inner seta on P4 exp-3 (formula 0.0.021) is therefore shared only with *N. pacificus* (a member of the *spinicaudatus*-group). *Neoleptastacus australis* is so far the only species displaying the combination of a 2-segmented P2 endopod and a 1-segmented P3 endopod (Table 2). The species is known from one female and two males collected at the type locality and has not been recorded again since its original description.

Neoleptastacus acanthus (Chappuis, 1954)

(Figs 1–5)

Arenopontia acantha Chappuis, 1954

Arenopontia (*Neoleptastacus*) *acantha* Chappuis, 1954: Wells (1967: 324)

Arenopontia acantha Chappuis, 1954: *lapsus calami* by Cottarelli (1969: 20)

Arenopontia (*Neoleptastacus*) *acantha acantha* Chappuis, 1954: Kunz (1971: 356)

Neoleptastacus acanthus (Chappuis, 1954) Sak *et al.* (2008: 412)

Neoleptastacus knidosensis—*nomen nudum* by Sak (2004: 230)

Original description. Chappuis (1954): 268–270; Figs 46–53.

Additional descriptions. Masry (1970—as *A. acantha*): 251–253; Fig. 13. Cottarelli (1973a—as *A. acantha*): Fig. 22 [mandibular palp]. Martínez Arbizu & Moura (1994—as *A. acantha*): 63; Fig. 2d, g [rostrum, anal somite and caudal rami]. Alper (2009): 45–46; Fig. 3.6 [♀ lateral habitus, photograph].

Type locality. Western Mediterranean. Chappuis (1954) collected the species in various localities in Italy, Algeria and Tunisia (see below) but did not specify a *locus typicus*. Since P.-A. Chappuis habitually ignored type fixation, all the specimens on which he established *A. acantha* are syntypes and collectively constitute the name-bearing type (ICZN Art. 72.1.1). According to ICZN Art. 73.2.3 the type locality encompasses all of the places where the syntypes were collected.

Material examined. One ♀ (dissected on eight slides) (reg. no NHMUK 2024.1050) and one ♂ (dissected on seven slides) (reg. no NHMUK 2024.1051); seven ♀♀ and three ♂♂ (in ethanol) (reg. nos NHMUK 2024.1052–1061); five ♀♀ and two ♂♂ (in ethanol) deposited in the collections of BUZM. All specimens collected from Hastanealtı Beach, Datça (Muğla Province), Türkiye on 24 November 2002; leg. A. Alper.

Body length. 450 μm (♀) [Chappuis 1954]; 380–420 μm (♀), 365–390 μm (♂) [Masry 1970]; 331 μm (♀), 325 μm (♂) [present account].

Redescription of female. Total body length from tip of rostrum to posterior margin of caudal rami 350 μm (mean = 331 μm ; $n = 10$). Maximum body width 36 μm (mean = 34 μm ; $n = 10$), measured near posterior margin of cephalothorax. Body slender and cylindrical without clear distinction between prosome and urosome. Sensillar pattern on body as figured. 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

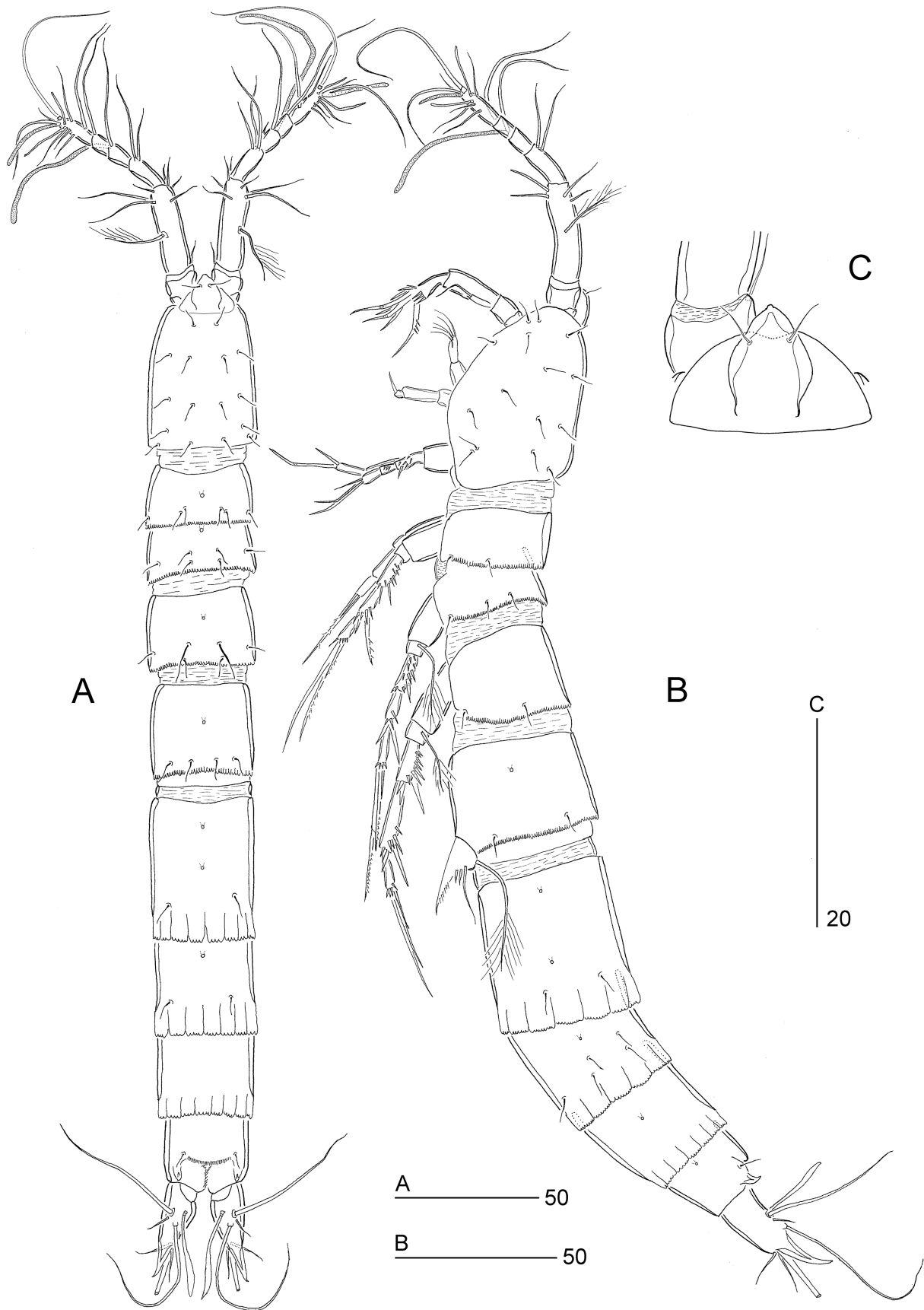


FIGURE 1. *Neoleptastacus acanthus* (Chappuis, 1954) (♀): (A) habitus, dorsal; (B) habitus, lateral; (C) rostrum, dorsal.

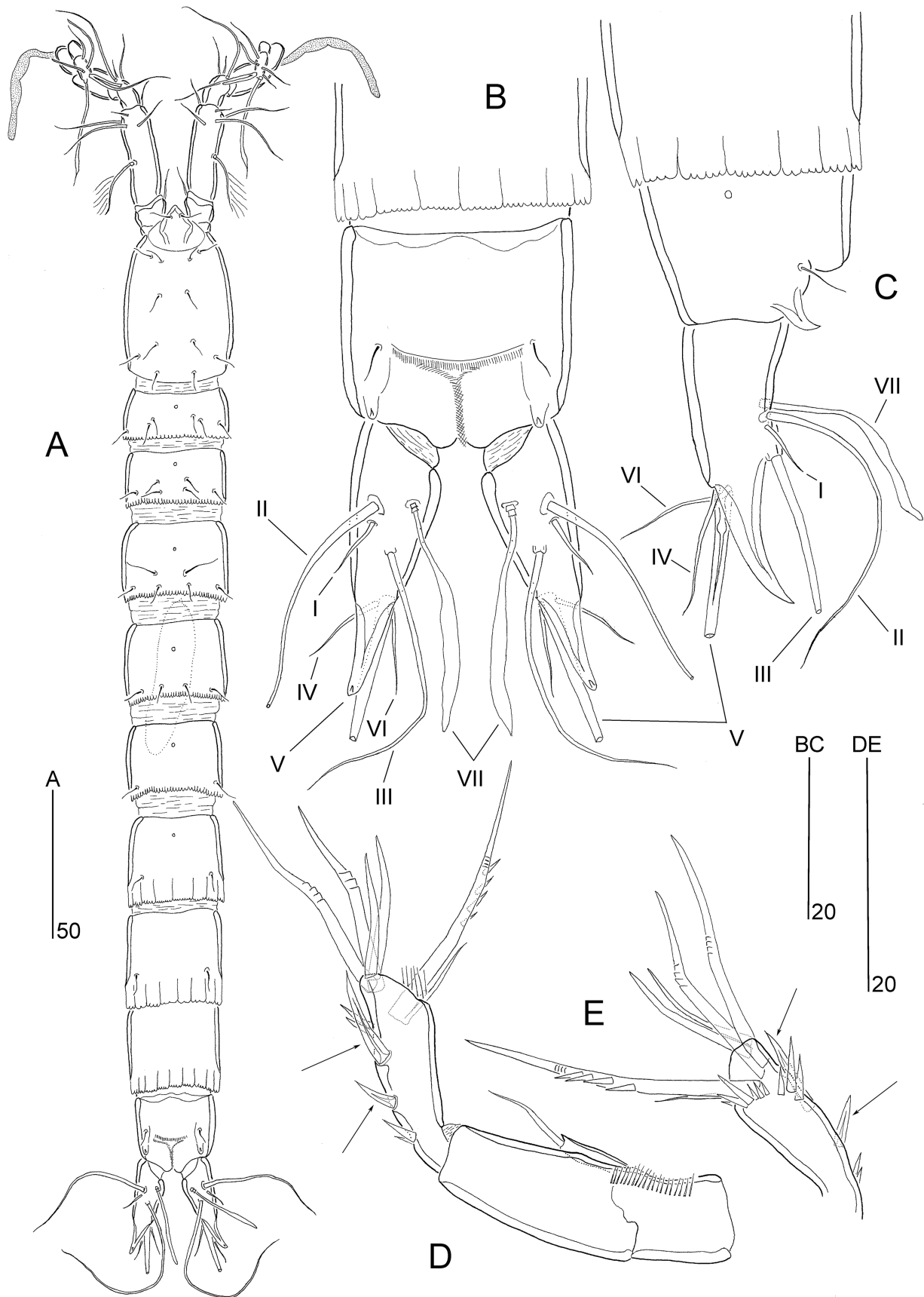


FIGURE 2. *Neoleptastacus acanthus* (Chappuis, 1954): (A) habitus (♂), dorsal; (B) anal somite and caudal rami (♀), dorsal; (C) anal somite and left caudal ramus (♀), lateral; (D) antenna (♀), medial; (E) antennary endopod (♀), outer. [Lateral spines of antennary endopod indicated by arrows in D–E]

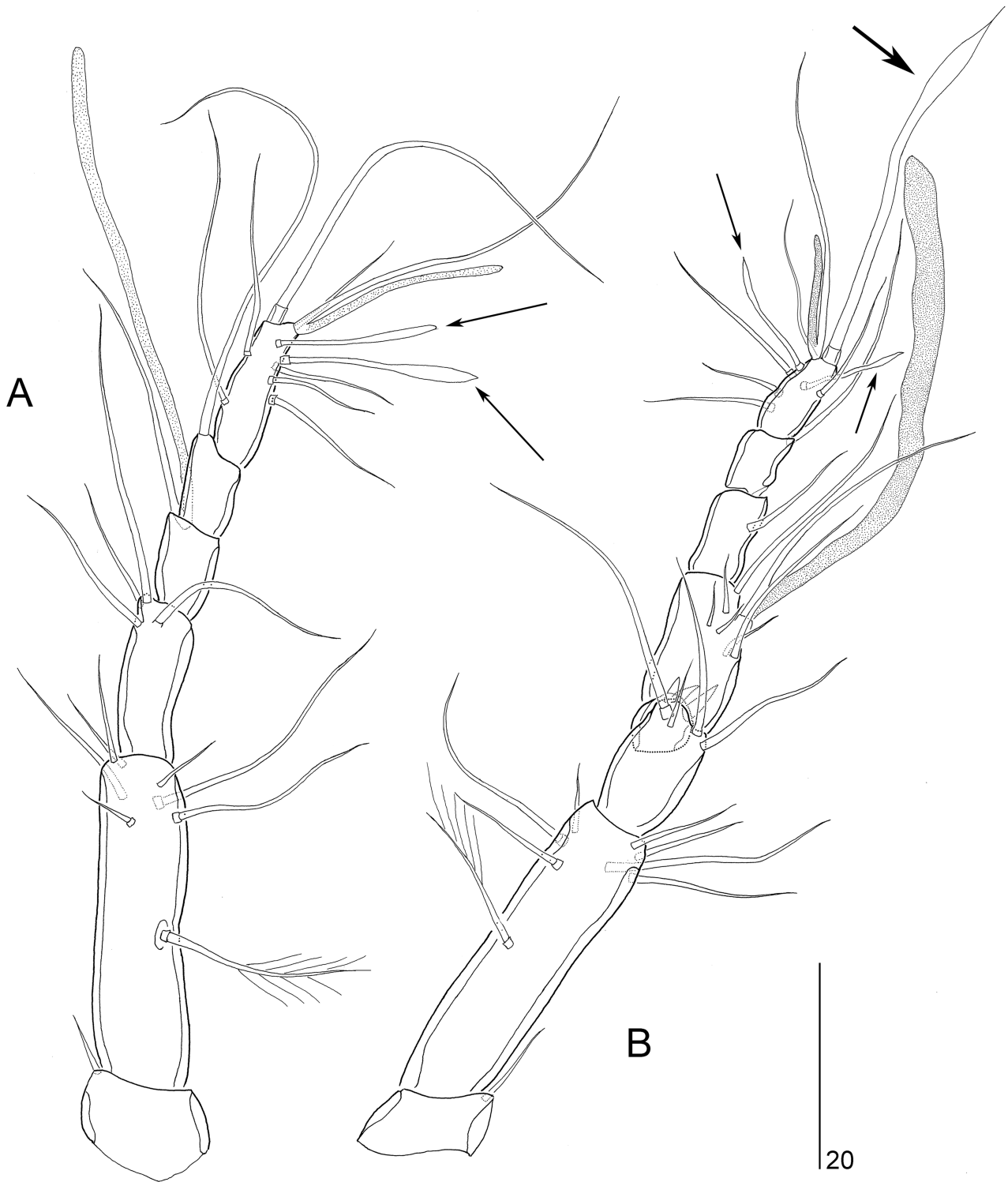


FIGURE 3. *Neoleptastacus acanthus* (Chappuis, 1954): (A) antennule (♀), dorsal; (B) antennule (♂), ventral. [spatulate setae indicated by arrows]

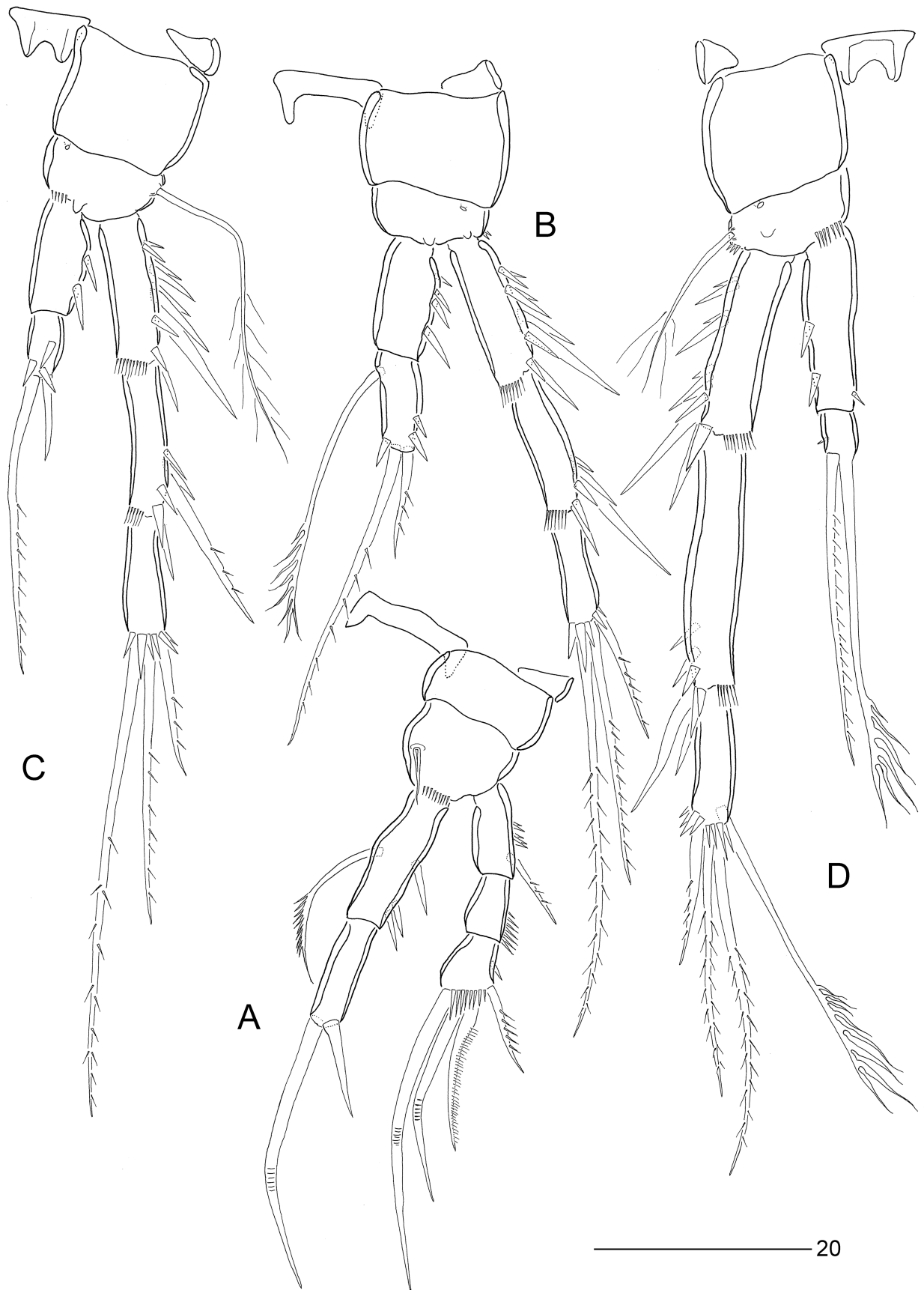


FIGURE 4. *Neoleptastacus acanthus* (Chappuis, 1954) (♀): (A) P1, anterior; (B) P2, anterior; (C) P3, anterior; (D) P4, anterior.

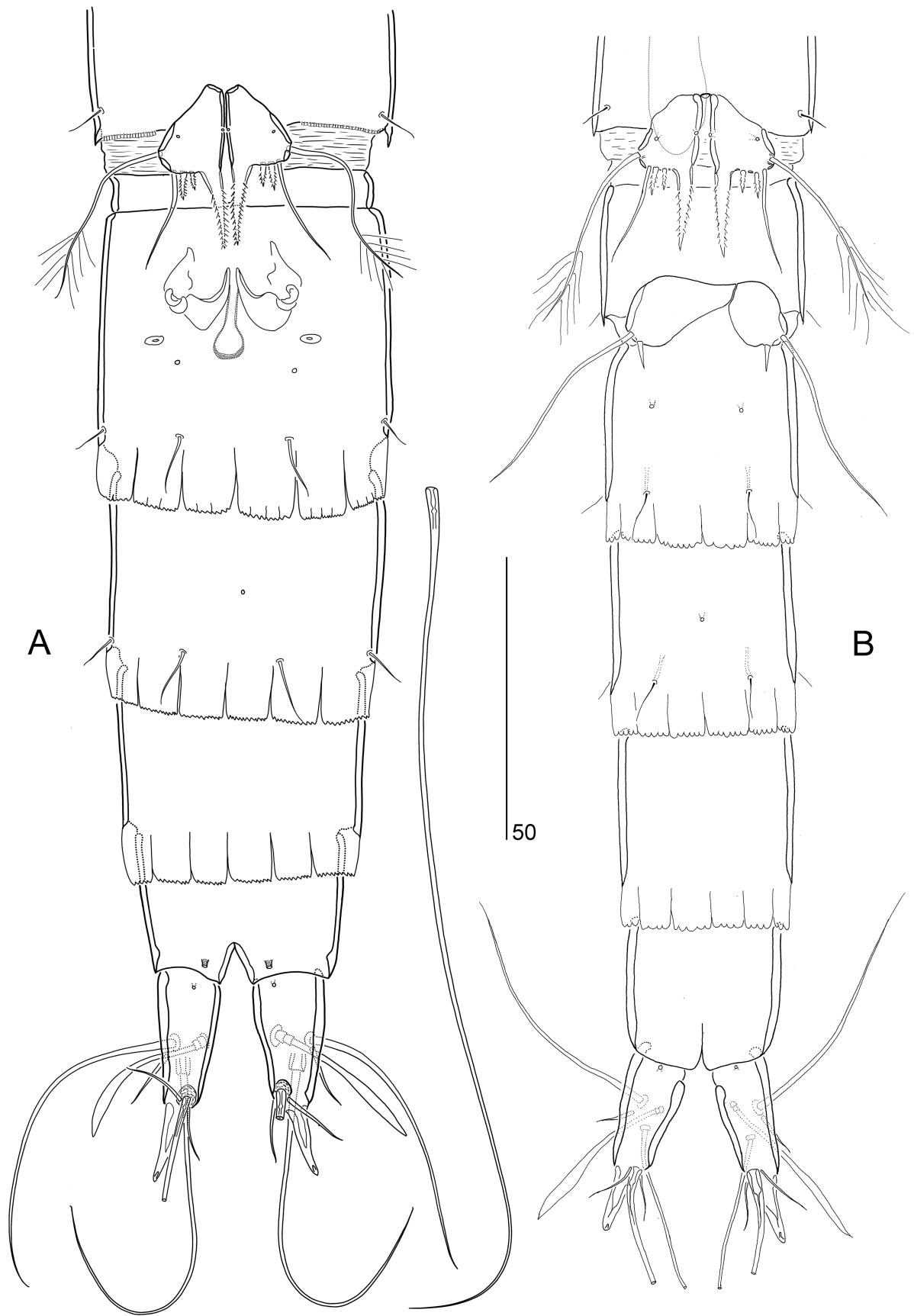


FIGURE 5. *Neoleptastacus acanthus* (Chappuis, 1954): (A) urosome (♀), ventral [caudal ramus seta V figured at full length in inset]; (B) urosome (♂), ventral.

1A, B; 2B; 5A). Somites connected by well-developed intersomitic membranes. Genital double-somite about 1.3 times longer than wide (measured in dorsal aspect); with two middorsal, four lateral and four ventral pores (Figs 1A, B; 5A). Anal somite (Figs 2B, C; 5A) with paired, dorsally recurved, spinous processes near posterior border either side of anal opening, and two lateral pores near anterior margin; with two conspicuous pores near ventral posterior margin. Anal frill triradiate, minutely incised (giving a spinulose appearance); anal operculum slightly convex, without ornamentation.

Caudal rami (Figs 2B, C; 5A) about three times longer than wide (measured in dorsal view from anterior margin to apex of spinous process), distinctly tapering posteriorly; with a pore near ventral proximal margin (Fig. 5A); outer distal corner produced into posteriorly directed, dorsally recurved spinous process; no spinular ornamentation discernible. Armature consisting of seven setae; seta I small; setae II and III (displaced to dorsal surface) long and naked; seta IV short, naked, located between seta V and posterior spinous process; seta V long, naked, with proximal fracture plane (Fig. 5A); seta VI small, naked and located at inner distal corner; seta VII distinctly foliaceous and tri-articulate at base.

Rostrum (Fig. 1C) small, broadly subtriangular, tapering distally; apical part lobate and demarcated by bilateral constrictions, with two delicate sensilla.

Antennule (Fig. 3A) long and slender, 6-segmented. Segment 1 with small seta near anterodistal margin. Segment 2 longest, about 3.4 times longer than wide. Segment 4 with long aesthetasc (L: 45 μ m) fused at base with seta. Distal segment with eight setae (two distinctly spatulate; indicated by arrows in Fig. 3A) and apical acrothek consisting of short aesthetasc (L: 20 μ m) and two setae. All setal elements naked except for plumose seta on dorsal surface of segment 2. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[8 + acrothek].

Antenna (Fig. 2D, E). Coxa small, without ornamentation (not figured). Basis and proximal endopodal segment forming incompletely fused allobasis, about 2.9 times as long as maximum width; original basis-endopod boundary marked by transverse surface suture at level of exopodal articulation; proximal part representing original basis with longitudinal row of small spinules near base of exopod. Exopod one-segmented, unornamented, and elongate, with a naked apical seta (about 1.3 times longer than exopod). Free endopodal segment with few lateral spinules proximally and transverse spinular row distally; medial armature consisting of two short spines (indicated by arrows in Fig. 2D, E); apical armature consisting of two naked spines and three geniculate setae, longest of which with spinules around geniculation and fused basally to naked accessory seta.

Mandible, maxillule, maxilla and maxilliped as in *N. spinicaudatus* (see Sak *et al.* 2008: Figs 16D, E; 17E, F). Mandibular gnathobase elongate, about as long as palp; with several curved, minute teeth and one tiny recurved seta at dorsal corner. Mandibular palp uniramous, consisting of elongate, unisetose basis and one-segmented endopod with one inner, two outer, and two apical setae. Maxillule comprising praecoxa, coxa, basis and vestigial rami; praecoxal arthrite with one anterior surface seta and five spines and two setae around distal margin; 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 comprising syncoxa, allobasis and endopod; syncoxa with two cylindrical endites, proximal endite with three setae (one fused at base) and 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 naked. Maxilliped comprising syncoxa, basis and endopod; syncoxa longer than wide, unarmed, with few spinules; basis elongate and unarmed; endopod with small accessory seta and slightly curved claw, bearing strong, subterminal spinule.

P1 (Fig. 4A). Intercoxal sclerite wide and subrectangular. Praecoxa small, triangular and naked. Coxa wider than long, without ornamentation. Basis with spinular row near base of endopod; anterior surface with a small inner spine near medial margin. Exopod three-segmented; exp-1 and -2 with several spinules around outer margin, exp-3 with single spinule; exp-1 longest, with unipinnate outer spine; exp-2 without outer element; exp-3 with short unipinnate outer spine, a long curved unipinnate spine and two geniculate setae distally. Endopod two-segmented, not prehensile, longer than exopod; enp-1 about 1.25 times longer than enp-2, with a serrate seta arising from halfway down inner margin and three coarse spinules along outer margin; enp-2 without spinules, distal margin with naked outer spine and geniculate inner seta.

P2–P4 (Fig. 4B–D). Intercoxal sclerites rectangular (P2) or squarish (P3–P4) with concave ventral margins. Praecoxae triangular, small and naked. Coxae squarish and without ornamentation. Bases smaller than coxae, with a spinular row near base of endopod (P3–P4) and a few spinules around outer corner in P2 and P4; anterior surface with a pore; outer basal seta absent in P2, long and plumose in P3–P4. Exopods three-segmented; segments with

coarse spinular ornamentation, as illustrated; outer spine of exp-1 and -2 naked (except for P3 exp-2 sparsely unipinnate); exp-3 with an outer unipinnate spine, and two setae distally (one unipinnate and one bipinnate in P2–P3 or two bipinnate setae in P4); P4 exp-2 elongate, distinctly longer than exp-1; inner seta of P4 exp-3 serrate in distal half and originating near distal margin from posterior surface. Endopods two-segmented; P2–P4 enp-1 unarmed, about 1.1, 1.6, and 4.1 times longer than their respective distal segments, with few coarse spinules along outer margin as figured, but without ornamentation along inner margin (except for single minute spinule near inner distal corner of P4 enp-1); P2 enp-2 with long, apically serrate, backwardly directed seta near proximal margin and two unequal unipinnate setae around distal margin, with two spinules along outer margin subdistally and with one spinule at inner distal corner; P3 enp-2 with three coarse spinules on anterior surface, apical margin with long, unipinnate, inner seta and short, naked, outer spine; P4 enp-2 with a spinule halfway along outer margin, apical margin with long, distally serrate and basally fused, inner seta, and long, unipinnate, outer seta. 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. 5A) closely set together, almost touching medially. Baseoendopod and exopod fused, forming a subrectangular plate; anterior surface with two pores; inner distal corner with strong, minutely bipinnate, spinous process (homologous to inner spine); distal margin with plumose outer basal seta, one long, naked seta, and two short, equally long, bipinnate spines.

Redescription of male. Total body length from tip of rostrum to posterior margin of caudal rami 336 μm (mean = 325 μm ; $n = 6$). Maximum body width 31 μm (mean = 32 μm ; $n = 6$), measured at posterior margin of cephalothorax. Body ornamentation (Fig. 2A) essentially as in female. Sexual dimorphism in antennule, genital segmentation, P5, and P6. Spermatophore length approximately 53 μm .

Antennule (Fig. 3B) 8-segmented, haplocer; geniculation between segments 6 and 7. Segment 1 with a slender naked seta; segment 2 longest and about 3.6 times longer than wide, with one plumose and seven naked setae; segment 3 with four setae and a spine; segment 4 an incomplete sclerite with two spiniform elements; segment 5 with six setae and a long aesthetasc (50 μm) fused basally to a slender seta; segments 6 and 7 with a seta; distal segment with seven setae (three of which spatulate and indicated by arrows in Fig. 3B) and apical acrothek consisting of short aesthetasc (12 μm) fused basally to two slender setae. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4 + 2 spines], 4-[2 spines], 5-[6 + (1 + ae)], 6-[1], 7-[1], 8-[7 + acrothek].

P5 (Fig. 5B) with armature as in female but inner spinous process slightly more slender.

Sixth legs (Fig. 5B) asymmetrical, with smallest P6 closing off functional gonopore; each with a long outer seta and a short inner spine, both elements naked.

Remarks. Kunz (1971) treated *A. longiremis* and *A. accraensis* as subspecies of *A. acantha*. Bodin (1976) adopted the division of *A. acantha* in three subspecies but reinstated *N. longiremis* in later editions of his catalogue (Bodin 1979, 1988, 1997). Kunz's (1971) subspecific classification was rejected by later revisers (Itô 1978; Bodiou & Colomines 1986; Wells 2007; Sak *et al.* 2008) who treated all three subspecific taxa as valid species. Within the *acanthus*-subgroup, *N. acanthus* differs from *N. chaufriassei* primarily in the proportional lengths of the endopodal segments of P1–P3 (enp-1:enp-2 length ratio 1.25, 1.20, 1.65 vs 1.65, 0.90, 1.20, respectively), the length and appearance of the inner subdistal seta on P4 exp-3, and the morphology of the P5 in both sexes. *Neoleptastacus huysi* is morphologically very close to its Mediterranean congener, *N. acanthus*, sharing the shape of the paired anal processes, the elongate P4 exp-2 (about 1.3 times the length of exp-1) and the morphology of P5. The only difference that distinguishes both species is the presence of only one outer spine on P1 exp-3 in *N. huysi*, raising the suspicion that the holotype female (and only known specimen) of the latter species was based on an aberrant or damaged individual.

Neoleptastacus acanthus has been recorded on multiple occasions in the Indian Ocean and the North and Southern Atlantic. Unfortunately, most of these records are not accompanied by illustrations which could have confirmed their authenticity. The species is widely distributed in the Western Mediterranean basin. Chappuis (1954)

and Delamare Deboutteville (1953a–c, 1960) recorded it from Italy (Lazio, Fregene), Algeria (El Kala = La Calle; Skikda = Philippeville; Jijel = Djidjelli; Beni Saf; Terga = Plage Turgot; Mers el Hadjad = Port aux Poules) and Tunisia (Gamarth-Plage, Rass Salakta). Reliable Italian records are those from near Cagliari (Cottarelli 1975) and Isola Tavolara (Cottarelli & Venanzetti 1989) in Sardinia, from Sperlonga in Lazio (Cottarelli 1969; 1971; Cottarelli *et al.* 1994), and from two localities (Tombolo della Giannella, Marina di Alberese) near Porto S. Stefano in Tuscany (Cottarelli 1973b). Martínez Arbizu & Moura (1994) published the only record from Spain (Valencia, El Saler).

Records from the Eastern Mediterranean include those from Elafonisi Beach and Pahia Ammos on the island of Crete, Greece (Sevastou 2005; Sevastou *et al.* 2011) and from the Datça-Bozburun peninsula (Muğla Province) (Sak 2004; Alper 2009; Alper *et al.* 2010; present account) and Dilek peninsula (Aydın Province) (Alper *et al.* 2015) in Türkiye. Masry's (1970) records from Nahariyya and Akhziv in Israel are the only published outliers in the Levantine Sea but note that his setal formula of P1 endopod and P4 exopod contradicts his illustrations, and that his report of an outer basal seta on P1–P2 is most probably false. The great variability alluded to by some authors (*e.g.* Karanovic 2000) has not yet been established as genuine.

Božić's (1967: 873, Fig. 3-3, 4) record from the Indian west coast (locality unknown but possibly Kerala) conceivably refers to *N. indicus* or a related species (see below). His illustrations of the female P5 and the anal somite including the caudal rami in dorsal aspect are of no use in deciding the identity of his material. Božić (1967) stated that the body length is about 400 µm and that the number of eggs in the egg-sac ranges between one and four. Munro *et al.* (1978) also reported "*Arenopontia acantha*" as one of the most abundant harpacticoids in the sandy beach of Cherthala (formerly Shertallai) in Kerala, India.

Lindgren's (1972, 1976) records from the beaches at Bogue Sound and Iron Steamer Pier, North Carolina (U.S.A.) are not accompanied by illustrations and are more likely based on the geographically close *N. gussoae*. Various South African workers (*e.g.* McLachlan 1980; Fricke *et al.* 1981; Hennig *et al.* 1983) have reported "*Arenopontia acantha*" in significant numbers in several beaches from around Cape Town in the west to Port Elizabeth and Algoa Bay in the east (Western Cape Province). It is highly likely that these authors were dealing with a different member of the *acanthus*-group which is probably conspecific with the species recorded as *Arenopontia* sp. from Algoa Bay (McLachlan & Furstenberg 1977). Wandeness (1998) recorded *N. acanthus* from a sandy beach in the Macaé region in Rio de Janeiro State, Brazil, but it is conceivable that this geographically disjunct record is also based on a different species.

***Neoleptastacus longiremis* (Chappuis, 1955)**

Arenopontia longiremis Chappuis, 1955

Arenopontia (*Neoleptastacus*) *longiremis* Chappuis, 1955: Wells (1967: 324)

Arenopontia (*Neoleptastacus*) *acantha longiremis* Chappuis, 1955: Kunz (1971: 356)

Neoleptastacus longiremis (Chappuis, 1955) Sak *et al.* (2008: 412)

Original description. Chappuis (1955): 54–55; Figs 38–47.

Additional description. Wells (1967): 326–327; Text-Fig. 66M–P.

Type locality. Madagascar, Toamasina Province (east coast), Ambila Lemaitso; sandy beach; muddy fine sand near high-tide mark.

Body length. 390 µm (♀ and ♂) [Chappuis 1955].

Remarks. The linear egg-sac contains three eggs (Chappuis 1955). The sexual dimorphism in shape and form of the P5 is remarkable but was not commented upon by Chappuis (1955). The fifth legs not only differ profoundly in general shape between both sexes but also in the relative length of the setal elements. Since such dimorphism has not been recorded elsewhere in the Arenopontiidae, it calls for confirmation whether the females and males recorded from Madagascar belong to the same species. Chappuis (1955) reported "quelques males et femelles" but did not expressly designate a holotype or syntypes. According to ICZN Art. 72.1.1, in the absence of such (or subsequent) designation, all specimens examined by Chappuis are syntypes and collectively constitute the name-bearing type. Since no name-bearing type specimen is believed to be extant or traceable we consider it desirable at present to designate such a specimen to define the nominal taxon objectively in the likely event that females and males attributed to *N. longiremis* turn out to be non-conspecific. Consequently, we here designate the male specimen illustrated in Chappuis (1955: Figs 41–43, 46–47) as the lectotype selected from the specimens that Chappuis had at his disposal in accordance with ICZN Art. 74.4.

The only potentially reliable records outside Madagascar are by Chappuis (1955) who recorded a single male from Anjouan (Comoro Islands) and by Wells (1967) who distinguished two varieties in littoral material from Ilha dos Portuguesos and Inhaca Island (Ponta Torres) in Mozambique. The long variety has an elongate caudal ramus resembling the type material, the short variety has a much shorter caudal ramus, more like that of *N. acanthus*. Re-examination of this material is required before these forms can be attributed with confidence to *N. longiremis* or, alternatively and more likely, be considered closely related sympatric species. It is noteworthy that the paired anal processes are laterally displaced and distinctly straight in Chappuis's types but dorsally recurved in the Inhaca material [J.B.J. Wells, pers. comm. in Itô (1978)]. The validity of Chappuis & Delamare Deboutteville's (1956) record from North Bimini (Sharktown beach) in the Bahamas (see also Renaud-Debyser 1963) was rightly questioned by Lang (1965), and Rouch's (1962) record from Mar del Plata in Argentina is probably equally unreliable. Chappuis & Rouch's (1961) material from Ghana belongs to *N. accraensis* (Lang 1965) which is treated here as a *species inquirenda* (see below). Rao (1980) listed "*Arenopontia longiremis* Chappuis ?" in his list of interstitial meiofauna species of the Andaman and Nicobar Islands but it is likely that this material refers to atypical populations of *N. indicus* (cf. Wells & Rao 1987: 165).

Although Wells (1967) advocated a close relationship between *N. acanthus* and *N. longiremis*, it is clear that the latter belongs to a different subgroup that unites at least seven closely related species characterized by the presence of only one distal element on P3 enp-2 (Table 2). Within this *gussoae*-subgroup, *N. longiremis* shares with *N. rectus* **sp. nov.** the straight outline of the backwardly directed paired spinous processes on the anal somite but can be differentiated from this species by (1) the shorter P1 endopod (enp/exp length ratio 1.15 vs 1.30) and (2) the length/maximum width ratio of the female (3.0 vs 1.7) and male (3.5 vs 2.25) P5.

***Neoleptastacus africanus* (Chappuis & Rouch, 1961)**

Arenopontia africana Chappuis & Rouch, 1961

Arenopontia (*Neoleptastacus*) *africana* Chappuis & Rouch, 1961: Wells (1967: 324)

Arenopontia (*Neoleptastacus*) *africana* f. *africana* Chappuis & Rouch, 1961: Kunz (1971: 358)

Neoleptastacus africanus (Chappuis & Rouch, 1961) Sak *et al.* (2008: 412)

Original description. Chappuis & Rouch (1961): 606–607; Figs 1–8.

Type locality. Ghana, Greater Accra Region, Accra; in front of lighthouse.

Body length. 380 µm (♀); unknown for ♂.

Remarks. *Neoleptastacus africanus* belongs to the *trisetosus*-group based on (1) P1 exp-1 without outer spine, (2) distal segment (exp-3, or exp-2 when exopod 2-segmented) with only one outer spine, (3) P2 exp-2 with very long outer setiform element (extending far beyond distal margin of exp-3), (4) P2–P3 endopods 1-segmented with reduced armature (010), and (5) outer seta of P4 enp-2 reduced. Within this group it is morphologically most similar to its geographically closest member, *N. angolensis* **comb. nov.**, with which it shares the 3-segmented condition of the P1 exopod, a distinctly elongate P4 exopod, the reduced armature on the fifth legs, and the presence of a middorsal process on the anal operculum. Kunz (1971) listed seven differences between *N. africanus* and *N. angolensis* **comb. nov.** but at least five of them appear unreliable or incorrect, e.g. (1) Kunz (1971) claimed that the outer spine on P1 exp-1 is present in *N. africanus* but the short outer element figured by Chappuis & Rouch (1961) appears too small to be a genuine spine (when present, its size invariably approaches that of the outer spines on exp-3) and is interpreted here as a spinule (as found in the same position in other species of the genus); (2) according to Kunz (1971), P4 enp-2 has only one seta but Chappuis & Rouch (1961) clearly stated (and illustrated) that the long distal seta is accompanied by "... une fine soie au bord externe"; (3) the difference related to the antennary exopod (represented by seta vs unisetose segment) is ambiguous because Chappuis & Rouch (1961) were not explicit about its condition ("Exopodite de l'antenne II, une soie courte et mince"; and (4) the pinnules bordering the anal operculum in *N. africanus* are not part of the opercular ornamentation but a misinterpretation of the underlying incised anal frill. Both species require thorough redescription but can be distinguished at present by the shape/curvature of the P5 and caudal rami. The number of spiniform armature elements on the P5 is reduced in both species, being one in *N. angolensis* **comb. nov.** and none in *N. africanus*. The species is known only from the type locality.

Neoleptastacus indicus (Rao, 1967)

Arenopontia indica Rao, 1967

Arenopontia (*Neoleptastacus*) *indica* Rao, 1967: Itô (1978: 52), Bodin (1979: 124)

Arenopontia (*Neoleptastacus*) *sakagamii* Itô, 1978: Wells & Rao (1987: 163)

Neoleptastacus indicus (Rao, 1967) Sak *et al.* (2008: 412)

Original description. Rao (1967): 129–131, Figs 1 and 2(1) [adults]; 131–136, Figs 2(2–7) and 3 [developmental stages].

Additional descriptions. Itô (1978—as *A. (N.) sakagamii*): 47–55; Figs 1–4; Table 1. Wells & Rao (1987): 163–165; Figs 132–133; Table 9. Rao (1989a): 64–65.

Type locality. India, Andhra Pradesh, Vishakhapatnam (= Waltair), Palm Beach; intertidal zone; salinity 24–34‰.

Body length. 560–600 µm (♀), 540–580 µm (♂) [Rao 1967]; 450–480 µm (♀), 430–470 µm (♂) [Itô 1978]; 380–600 µm (♀) [Wells & Rao 1987]; 520–560 µm (sex not specified) [Rao 1989a, 1991]; 520–540 µm (sex not specified) [Rao 1993].

TABLE 3. Records of *Neoleptastacus indicus* (Rao, 1967) from Indian archipelagos.

Archipelago	Island	Locality	References
Lakshadweep		Agatti	Rao & Misra (1983), Rao (1991)
		Amini	Rao (1991)
		Androth	Rao & Misra (1983)
		Kavaratti	Rao & Misra (1983), Rao (1991)
Andaman Islands	Middle Andaman	Rangat Bay	Rao (1975), Wells & Rao (1987)
		Chiriatapu	Rao (1975), Wells & Rao (1987)
		Rutland	Rao (1987)
	South Andaman	Wandur	Rao (1975)
		Port Blair	Rao (1989b)
		Kodiyaghat	Jayabarathi <i>et al.</i> (2012)
		Little Andaman	Harmindar Bay
Nicobar Islands	Car Nicobar Island	South Bay	Rao (1993)
		Hut Bay	Rao (1975), Wells & Rao (1987)
		[locality not specified]	Rao (1980)
		East Point	Rao (1975)
		Sawai Bay	Wells & Rao (1987)

Remarks. Rao (1967) showed two setae on the antennary exopod of *N. indicus*, a character he claimed to be already expressed at copepodid I stage. A similar condition was reported by Cottarelli (1973a: Fig. 14) for the closely related *N. gussoae* (Cottarelli, 1973a). Both reports are based on observational errors since the shorter outer element is a mere extension of the distal corner of the segment and can be variable in length among members of the genus. Wells & Rao (1987) and Rao (1989a, 1991) noted that the spur illustrated by Rao (1967) on the outer lateral surface of the caudal ramus [and which was considered potentially homologous with seta I by Itô (1978)] in reality arises from the medial surface [as already suspected by Mielke (1987: 334)]. Unfortunately, Wells & Rao (1987) also introduced an error with regard to the P1 which was described (*cf.* setal formula) and illustrated (their Fig. 133a) with two geniculate setae and one spine on enp-2. Similarly, they illustrated the inner apical seta of P4 enp-2 as distinctly shorter than the outer apical one (their Fig. 133d) while it is consistently longer in all other members of the *gussoae*-subgroup.

Cottarelli (1973a) discussed the close relationship between *N. indicus* and *N. gussoae*, pointing out differences in mandibular palp segmentation, abdominal hyaline frill structure, morphology of P5 and caudal ramus, number

of eggs contained in the egg-sac, and body length. Itô (1978) expanded the discussion on the *gussoae*-complex by including *N. longiremis* and a new species—originally described as *Arenopontia* (*Neoleptastacus*) *sakagami* Itô, 1978—from Kita Harbour on Hahajima in the Bonin Islands (= Ogasawara Gunto), Japan. He maintained all four species as distinct taxa based on a comparison of five characters: (1) caudal ramus with/without medial spur, (2) anal spinous processes straight/recurved, (3) P5 inner spinous process naked/bipinnate, (4) P6 ♂ with two setae/one seta and one spine, and (5) sixth pair of legs in ♂ forming a common plate/separated opercula. Itô's (1978) type material of *A. (N.) sakagami* lacks the spur on the caudal rami and displays recurved anal processes, a naked spinous process on P5 of both sexes, and separated male sixth legs bearing two setae each.

TABLE 4. Distribution and morphological characteristics displayed by members of the *gussoae*-subgroup (excluding *N. emendatus* and *N. longiremis*); L = length, W = width.

	<i>N. indicus</i>	<i>N. gussoae</i>	<i>N. rectus</i>	<i>N. abbreviatus</i>	<i>N. chilensis</i>	uncertain status	uncertain status	uncertain status
Previous identification	<i>N. indicus</i> [Rao 1967]	<i>N. gussoae</i> [Cottarelli 1973a]	<i>N. ? gussoae sensu</i> Mielke (1982b)	<i>N. ? gussoae sensu</i> Mielke (1982b)	<i>N. ? gussoae sensu</i> Mielke (1987)—normal form	<i>N. ? gussoae sensu</i> Mielke (1982b)	<i>N. ? gussoae sensu</i> Mielke (1982b)	<i>N. ? gussoae sensu</i> Mielke (1987)—2 nd form
Distribution	India (incl. Lakshadweep, Andaman and Nicobar Islands), Japan	Cuba	Panamá, Atlantic coast (Isla Nalunega)	Panamá, Pacific coast (Isla Melones)	Chile (Antofagasta, Coquimbo, Iquique)	Panamá, Pacific coast (Playa Nueva Gorgona)	Panamá, Pacific coast (Playa Avenida Balboa)	Chile (Coquimbo, Iquique)
Body size (µm)	560–600 (♀) ^a 540–580 (♂) ^a	317 (♀) 281 (♂)	360–380 (♀) 310–330 (♂)	360–400 (♀) 350–360 (♂)	290–410 (♀) ^b 270–400 (♂) ^b	360 (♀) 300 (♂)	320 (♀) unknown (♂)	unknown
P1 enp:exp ^c	1.25	1.30	1.30	0.85	1.00	unknown	unknown	unknown
P1 enp-1: enp-2	1.65	1.25	1.45	1.45	1.25	unknown	unknown	unknown
P5 ♀ L:max W	2.7	2.0	1.7	2.6	2.4	unknown	unknown	unknown
Anal processes	recurved	recurved	straight	recurved	recurved	recurved	unknown	virtually straight
Caudal ramus spinous process ^d	55% not recurved ^c	45% recurved	45% not recurved	45–50% recurved	35% recurved	45% recurved	unknown	50% not recurved

^a Based on Rao (1967). Measurements provided by other authors: 450–480 µm (♀), 430–470 µm (♂) [Itô 1978]; 520–560 µm (sex not specified) [Rao 1989a, 1991]; 520–540 µm (sex not specified) [Rao 1993]. The broad size range reported for females (380–600 µm) by Wells & Rao (1987) is likely a reflection of the presence of potentially sympatric cryptic species in their collections.

^b Mielke (1987) gave measurements for individual populations: (1) Antofagasta: 320–380 µm (♀), 270–360 µm (♂); (2) Coquimbo: 340–410 µm (♀), 320–390 µm (♂); (3) Iquique (Playa Cavancha): 290–340 µm (♀), 270–300 µm (♂); and (4) Iquique (Playa Brava): 350–410 µm (♀), 340–400 µm (♂).

^c Length of rami calculated as sum of segment lengths.

^d Ratio of spinous process length (measured from tip to insertion of seta V) to caudal ramus length (measured in lateral aspect along ventral curvature). Shape of distal half of process as viewed in lateral aspect.

^e Based on Rao (1967) and Wells & Rao (1987—but not their Fig. 132h which represents a different species).

Wells & Rao (1987) compared their material of *N. indicus* from the Andaman Islands (Middle Andaman, South Andaman and Little Andaman) and Car Nicobar Island with the types from Vishakhapatnam (= Waltair) and found the same range of variability in both sets of specimens (see their Table 9). As a result of their comparative study, they concluded that the different “setation” of the antennary exopod was the only diagnostic difference separating *N. indicus* and *N. sakagamii*, and consequently sank the latter as a junior subjective synonym of the former. However, Mielke’s (1982b, 1987) detailed studies of the *gussoae*-“Verwandtschaftskreis” in Central and South America suggest that the extensive interspecific variability of *N. indicus* documented so far should be re-evaluated before Wells & Rao’s (1987) conclusions can be accepted. In particular the variability observed in body length and caudal ramus morphology, including the ratio of length of the terminal process to the basal portion of the ramus (1.88–2.21:1) and degree of curvature of the former, may be indicative for the existence of potentially sympatric cryptic species and calls for examination of a larger number of individuals from Andhra Pradesh and the Andaman Islands. Other sources of variability are the shape and ornamentation of the inner spinous process on P5, the shape of the inner element on the male P6 and curvature of the paired spinous processes on the anal somite. *Neoleptastacus indicus* differs from other members of the *gussoae*-subgroup by the relative lengths of the endopodal segments of P1 (enp-1:enp-2 = 1.65 vs 1.25–1.45), the elongate female P5 (length:maximum width 2.7) and caudal ramus process (55% of ramus length) (Table 4). The body size given by Rao (1967) is significantly larger than that reported for its congeners in this subgroup (Table 4).

Rao (1967) recorded highest densities near half-tide level, with a preference for medium particle size 300–500 µm. Breeding shows a peak in summer and the species appears to feed on detritus, bacteria and diatoms. The egg-sac contains 5–9 eggs (36–42 µm in diameter) arranged in one or two rows. Rao (1967) described six naupliar and six copepodid stages and noted that development under laboratory conditions was completed in about 25–30 days (the naupliar phase takes about 10–12 days). Sex differentiation is possible from copepodid IV onwards. The serrate setae on P2 enp-2, P4 exp-3 and P4 enp-2 first appear as spindle-shaped elements in copepodid V. The species occurs in very high numbers (> 12,000 ind.10 cm⁻²) in sandy beaches of the Chennai coast (Mantha *et al.* 2012).

In addition to the type locality (Rao 1967, 1973; Rao & Clausen 1970), the coasts of Odisha (formerly Orissa) (Rao 1970, 1989a; Nagabhushanam 1972; Pati *et al.* 2009) and Chennai (Mantha *et al.* 2012), and Manamelkudi in Palk Bay (Sugumaran & Padmasai 2019), all located on mainland India, *N. indicus* has also been recorded from three archipelagos in the Indian Ocean: Lakshadweep (= Laccadive Archipelago), Andaman Islands and Nicobar Islands (Table 3). Kazmi & Naushaba (2000) claimed to have found *N. indicus* in a sandy beach in Karachi, Pakistan. It is impossible to verify this record since it is based on a single copepodid IV (their Fig. 8). Silva (2006) recorded *A. (N.) indica* as one of the three dominant harpacticoid species of Maracaípe beach in Pernambuco State, Brazil, but this record probably refers to another member of the *acanthus*-group.

***Neoleptastacus ishikarianus* (Itô, 1968)**

Arenopontia ishikariana Itô, 1968

Arenopontia (Neoleptastacus) ishikariana Itô, 1968: Bodin (1979: 124)

Neoleptastacus ishikarianus (Itô, 1968) Sak *et al.* (2008: 412)

Original description. Itô (1968): 274–377; Figs 4–5 [based on small form].

Type locality. Japan, Hokkaido, Sea of Japan coast, Bannaguro, near Ishikari; sandy beach.

Body length. 280 µm (♀), slightly smaller (♂). A larger (♀: 330 µm), morphologically similar form was also recorded.

Remarks. Itô’s (1968) claim (text and illustrations) of an outer basal seta on P1–P2 (always absent in arenopontiids) must be based on observational errors. The discrete nature of the outer distal spine on P3 enp-2 requires confirmation since it is always fused in other members of the *spinicaudatus*-group. Within this group, *N. ishikarianus* is morphologically most similar to *N. pseudishikarianus* **sp. nov.** The latter is proposed here for Mielke’s (1987) Chilean material that was tentatively identified as *A. ? ishikariana*. Both species lack conspicuous plate-like surface ornamentation on the urosomites and the dorsolateral spur (near the origin of seta VII) on the caudal ramus while maintaining the inner seta on P4 exp-3. They can primarily be distinguished from one another by differences in the anal operculum, abdominal hyaline frills, P1 and P5 (see below).

Itô (1968) reported the species from two localities (*locus typicus* and Oshoro, Ranshima) along the Sea of Japan (East Sea) coast of Hokkaido, while Kajihara *et al.* (2015) rediscovered it at Ishikari beach. The species displays a wide horizontal zonation and vertical distribution at the type locality where it is the dominant species, occurring in densities of up to 4,045 individuals per 100 cc sediment (Itô 1984). According to Itô (1968, 1973), the egg-sac contains 2–4 eggs. There are no morphological differences between the two size morphs.

Chertoprud *et al.* (2015) recorded *N. ishikarianus* from estuaries and brackish lagoons on the Kunashir and Iturup Islands in the southern Sea of Okhotsk. The fact that these records came from localities with a reported salinity of 4–6 ‰ casts doubt on their identification.

***Neoleptastacus gussoae* (Cottarelli, 1973a)**

Arenopontia gussoae Cottarelli, 1973a

Arenopontia (*Neoleptastacus*) *gussoae* Cottarelli, 1973a: Bodin (1979: 124)

Neoleptastacus gussoae (Cottarelli, 1973a) Sak *et al.* (2008: 412)

Original description. Cottarelli (1973a): 49–56; Figs 1–21.

Type locality. Cuba, Matanzas Province; north coast, 3 km from Varadero, Playa Arenas Blancas; sandy beach.

Body length. 317 µm (♀), 281 µm (♂).

Remarks. Cottarelli (1973a) claimed that the mandibular palp displays a 2-segmented endopod and used it to differentiate the species from *N. acanthus* and *N. indicus*. Although the endopod has been illustrated as 2-segmented in several contemporary arenopontiid descriptions with the boundary between both segments often ill-defined (*e.g.* Mielke 1982b, 1985, 1987), others have shown it to be clearly 1-segmented (Itô 1978; Mielke 1982a; Wells & Rao 1987; Sak *et al.* 2008, 2024). The validity of the observations of a 2-segmented condition and the usefulness of mandibular endopod segmentation as a species discriminant are questionable since it is generally assumed that this ramus is primitively 1-segmented in the Harpacticoida (Huys & Boxshall 1991). The alleged presence of an outer basal seta on P1–P2 and the absence of an inner basal spine on P1 in the original description are based on observational errors. The linear egg-sac typically contains 3–5 eggs. Species discrimination in the *gussoae*-subgroup is notoriously difficult, however *N. gussoae* can be differentiated from the other two members (*N. abbreviatus* **sp. nov.**, *N. chilensis* **sp. nov.**) that have both the anal processes and terminal extensions of the caudal rami dorsally recurved, by the elongate P1 endopod (1.30 times as long as exopod vs 0.85–1.00) and the shorter and broader female P5 (length/maximum width ratio 2.0 vs 2.4–2.6) (Table 4).

Neoleptastacus gussoae is so far known only from several sandy beaches in the Matanzas Province in Cuba. In addition to the type locality (Cottarelli 1973a), the species was also recorded from the Varadero beach on the Península de Hicacos, and from Playa Sirena of Cayo Largo, a small resort island 80 km south of the Península de Zapata (Mielke 1988).

Mielke (1982b, 1987) provisionally assigned a number of populations from Panamá and Chile to the geographically closest member of the *acanthus*-group, as “*N. ? gussoae*”. In his first report (Mielke 1982b) he recorded the form from both the Atlantic (Comarca de Guna Yala: San Blas Islands, Isla Nalunega) and Pacific (Panamá Province: Isla Melones, Playa Nueva Gorgona and Playa Avenida Balboa) seaboards of Panamá but remained ambiguous in his view on their identity. Although he considered the presence of a *gussoae*-complex of cryptic species in Panamá likely since no variability within the various populations was recorded, the possibility that *N. gussoae* represented a highly variable species was not ruled out. Mielke (1982b) finally stated that a definitive clarification can only be obtained through cross-breeding experiments and that *N. gussoae* is to be considered as an amphi-American species or a species complex that is in the process of splitting. Wells (1986a–b) regarded it as a trans-Panamanian species. This view is not accepted here (see below *N. abbreviatus* **sp. nov.** and *N. rectus* **sp. nov.**).

In contrast to the Panamanian material, considerably more morphological uniformity was found in the widely disjunct populations of the so-called “normal form” (Mielke, 1987) of *N. ? gussoae* along the Chilean coast (Coquimbo, Antofagasta, Iquique). Mielke (1987) distinguished a second form which co-occurs with the “normal form” in at least Coquimbo and Iquique and differs in the wider rostrum, spinulation of the inner spinous process of P5, sharper and not dorsally recurved spinous processes on the anal somite, and absence of a dorsal spur and different insertion site of seta III on the caudal ramus. Breeding experiments are needed to confirm or disprove

the conspecificity of these two co-occurring forms. Except for the anal somite and caudal ramus in lateral aspect, Mielke (1987) did not provide any illustrations of the second form, however, the normal form is here treated as a distinct species, *N. chilensis* **sp. nov.** (see below).

***Neoleptastacus trisetosus* (Mielke, 1982a)**

Arenopontia trisetosa Mielke, 1982a

Pararenopontia trisetosa (Mielke, 1982a) Bodiou & Colomines (1986: 61)

Arenopontia (*Arenopontia*) *trisetosa* Mielke, 1982a: Bodin (1988: 166)

Arenopontia (*Pararenopontia*) *trisetosa* Mielke, 1982a: Bodin (1997: 165)

Neoleptastacus trisetosus (Mielke, 1982a) Sak *et al.* (2008: 412)

Original description. Mielke (1982a): 42–48; Abb. 25–27, 28 (distribution map).

Additional description. Mielke (1982b): 200–201; Fig. 2D.

Type locality. Ecuador, Galápagos, Barrington; strongly exposed sandy beach, north side of island.

Body length. 230–270 µm (♀), 250–260 µm (♂) [Mielke 1982a]; 280–290 µm (♀), 260–280 µm (♂) [Mielke 1982b].

Remarks. Mielke (1982a) reported *N. trisetosus* from a second beach on Barrington and from Puerto Nuñez on Santa Cruz (Galápagos archipelago). The specimens from the latter site differed slightly in the length of the outer spine on P2 exp-2 (Mielke 1982b). Members of the genus *Neoleptastacus* typically display well developed hyaline frills on the abdominal somites which are characteristically incised, forming rectangular or apically rounded lappets. Mielke (1982a) failed to observe such frills in *N. trisetosus* but reported a plain frill on the penultimate somite (his Abb. 27A). The long pectinate seta on P4 enp-2 was described as an articulating element which is possibly based on an observational error since it is typically fused at the base in other members of the genus. The only ovigerous female found by Mielke (1982a) had one egg in the egg-sac but this is most likely due to damage. Mielke (1982b: Fig. 2D) provided a more accurate drawing of the caudal ramus which confirms the presence of coarse spinules near the base of dorsal seta VII (as in *N. supersetosus* **sp. nov.** and possibly *N. panamensis* **sp. nov.**—see below).

Mielke (1982b) reported specimens from two localities along the Pacific side of Panamá which he identified as *N. trisetosus* despite some morphological differences. The Panamanian population is here treated as a discrete species, *N. panamensis* **sp. nov.**, which can be differentiated from *N. trisetosus* by differences in the female genital field, P1, P2, P4 and caudal ramus ornamentation (see below). Both species differ from other members in the genus by the discrete inner spine of the P5 in both sexes (which forms a spinous process in other congeners).

***Neoleptastacus clasingi* (Mielke, 1985)**

Arenopontia clasingi Mielke, 1985

Arenopontia (*Arenopontia*) *clasingi* Mielke, 1985: Bodin (1988: 162)

Neoleptastacus clasingi (Mielke, 1985) Sak *et al.* (2008: 412)

Original description. Mielke (1985): 222–227; Abb. 3B, 26–28.

Additional description. Mielke (1987): 329 [no illustrations].

Type locality. Chile, Los Ríos Region, Valdivia Province, Mehuín (about 60 km north of Valdivia); Playa Universitaria, in front of marine laboratory of UACH (University of Valdivia); dark substratum, grain size 125–250 µm.

Body length. 390–420 µm (♀), 390–410 µm (♂) [Mielke 1985]; 400–440 µm (♀), 410 (♂) (Coquimbo population) and 340–390 µm (♀), 350–400 µm (♂) (Antofagasta population) [Mielke 1987].

Remarks. *Neoleptastacus clasingi* is unique within the *spinicaudatus*-group because of the conspicuous integumental pattern of the abdominal somites, which deceptively appears as surface sculpturing but, in reality, reflects internal longitudinal reinforcements of the body wall. This character, which enhances flexibility of the urosome, evolved convergently in the two known species of the *ornamentus*-subgroup (*N. ornamentus*, *N. reductaspina*). The middle exopodal segment of P4 appears expanded along its transversal axis and the inner and distal elements of the distal segment are swollen proximally. Mielke (1985) recorded a minute middorsal extension (“Nippel”) on the anal operculum.

Mielke (1987) added Chilean records from Las Lozas (south of Coquimbo) and La Rinconada (north of Antofagasta). The species appears therefore to be distributed along the Chilean coast from at least Antofagasta (Antofagasta Region) in the north to Valdivia (Los Ríos Region) in the south (Mielke 1985, 1987). It occurs sympatrically with *N. spicatus* in sandy beaches around Antofagasta and Coquimbo.

Neoleptastacus pacificus (Mielke, 1985)

Arenopontia pacifica Mielke, 1985

Arenopontia (Arenopontia) pacifica Mielke, 1985: Bodin (1988: 162)

Neoleptastacus pacificus (Mielke, 1985) Sak *et al.* (2008: 412)

Original description. Mielke (1985): 209–215; Abb. 3A, 18–21.

Type locality. Chile, Los Lagos Region, Chiloé Province, east coast of Isla de Chiloé, Quellón, beach of Quellón Viejo; primarily coarse sand.

Body length. 340–430 μm (♀), 300–390 μm (♂).

Remarks. *Neoleptastacus pacificus* can readily be differentiated from other members of the *spinicaudatus*-group by (1) the absence of the inner seta on P4 exp-3, (2) the presence of two-three coarse spinules at the dorsal outer corners of the anal somite, either side of the operculum (in the same position as the anal processes in the *acanthus*-group), and (3) an extremely long, spinous, caudal process which is as long as the rest of the ramus (*vs* distinctly shorter) and virtually straight (*vs* typically dorsally recurved). The two spiniform elements on the P5 of both sexes are also larger than those of the other members of the species-group. The multiseriate egg-sac typically contains six eggs.

Mielke (1985) reported the species also from Viña del Mar (Reñaca) in Central Chile (Valparaíso Region) and noted slight variability between the Reñaca and Quellón populations in body size, slenderness of the swimming legs, and in the length of the spines on the P5 of both sexes and the terminal process of the caudal ramus. His claim that the male P6 shows a supernumerary seta (dorsal to the outer basal seta) is extremely unlikely and probably based on a misinterpretation of a different structure such as a sensillum or posterior somite margin.

Neoleptastacus spicatus (Mielke, 1985)

Arenopontia spicata Mielke, 1985

Arenopontia (Arenopontia) spicata Mielke, 1985: Bodin (1988: 162)

Neoleptastacus spicatus (Mielke, 1985) Sak *et al.* (2008: 412)

Original description. Mielke (1985: 216–222; Abb. 3C, 22–25).

Additional description. Mielke (1987): 334–336; Abb. 13A.

Type locality. Chile, Valparaíso Region, Valparaíso Province, Viña del Mar, Playa de Reñaca, about 500 m from Instituto de Oceanología (University of Valparaíso); medium to coarse sand.

Body length. 300–360 μm (♀), 280–310 μm (♂) [Mielke 1985]. 240–260 μm (♀), 240 μm (♂) (Coquimbo, La Herradura population); 300–330 μm (♀), 280–320 μm (♂) (Coquimbo, Las Lozas population); 270–290 μm (♀), 220–270 μm (♀) (Antofagasta population); 310–380 μm (♀), 340–350 μm (♂) (Punta Arenas population) [Mielke 1987].

Remarks. As noted above, *N. spicatus* is morphologically closest to its Australian congener, *N. spinicaudatus*, from which it differs in the shape of the abdominal hyaline frills, the length of the inner distal seta on P2–P3 enp-2, the length:width ratio of the P5 and ornamentation of its apical spinous process.

The species is so far restricted to Chile. In addition to the type locality, Mielke (1985) recorded it also from Isla Maiquillahue (Los Lagos Region), Dichato (Biobío Region) and a second locality in Viña del Mar (Playa los Lilenes). A later paper by Mielke (1987) considerably extended the distribution of *N. spicatus* with records from Antofagasta (Antofagasta Region), Coquimbo (Coquimbo Region) and Punta Arenas (Magallanes and Antártica Chilena Region). The latter record is the southernmost for the family at a distance of over 3,000 km from the type locality of *N. spicatus* where it co-occurs with *N. pacificus*. Some variability was observed in body size (possibly

related to sediment grain size), the size of the spinous process on the caudal ramus, and the relative setal lengths on P2 endopod and P4 exp-3 (Mielke 1987).

Neoleptastacus angolensis (Bodiou & Colomines, 1986) **comb. nov.**

Arenopontia (*Neoleptastacus*) *africana* Chappuis & Rouch, 1961 f. *angolensis* Kunz, 1971

Arenopontia (*Neoleptastacus*) *angolensis* Kunz, 1971—unavailable name attributed to Kunz (1971) by Bodiou & Colomines (1986: 60) [ICZN Art. 45.5.1]

Neoleptastacus angolensis (Kunz, 1971) Sak *et al.* (2008: 412)—unavailable name

Original description. Kunz (1971): 356–358; Abb. 34–42 (♀ only).

Type locality. Angola, Luanda Province, south of Fastaleza (near Luanda); coarse sandy beach, 8 m from low-tide mark, salinity 35‰.

Body length. 290–350 µm (♀).

Remarks. Kunz (1971) distinguished two varieties of *Arenopontia* (*Neoleptastacus*) *africana* Chappuis & Rouch, 1961 (*africana* and *angolensis* n. f.). Bodiou & Colomines (1986), taking a rather pragmatic approach, upgraded *A. (N.) africana* f. *angolensis* to species level as *A. (N.) angolensis* and attributed authorship to Kunz (1971). However, a form, if published after 1960, is deemed to denote infrasubspecific rank and is therefore not regulated by the Code (ICZN Arts 15.2 & 45.6.3). According to ICZN Art. 45.5.1, names of infrasubspecific rank cannot be made available from their original publication by subsequent elevation in rank except by a ruling of the Commission. When a subsequent author applies the same word to a species or subspecies in a manner that makes it an available name, even if authorship of the name is attributed to the author of its publication as an infrasubspecific name, that subsequent author thereby establishes a new name with its own authorship and date. Although Bodiou & Colomines (1986) did not explicitly provide a diagnosis of *A. (N.) angolensis*, they do include the species in an identification key. The characters used in the key, leading to the couplet where *A. (N.) angolensis* keys out, collectively serve as a definition of the taxon which satisfies the provisions of ICZN Art. 13.1.1 and makes the name available. Hence the binomen *A. (N.) angolensis* becomes available from Bodiou & Colomines (1986) and is here treated as a new combination, *Neoleptastacus angolensis* (Bodiou & Colomines, 1986) **comb. nov.** Sak *et al.* (2008) had previously incorrectly attributed this combination to Kunz (1971).

According to Kunz's (1971) setal formula, P2 exp-2 possesses an inner seta on P2 exp-2 which is a unique character in the family (except for the inadequately described *Arenopontia pontica*). However, since Kunz did not illustrate the P2 nor mentioned this character in the text or the table comparing *A. africana* f. *africana* and f. *angolensis* (he does state that the P2 is as in the nominate form apart from the ornamentation of the inner seta on exp-2), we strongly suspect that his report is based on a slip of the pen in his table rather than on an observational error. As pointed out by Mielke (1982a: 45) Kunz's (1971) setal formula for P3 exp-3 should read 021 (not 010). The species is known from the type locality only and its male remains unknown.

Neoleptastacus chaufriassei (Bodiou & Colomines, 1986)

Arenopontia (*Neoleptastacus*) *chaufriassei* Bodiou & Colomines, 1986

Neoleptastacus chaufriassei (Bodiou & Colomines, 1986) Sak *et al.* (2008: 412)

Original description. Bodiou & Colomines (1986): 55–59; Figs 1–2.

Type locality. French Southern and Antarctic Lands (Terres Australes et Antarctiques Françaises), Crozet Islands; Bodiou & Colomines (1986) collected the type material (syntypes in the absence of an explicit designation of a holotype) from two sandy beaches but did not designate the exact type locality: (1) north of Cap Verdoyant on the west coast of Île aux Cochons, and (2) Baie de l'Aventure on the north coast of Île de l'Est. According to ICZN Art. 73.2.3 the type locality encompasses both places where the syntypes were collected.

Body length. 520 µm (♀), 460 µm (♂).

Remarks. *Neoleptastacus chaufriassei* is one of three species in the *acanthus*-group that has retained the plesiomorphic armature pattern on P2–P4, the others being *N. acanthus* and *N. huysi* (Table 2). Although Bodiou &

Colomines (1986) did not explicitly provide the justification for its proposal, the species can readily be distinguished by the unusual armature of the P5 in both sexes. The presence of a single minute dentiform spine (♀) or process (♂) (instead of the usual two spines) located at the distal margin of the P5, between the inner bipinnate spinous process and the outer marginal seta, is unique in the genus. This condition is vaguely reminiscent of that in *N. angolensis* **comb. nov.** (Kunz 1971: Abb. 38) but the relative position of the two marginal elements (one short spine and one seta) in the latter rules out homology (a similar but more derived condition is shown by *N. africanus*; Chappuis & Rouch 1961: Figs 6–7). Convergent evolution in reduced P5 armature has also been postulated for *N. reductaspina* (Mielke 1987: 344, Abb. 18B, C). An additional character that differentiates *N. chaufriassei* from its congeners is the length and ornamentation of the inner subdistal seta of P4 exp-3 which is remarkable short and pinnate, a condition shared only with the unrelated *N. africanus* (Chappuis & Rouch 1961: Fig. 4). In all species for which the P4 exopod was figured (not known for *N. longiremis*) it is much longer and distally serrate which, by comparison with other genera that have retained this seta (*Mesopontia*, *Phreatipontia* **gen. nov.**), appears to be the plesiomorphic condition in the family.

Bodiou & Colomines (1986) do not provide information on the form of the abdominal hyaline frills and their illustration of the caudal ramus is confusing since all seven setae appear to originate from the ventral surface, including seta VII which has a conspicuous swollen section halfway (this “renflement” is more likely a misrepresentation of the foliaceous nature of this seta).

The species is only known from two of the Crozet Islands with no variability recorded between sampling sites. Block (1992) cited an unnamed species of *Arenopontia* in his annotated bibliography of terrestrial and freshwater Antarctic invertebrates but this in reality refers to Bodiou & Colomines’s (1986) description of *A. chaufriassei* from sandy beaches in the Crozet Islands (see also Pugh *et al.* 2002).

Neoleptastacus ornamentus (Mielke, 1987)

Arenopontia ornamenta Mielke, 1987

Arenopontia (*Neoleptastacus*) *ornamenta* Mielke, 1987: Bodin (1988: 163)

Neoleptastacus ornamentus (Mielke, 1987) Sak *et al.* (2008: 412)

Original description. Mielke (1987): 338–342; Abb. 15–17.

Type locality. Chile, Antofagasta Region, Antofagasta Province, 25 km north of Antofagasta, La Rinconada, few km north of La Portada; fine grey-brown sandy beach.

Body length. 300–410 µm (♀), 350–380 µm (♂).

Remarks. *Neoleptastacus ornamentus* and *N. reductaspina* are the only species of the *acanthus*-group that exhibit a conspicuous integumental pattern of elongate rectangular plates on the ventral and dorsal surfaces of the urosomites (except the anal somite). Similar plates have also been reported in a single species, *N. clasingi*, of the *spinicaudatus*-group. Such internal integumental reinforcements interspersed with areas of almost membranous cuticle is an obvious adaptation to life in the interstitial habitat, enhancing flexibility and wriggling ability in the lacunae between the sediment grains. Similar integumental patterns have been observed on the prosome and/or urosome of members of other marine mesopsammic families, including the Leptastacidae (Huys 1992; Huys *et al.* 1996a), Paramesochridae (Huys 1995; Mielke 1987, 1988) and Psammopsyllidae (Mielke 1983; Karaytuğ & Sak 2005).

The species is so far restricted to northern Chile, having been reported from Iquique (Tarapacá Region) and north of Antofagasta (Mielke 1987). It can be differentiated from *N. reductaspina* by differences in P3–P5, anal somite and caudal rami (see below).

Neoleptastacus reductaspina (Mielke, 1987)

Arenopontia reductaspina Mielke, 1987

Arenopontia (*Neoleptastacus*) *reductaspina* Mielke, 1987: Bodin (1988: 163)

Neoleptastacus reductaspina (Mielke, 1987) Sak *et al.* (2008: 412)

Original description. Mielke (1987): 343–344; Abb. 18.

Type locality. Chile, Tarapacá Region, Iquique Province, Iquique, Playa Cavancha; public beach, fine greyish sand.

Body length. 360–380 µm (♀), 360–370 µm (♂).

Remarks. *Neoleptastacus reductaspina* can be distinguished from *P. ornamentus* by (1) P3 enp-1 with only one seta (*vs* two setae), (2) P4 enp-2 outer seta only half the length of inner one (*vs* 3/4 length), (3) P5 of both sexes with only two elements between outer basal seta and inner spinous process (*vs* three elements), (4) shorter caudal ramus, and (5) posterior margin of anal somite without spinules between bases of caudal rami (*vs* with). The species is so far known only from the type locality where it occurs sympatrically with *N. ornamentus* (Mielke 1987).

Neoleptastacus huysi (Karanovic, 2000)

Arenopontia (*Neoleptastacus*) *huysi* Karanovic, 2000

Neoleptastacus huysi (Karanovic, 2000) Sak *et al.* (2008: 412)

Original description. Karanovic (2000): 34–36; Figs 1–13 (♀ only).

Type locality. Montenegro, Ulcinj Municipality, Island of Ada Bojana, near Ulcinj; 41°51'30" N, 19°21'10" E; sandy beach.

Body length. 320 µm (♀).

Remarks. The species has not been recorded again since its original description which was based on a single ovigerous female. The combined presence of an inner seta on P2 enp-2 and two distal elements on P3 enp-2 places *N. huysi* in the *acanthus*-subgroup, together with *N. acanthus* and *N. chaufriassei*. Karanovic (2000) considered the species most closely related to *N. acanthus* but did not provide evidence for this, probably because the latter was conceived at the time as a species that displayed significant variability. *Neoleptastacus huysi* differs from the other two members of the *acanthus*-subgroup by the presence of three elements on P1 exp-3 (instead of four), a condition that is shared with the unrelated *trisetosus*-group (Table 2). Karanovic (2000) described the spatulate caudal ramus seta VII as “aesthetasc-like” and erroneously used it as a character to differentiate *N. huysi* from *N. acanthus*. Some armature elements on the antennule were overlooked on most segments (particularly 1, 2, 3 and 6). The author also stated “Hind margins of all body somites smooth. First, second and third free thoracic somites with a chitinous suture dorsolaterally, which bears a row of very fine spinules”. The spinular rows referred to by Karanovic in reality represent the crenulated hyaline frills on these somites while the strongly developed abdominal frills, consisting of rectangular digitate lappets, were obviously overlooked. The linear egg-sac of the holotype female contained three eggs. The species is potentially conspecific with *N. acanthus* (see above).

Neoleptastacus abbreviatus sp. nov.

<https://zoobank.org/0BABE6B9-3B09-4AA0-838D-2880AAB1DE6D>

Arenopontia ? *gussoae* Cottarelli, 1973a *sensu* Mielke (1982b) [partim: material from Isla Melones, Panamá]

Original description. Mielke (1982b—as *Arenopontia* ? *gussoae*): 202–203; Figs 4A–H, 5, 6A, C, 7A–C).

Type locality. Panamá, Pacific seaboard; Panamá Province, Isla Melones (situated between the mainland and Taboga Island), sandy beach; fine-medium sand with little detritus.

Body length. 360–400 µm (♀), 350–360 µm (♂) [Mielke 1982b].

Etymology. The specific epithet (derived from the Latin *abbreviatus*, past participle of *abbreviare*, meaning to shorten, make brief) refers to the short P1 endopod which is shorter than in any other member of the *gussoae*-subgroup.

Remarks. Mielke (1982b) considered it plausible that his specimens of “*Arenopontia* ? *gussoae*” from Isla Melones represented a distinct species but refrained from formally proposing it. The Panamanian material is characterized by a P1 endopod that is clearly shorter than its corresponding exopod (length ratio 0.85). Within the *gussoae*-subgroup only *N. chilensis* sp. nov. and *N. emendatus* sp. nov. have a comparatively short endopod, being as long as the exopod, while in all other members it is distinctly longer than the exopod (Table 4). Additional

character states that differentiate the Isla Melones form from typical *N. gussoae* include (1) the pointed rostrum, (2) the length ratio between P1 enp-1 and enp-2 (1.45 vs 1.25), (3) the longer female P5 (length/maximum width ratio 2.6 vs 2.0) and (4) the spiniform elements on the female P5 being unequal in length (inner one distinctly shorter than outer one) vs equally long. Mielke (1982b: Fig. 5A) illustrated a fine outer seta on the basis of P1 but this must be an observational error.

The female specimen illustrated by Mielke (1982b: Figs 4A–C, E–H, 5, 6A, 7A–C) and deposited in the Zoologisches Institut und Museum der Universität Göttingen is here designated as the holotype of *N. abbreviatus* **sp. nov.** in accordance with ICZN Arts 16.4, 72.5.6 and 73.1.4. The species can be differentiated by the characters listed above (ICZN Art. 13.1).

***Neoleptastacus chilensis* sp. nov.**

<https://zoobank.org/AA740537-8778-4985-A099-91E5416169BE>

Arenopontia ? *gussoae* Cottarelli, 1973a *sensu* Mielke (1987) [partim: “normal form”]

Original description. Mielke (1987—as *Arenopontia* ? *gussoae*): 330–334; Figs 10–12.

Type locality. Chile, Antofagasta Region, Antofagasta Province, 25 km north of Antofagasta, La Rinconada (few km north of La Portada); fine grey-brown sandy beach.

Body length. 320–380 µm (♀), 270–360 µm (♂) (Antofagasta type population); 340–410 µm (♀), 320–390 µm (♂) (Coquimbo population); 290–340 µm (♀), 270–300 µm (♂) (Iquique, Playa Cavancha population); 350–410 µm (♀), 340–400 µm (♂) (Iquique, Playa Brava population) [Mielke 1987].

Etymology. The specific epithet refers to the geographical place of collection (in this case the country of origin) of the name-bearing type.

Remarks. Mielke (1987) reported several populations of *Arenopontia* ? *gussoae* from northern Chile with most of them belonging to the “normal form”. Some specimens from Coquimbo and Iquique that co-occurred with this form were attributed to a “second form” but were not formally described (see below). The normal form can be differentiated from the type population of *N. gussoae* by (1) the shorter P1 endopod (being as long as the exopod vs distinctly longer), (2) the longer and broader female P5 (length/maximum width ratio 2.4 vs 2.0), (3) the shorter terminal spinous process on the caudal ramus (35% of ramus length vs 45%), and (4) the presence of a conspicuous medial spur near the origin of caudal ramus seta VII. The combination of these characters is regarded here as sufficient evidence to attribute distinct specific status to the normal form. It differs from the “second form” in rostrum shape, spinular ornamentation of the inner spinous process of P5, absence of the medial spur on the caudal ramus, and position of caudal ramus seta III.

The female specimen illustrated by Mielke (1987: Figs 10, 11A–D, 12) and deposited in the Zoologisches Institut und Museum der Universität Göttingen is here designated as the holotype of *N. chilensis* **sp. nov.** in accordance with ICZN Arts 16.4, 72.5.6 and 73.1.4. The species can be differentiated by the characters listed above (ICZN Art. 13.1). Mielke (1987) collected the species from four localities in northern Chile but explicitly indicated that his illustrations were based on specimens from La Rinconada beach which consequently becomes the type locality (ICZN Art. 76.1).

***Neoleptastacus emendatus* sp. nov.**

(Figs 6–8)

<https://zoobank.org/AA0F3DBD-38CC-4B1D-8877-39C901FB6F27>

Arenopontia (*Neoleptastacus*) *acantha accraensis* Lang, 1965 *sensu* Kunz (1971: 354)

Neoleptastacus emendatus—*nomen nudum* by Sak (2004: 211)

Original description. Kunz (1971—as *Arenopontia* (*N.*) *acantha accraensis*): 354–356; Abb. 25–32 (♀ only). Abb. 33 is probably based on a different species.

Type locality. Angola, Luanda Province, south of Fastaleza (near Luanda); coarse sandy beach, 8 m from low-tide mark, salinity 35‰.

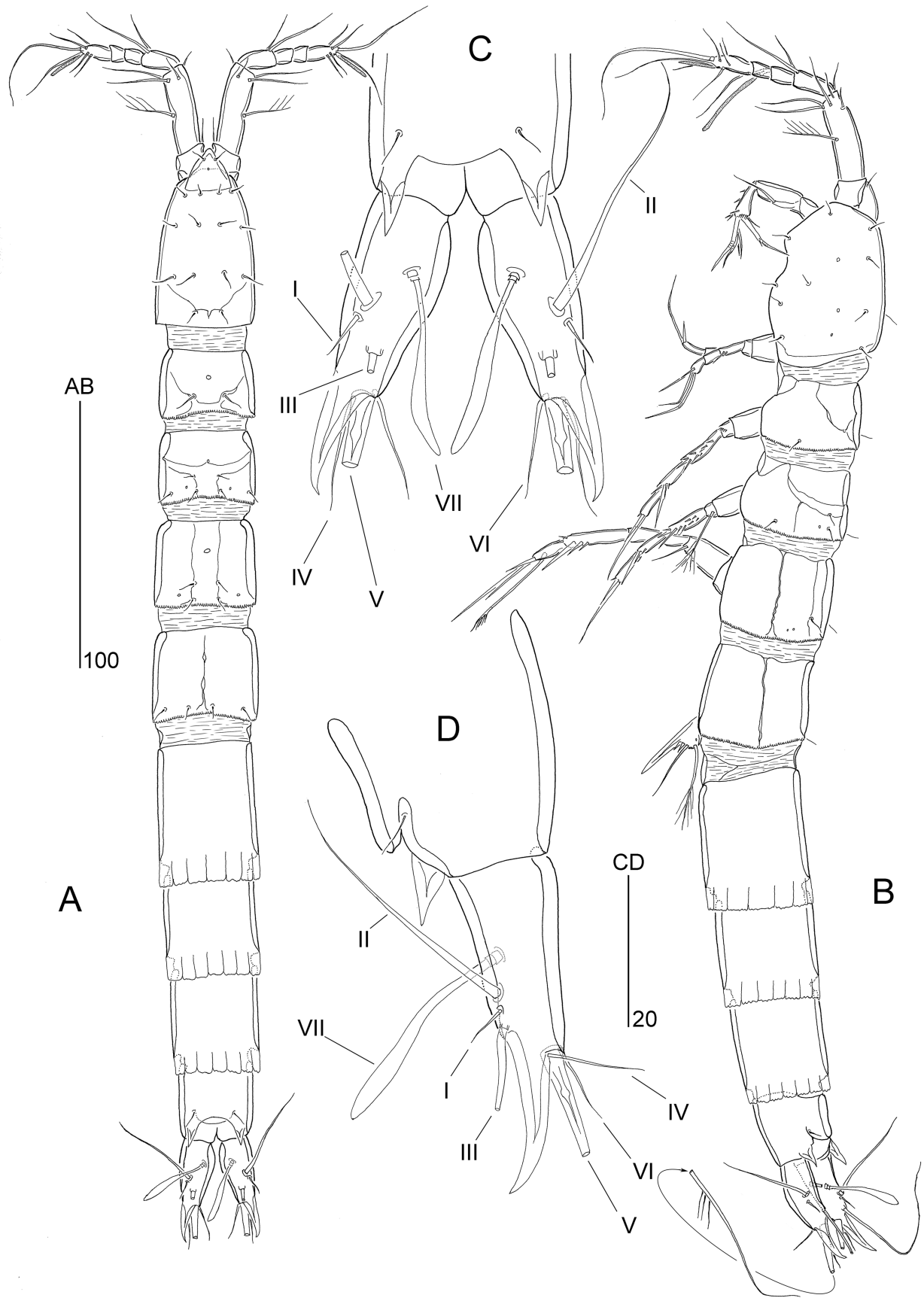


FIGURE 6. *Neoleptastacus emendatus* sp. nov. (♀): (A) habitus, dorsal; (B) habitus, lateral; (C) anal somite and caudal rami, dorsal; (D) anal somite and right caudal ramus, lateral.

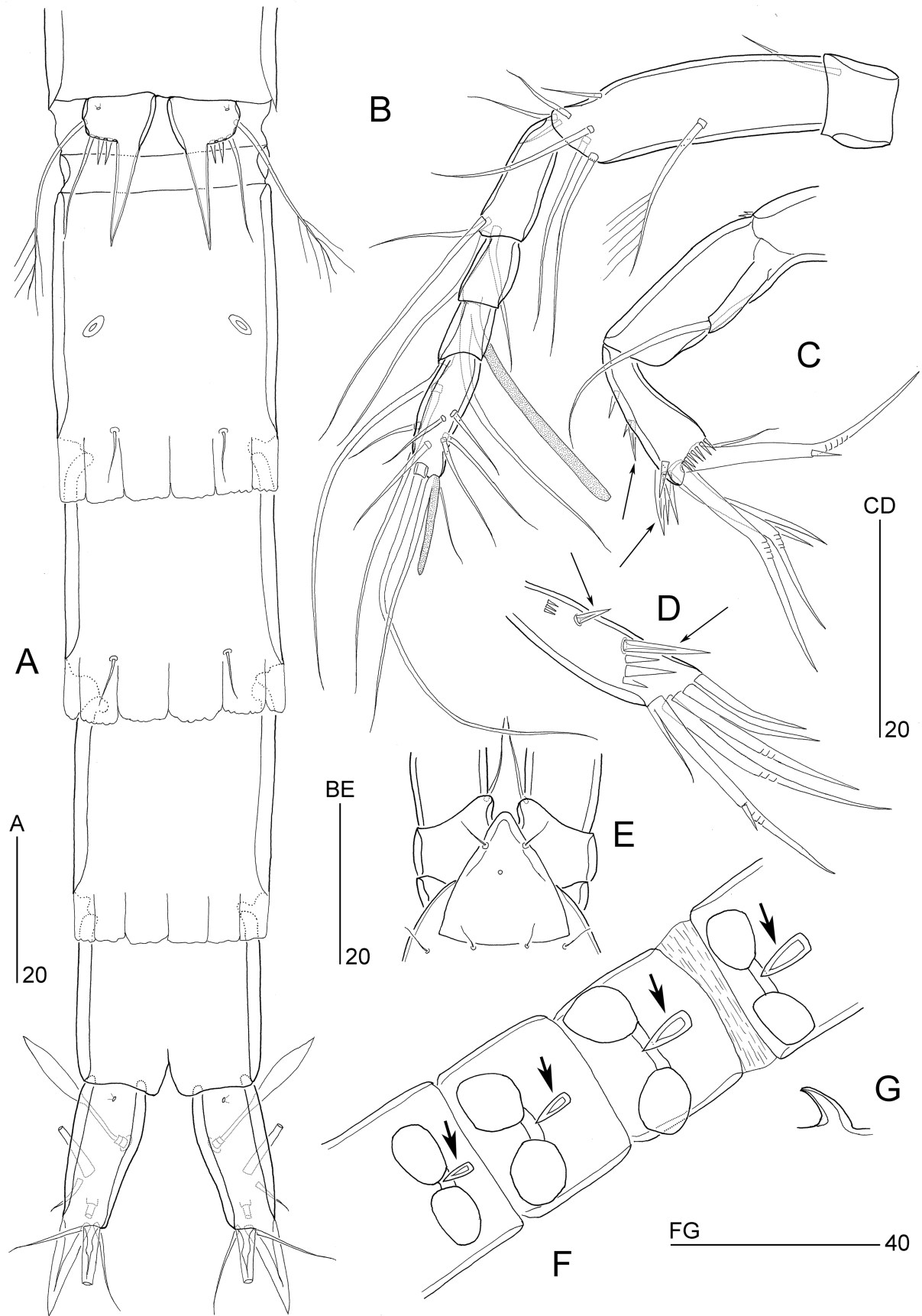


FIGURE 7. *Neoleptastacus emendatus* sp. nov. (♀): (A) urosome, ventral; (B) antennule, dorsal; (C) antenna, outer; (D) antennary endopod, medial; (E) rostrum, dorsal; (F) midventral hook-like processes [indicated by arrows] on pedigerous somites; (G) hook-like process, lateral. [lateral endopodal spines indicated by arrows in C–D]

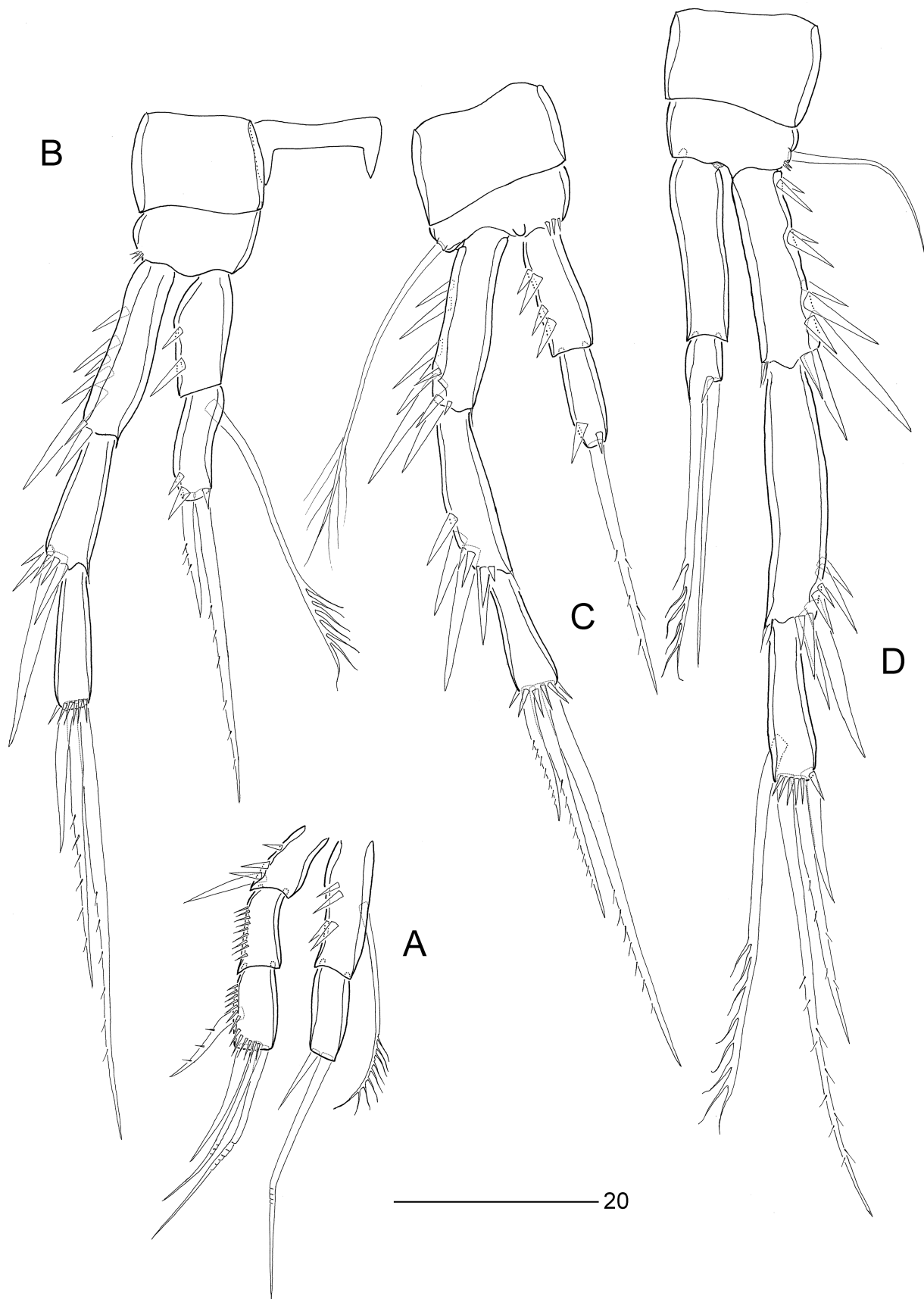


FIGURE 8. *Neoleptastacus emendatus* sp. nov. (♀): (A) P1, anterior; (B) P2, anterior; (C) P3, anterior; (D) P4, anterior.

Type material. Undissected holotype ♀ in alcohol (reg. no NHMUK 2024.1062).

Body length. Not given in Kunz (1971); 390 µm (♀) [present account].

Description of female. Total body length from tip of rostrum to posterior margin of caudal rami 390 µm ($n = 1$). Maximum body width 34 µm, measured near posterior margin of cephalothorax. Body (Fig. 6A, B) slender and cylindrical, without clear distinction between prosome and urosome. Sensillar pattern on body as figured. Hyaline frills of thoracic somites weakly developed and crenulated; those of genital double-somite and free abdominal somites strongly developed and consisting of rectangular lappets with weakly incised free margin (Figs 6A, B; 7A). Integument of cephalothorax and pedigerous somites with internal pattern of ridges. Somites connected by well-developed intersomitic membranes. Cephalothorax and somites bearing P2–P4 with midventral, backwardly directed, spinous process located anterior to intercoxal sclerites of swimming legs 1–4 (Fig. 7F, G).

Genital double-somite about 1.5 times longer than wide (measured in dorsal aspect); with two conspicuous ventrolateral pores (Figs 6A, B; 7A). Anal somite (Figs 6C, D; 7A) with paired, posteriorly directed, spinous processes near posterior border either side of anal opening. Anal frill triradiate, minutely incised.

Caudal rami (Figs 6C, D; 7A) about 3.5 times longer than maximum width (measured in dorsal view from anterior margin to apex of spinous process), only slightly tapering in anterior two-thirds; inner margin expanded medially in anterior third; with a pore near ventral proximal margin (Fig. 7A); outer distal corner produced into posteriorly directed, dorsally recurved spinous process; no spinular ornamentation discernible. Armature consisting of seven setae; seta I small; setae II and III (displaced to dorsal surface) long and naked; seta IV short, naked, located between seta V and posterior spinous process; seta V long, naked, with proximal fracture plane and few long setules at around 1/3 its length (Fig. 6B); seta VI small, naked and located at inner distal corner; seta VII weakly foliaceous and tri-articulate at base.

Rostrum (Fig. 7E) small, subtriangular, tapering distally and rounded apically; with two delicate sensillae and one midventral pore.

Antennule (Fig. 7B) long and slender, 6-segmented. Segment 1 with well developed seta near anterodistal margin. Segment 2 longest, about 3.2 times longer than wide. Segment 4 with long aesthetasc (L: 29 µm) fused at base with seta. Distal segment with eight setae (none of them noticeably spatulate) and apical acrothek consisting of short aesthetasc (L: 10 µm) and two setae. All setal elements naked except for plumose seta on dorsal surface of segment 2. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[8 + acrothek].

Antenna (Fig. 7C, D). Coxa small, without ornamentation (not figured). Basis and proximal endopodal segment forming incompletely fused allobasis, about 3.4 times as long as maximum width; original basis-endopod boundary marked by transverse surface suture at level of exopodal articulation; proximal part representing original basis with few small spinules at distal exopodal corner. Exopod one-segmented, unornamented and elongate, with a long naked apical seta (about twice longer than exopod). Free endopodal segment with few lateral spinules proximally and transverse spinular row distally; medial armature consisting of two short spines (indicated by arrows in Fig. 7C, D); apical armature consisting of two naked spines and three geniculate setae, longest of which with spinule around geniculation and fused basally to naked accessory seta.

Mandible, maxillule, maxilla and maxilliped as in *N. spinicaudatus* (see Sak *et al.* 2008: Figs 16D, E; 17E, F).

P1 (Fig. 8A). Praecoxa, coxa, basis and intercoxal sclerite not observed. Exopod three-segmented; all segments with several spinules around outer margin; exp-1 with outer spine; exp-2 without outer element; exp-3 with unipinnate outer spine, a long naked spine and two geniculate setae distally; distal margin of exp-3 with spinules. Endopod two-segmented, about as long as exopod; enp-1 about 1.6 times longer than enp-2, with a serrate seta arising from halfway down inner margin and two sets of two coarse spinules along outer margin; enp-2 without spinules, distal margin with naked outer spine and geniculate inner seta.

P2–P4 (Fig. 8B–D). Intercoxal sclerite of P2 rectangular with concave ventral margin; not observed in P3–P4. Praecoxae triangular, small and naked (not figured). Coxae broadly rectangular and without ornamentation. Bases smaller than coxae, with few spinules near base of P3 endopod and around outer corner in P2 and P4; anterior surface pore not discerned; outer basal seta absent in P2, long and either plumose (P3) or naked (P4) in remaining legs. Exopods three-segmented; exp-1 and -2 with coarse spinular ornamentation as illustrated; outer spine of exp-1 and -2 naked; exp-3 with an outer unipinnate (P3) or naked (P2, P4) spine, and two unipinnate (P2–P3) or bipinnate (P4) setae apically; P4 exp-2 elongate, distinctly longer than exp-1; inner seta of P4 exp-3 serrate in distal half and originating near distal margin from posterior surface. Endopods two-segmented; P2–P4 enp-1 unarmed, about 1.0, 1.3, and 4.0 times longer than their respective distal segments, with few coarse spinules along outer margin in

P2–P3, but without ornamentation along inner margin; P2 enp-2 with long, apically serrate, backwardly directed seta near proximal margin and two unequal unipinnate setae around distal margin; apical margin of P3 enp-2 with long, sparsely bipinnate seta; apical margin of P4 enp-2 with long, distally serrate and basally fused, inner seta, and long, naked outer seta. Spine and seta formula as follows:

	Exopod	Endopod
P2	0.0.021	0.120
P3	0.0.021	0.010
P4	0.0.121	0.020

Fifth legs (Fig. 7A) closely set together, but not touching in ventral midline. Baseoendopod and exopod fused, forming elongate plate (about 2.3 times as long as maximum width); anterior surface with one pore; inner distal corner with long and straight, unornamented spinous process (homologous to inner spine); distal margin with one naked seta, and two short, equally long, bipinnate spines; outer basal seta plumose.

Male. Unknown.

Etymology. The specific epithet is derived from the Latin *emendatus*, past participle of *emendare*, meaning to correct or improve, and refers to the present redescription which amends Kunz's (1971) original description, leading to the proposal of the new species.

Remarks. Kunz (1971) reported several females from Angola which he attributed to *Arenopontia* (*Neoleptastacus*) *acantha accraensis* Lang, 1965. Our re-examination of the only extant female of Kunz's (1971) original material revealed several differences with Chappuis & Rouch's (1961) type population of *N. accraensis*, warranting the proposal of a new species for the former in the *acanthus*-group. *Neoleptastacus emendatus* **sp. nov.** is so far the only species of the genus that displays strongly developed, median sternal processes on the posterior part of the cephalothorax and on the pedigerous somites bearing P2–P4. The midventral chitinous projections are typically hook-shaped and originate anterior to the intercoxal sclerites of the first four pairs of swimming legs. The function of the processes is unknown but it is conceivable that they enhance the wriggling ability of these tiny copepods in the interstitial habitat. Kunz (1971) observed some variability in the degree of their development and claimed that in some specimens they are replaced altogether by chitinous nodular outgrowths. The significance of the latter observation is difficult to assess because his reported variability in caudal ramus structure and presence/absence of anal processes (compare his Abb. 32–33) almost certainly reflects an amalgam of two species in his sample. The second form illustrated by Kunz (1971) in his Abb. 33 (and underrepresented in his sample) that displays a straight spinous terminal process on the caudal ramus and lacks the paired anal processes does not belong to the *acanthus*-group. Note that Kunz (1971) did not list the inner seta on P1 enp-1 in his setal formula table. The species is so far known from the type locality only.

***Neoleptastacus panamensis* sp. nov.**

<https://zoobank.org/F27ED4EA-EC4C-4238-AB97-8414660E0190>

Arenopontia trisetosa Mielke, 1982a *sensu* Mielke (1982b)

Original description. Mielke (1982b—as *Arenopontia trisetosa*): 200–201; Fig. 2A–C, E.

Type locality. Panamá, Pacific seaboard, Panamá Province. Mielke (1982b) collected his specimens from two sandy beaches west of Panamá City, *i.e.* Playa Nueva Gorgona and Playa Río Mar, but did not specify which site the illustrated female specimen (here designated as the holotype) originated from.

Body length. 280–290 µm (♀), 260–280 µm (♂) [Mielke 1982b].

Etymology. The specific epithet refers to the geographical place of collection (in this case the country of origin) of the name-bearing type.

Remarks. Mielke (1982b) noted several differences between the type population of *N. trisetosus* from the Galápagos (Mielke 1982a) and morphologically similar but not identical specimens from the Pacific seaboard of Panamá. Although he viewed these differences as a reflection of intraspecific variability, we consider them as sufficient evidence to attribute separate specific rank to the Panamanian material. The marked and consistent

difference in female genital field structure may indicate that the Panamanian population is reproductively isolated from the Galápagos one. In the former the copulatory duct [misinterpreted as the seminal receptacle by Mielke (1982b)] is markedly longer than in the Galápagos specimens. Additional morphological differences include (1) proportional lengths and slenderness of P1 segments with enp-1 being comparatively longer in the Galápagos population (enp-1/exp-1 length ratio 1.8 vs 1.25; enp-1:enp-2 length ratio 1.4 vs 1.15; endopod/exopod length ratio 1.3 vs 1.1), (2) the length of the outer spine on P2 exp-2 which is as long as the entire exopod and reaches well beyond the tip of the outer spine of exp-3 in the Panamanian population [vs distinctly shorter than the exopod and not reaching beyond the outer spine of exp-3 although some specimens from Puerto Nuñez on Santa Cruz display a longer spine but not to the same degree according to Mielke (1982b)], (3) the segment representing the P2 endopod is as long as exp-1 and subrectangular in shape and tapers only slightly distal to the insertion of the inner seta (vs shorter than exp-1 and distinctly flask-shaped), and (4) all exopodal segments of P4 are comparatively longer in the Panamanian population (exopod/endopod length ratio 2.6 vs 2.25) and the inner seta on exp-3 inserts more distally (at > 80% of the inner margin length vs 55%).

The female specimen illustrated by Mielke (1982b: Fig. 2B, C, E) and deposited in the Zoologisches Institut und Museum der Universität Göttingen is here designated as the holotype of *N. panamensis* **sp. nov.** in accordance with ICZN Arts 16.4, 72.5.6 and 73.1.4. The species can be differentiated by the characters listed above (ICZN Art. 13.1). Although Mielke (1982b) did not illustrate the caudal ramus of *N. panamensis* **sp. nov.**, it is likely that it resembles the condition shown by him (his Fig. 2D) for *N. trisetosus*, i.e. with coarse spinules around the base of seta VII (as in *N. supersetosus* **sp. nov.** (see below).

***Neoleptastacus pseudishikarianus* sp. nov.**

<https://zoobank.org/71936DF5-742B-48DC-8FA7-C1531885AF72>

Arenopontia ? *ishikariana* Itô, 1968 *sensu* Mielke (1987: 336)

Original description. Mielke (1987—as *Arenopontia* ? *ishikariana*): 335–337; Abb. 13B–E, 14.

Type locality. Chile, Antofagasta Region, Antofagasta Province, 25 km north of Antofagasta, La Rinconada (few km north of La Portada); fine grey-brown sandy beach.

Body length. 270–310 µm (♀), 230–300 µm (♂).

Etymology. The specific epithet refers to the close similarity with *N. ishikarianus*.

Remarks. Mielke (1987) provided a partial description of a *Neoleptastacus* species from northern Chile but expressed reservations about its identity within the *spinicaudatus*-group. Rather than considering them as a new species he tentatively assigned his specimens to *N. ishikarianus*. The South American material differs from the latter in the following characteristics: (1) anal operculum with middorsal rounded projection (vs absent), (2) lappets of abdominal hyaline frills non-digitate and with rounded distal margins (vs digitate with straight margins), (3) P1 rami approximately equal in length (vs endopod distinctly longer than exopod), and (4) P5 with shorter, straight and more robust inner spinous projection (vs longer, slightly curved and slender) and size of marginal spines larger [longest (= outer) spine in ♀ about half the length of spinous process vs about one-quarter]. Mielke (1987) also pointed out that caudal ramus seta III is distinctly longer than in the Japanese specimens but it is unclear if this seta was presented in a foreshortened view in Itô's (1968: Fig. 4-3) illustration. Similarly, Mielke also commented on setal length differences on the P4 endopod but no such discrepancies could be discerned when comparing both descriptions. Based on the differences outlined above, *Arenopontia* ? *ishikariana* Itô, 1968 *sensu* Mielke (1987) is attributed discrete specific rank as *N. pseudishikarianus* **sp. nov.**

The female specimen illustrated by Mielke (1987: Abb. 13B–E; 14 A, B) and most likely deposited in the Zoologisches Institut und Museum der Universität Göttingen is here designated as the holotype of *N. pseudishikarianus* **sp. nov.** in accordance with ICZN Arts 16.4, 72.5.6 and 73.1.4. The species can be differentiated by the characters listed above (ICZN Art. 13.1). Mielke (1987) recorded the species from three different sandy beaches in Arica (Arica and Parinacota Region), Iquique (Tarapacá Region) and La Rinconada (all in northern Chile) but based his illustrations solely on material from the latter which consequently becomes the type locality (ICZN Art. 76.1). At the latter it occurs sympatrically with three members of the *spinicaudatus*-group, *N. clasingi*, *N. ornamenta*, *N. spicata*, in addition to a fourth species tentatively identified as *N. ? gussoae* (= *N. chilensis* **sp. nov.**) (Mielke 1987).

***Neoleptastacus rectus* sp. nov.**

<https://zoobank.org/C916BDF2-CD13-421B-A8C2-8DFDE9D80D9F>

Arenopontia ? *gussoae* Cottarelli, 1973a *sensu* Mielke (1982b) [partim: material from Isla Nalunega, Panamá]

Original description. Mielke (1982b—as *Arenopontia* ? *gussoae*): 204; Figs 4I, 6D, 7D).

Type locality. Panamá, Atlantic seaboard; Comarca de Guna Yala, San Blas Islands, Isla Nalunega; sandy beach, fine-medium sand with medium amount of detritus.

Body length. 360–380 μm (♀), 310–330 μm (♂) [Mielke 1982b].

Etymology. The specific epithet (derived from the Latin *rectus*, meaning straight) refers to the shape of the paired anal processes which are not dorsally recurved as in most other members of the *gussoae*-subgroup (except *N. longiremis*).

Remarks. Mielke (1982b) recorded “*Arenopontia* ? *gussoae*” from both oceanic seaboard of Panamá. His specimens from the Atlantic seaboard are similar to *N. gussoae* in the relative length of the caudal spinous process (45% of ramus length) and the length ratio of the rami of P1 (endopod 1.3 times longer than exopod) but differ from the Cuban population in (1) the paired anal processes are straight and pointed, (2) the caudal ramus is more angular and its terminal process is not recurved in its distal half, (3) P1 enp-1 is 1.45 times longer than enp-2 (*vs* 1.25), and (4) the female P5 is atypically short and broad (length/maximum width 1.7 *vs* at least 2.0 in other members of the *gussoae*-subgroup (Table 4). Mielke (1982b) also mentioned that the rostrum is less tapered towards its apex (compared to *N. abbreviatus* **sp. nov.**) and that the free endopodal segment of the antenna has long hairs on its posterior surface (this feature possibly refers to the endopodal surface frill) but both characters are of limited value for comparing *N. gussoae* with the Isla Nalunega population. Note that Mielke (1982b: Fig. 6D) illustrated a fine outer seta on the basis of P1 but this must be an observational error.

The differences displayed by the Isla Nalunega population are here considered as sufficient evidence to accord it distinct specific rank. The female specimen illustrated by Mielke (1982b: Figs 4I, 6D, 7D) and deposited in the Zoologisches Institut und Museum der Universität Göttingen is here designated as the holotype of *N. rectus* **sp. nov.** in accordance with ICZN Arts 16.4, 72.5.6 and 73.1.4. The species can be differentiated from its congeners in the *gussoae*-subgroup by the characters listed above (ICZN Art. 13.1).

***Neoleptastacus supersetosus* sp. nov.**

(Figs 9–11)

<https://zoobank.org/316E69F8-8817-4599-9126-F24A67BE3579>

Pararenopontia polisetata—*nomen nudum* by Sak (2004: 273)

Type locality. Kuwait, Shuwaikh (29°21'41.8" N, 47°57'19.2" E) mid- and upper tide levels on public recreational beach within Kuwait Bay adjacent to the commercial port, surrounded by extensive urban development. Relatively steeply sloping sandy beach, bounded to seaward by extensive limestone flats.

Type material. Holotype ♀ (dissected on eight slides) (reg. no NHMUK 2024.1063). Paratypes are one ♂ (dissected) and one ♀ and one ♂ preserved in alcohol (reg. nos NHMUK 2024.1064–1066). All specimens were collected from the type locality; leg. S. Livesey and N. O'Brien, 3 June 2004.

Description of female. Total body length from tip of rostrum to posterior margin of caudal rami 225 μm (*n* = 1). Body (Fig. 9A) slender and cylindrical without clear distinction between prosome and urosome. Hyaline frills of thoracic somites weakly developed and smooth; those of genital double-somite and free abdominal somites strongly developed and consisting of rectangular digitate lappets (Figs 9A; 10A; 11C). Somites connected by well-developed intersomitic membranes. Somites bearing P2–P5, genital double-somite and second abdominal somite with internal semicircular reinforcements forming pattern as figured. Genital double-somite (Figs 9A; 10A) about as long as wide (measured in ventral aspect); with two ventral pores in posterior half (Figs 10A).

Anal somite (Fig. 10A; 11C, D) without paired, dorsally recurved, spinous processes; with two sensilla dorsally and few spinules either side of ventral midline. Anal operculum well developed, semicircular, without ornamentation; covering terminally positioned anal opening. Anal frill triradiate, distinctly incised (giving a spinulose appearance underneath anal operculum).

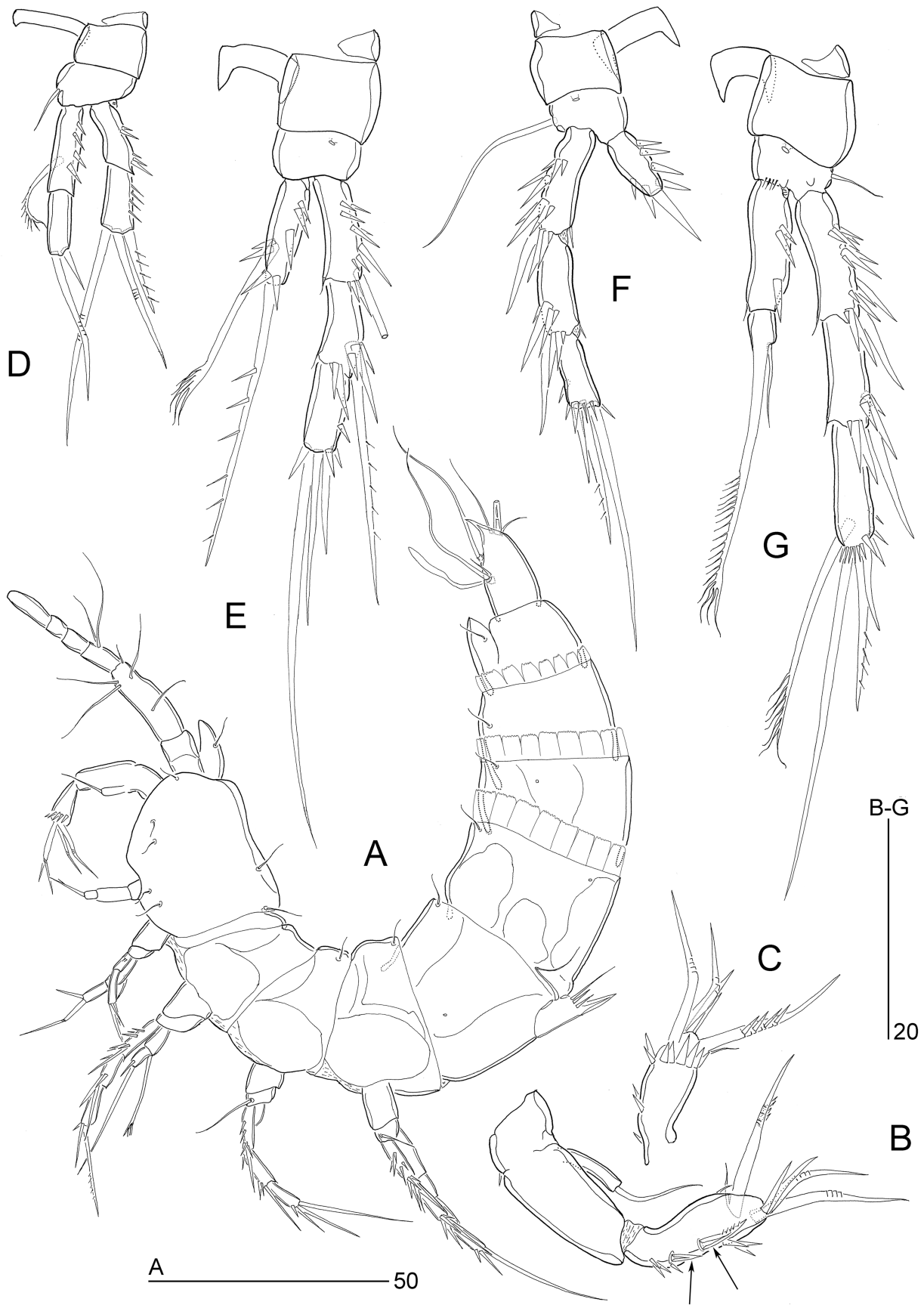


FIGURE 9. *Neoleptastacus supersetosus* sp. nov. (♀): (A) habitus, lateral; (B) antenna, medial [lateral endopodal spines indicated by arrows]; (C) antennary endopod, outer [lateral spines omitted]; (D) P1, anterior; (E) P2, anterior [outer spine of exp-1 broken]; (F) P3, anterior; (G) P4, anterior.

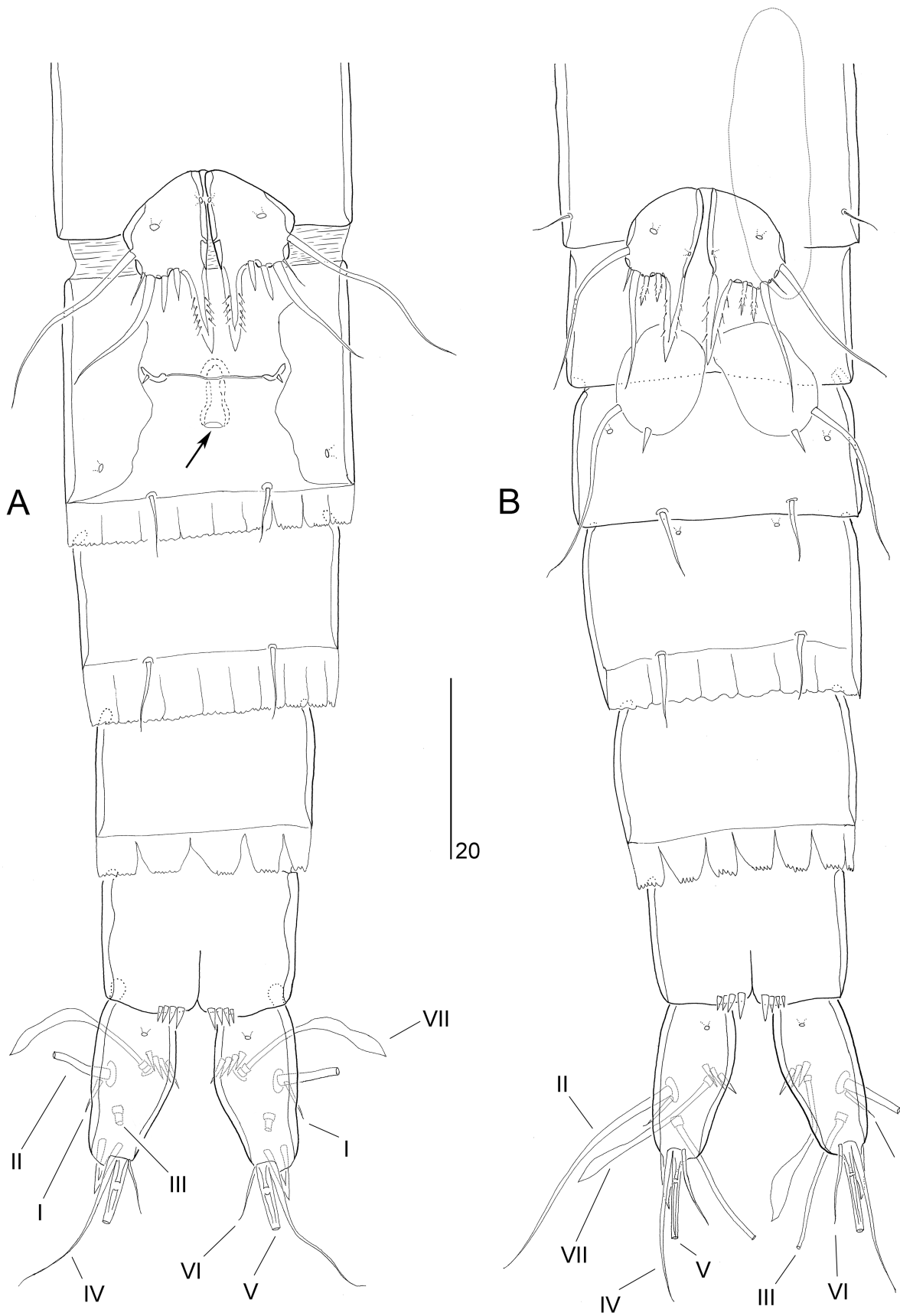


FIGURE 10. *Neoleptastacus supersetosus* sp. nov.: (A) urosome (♀), ventral [arrow indicating copulatory pore]; (B) urosome (♂), ventral.

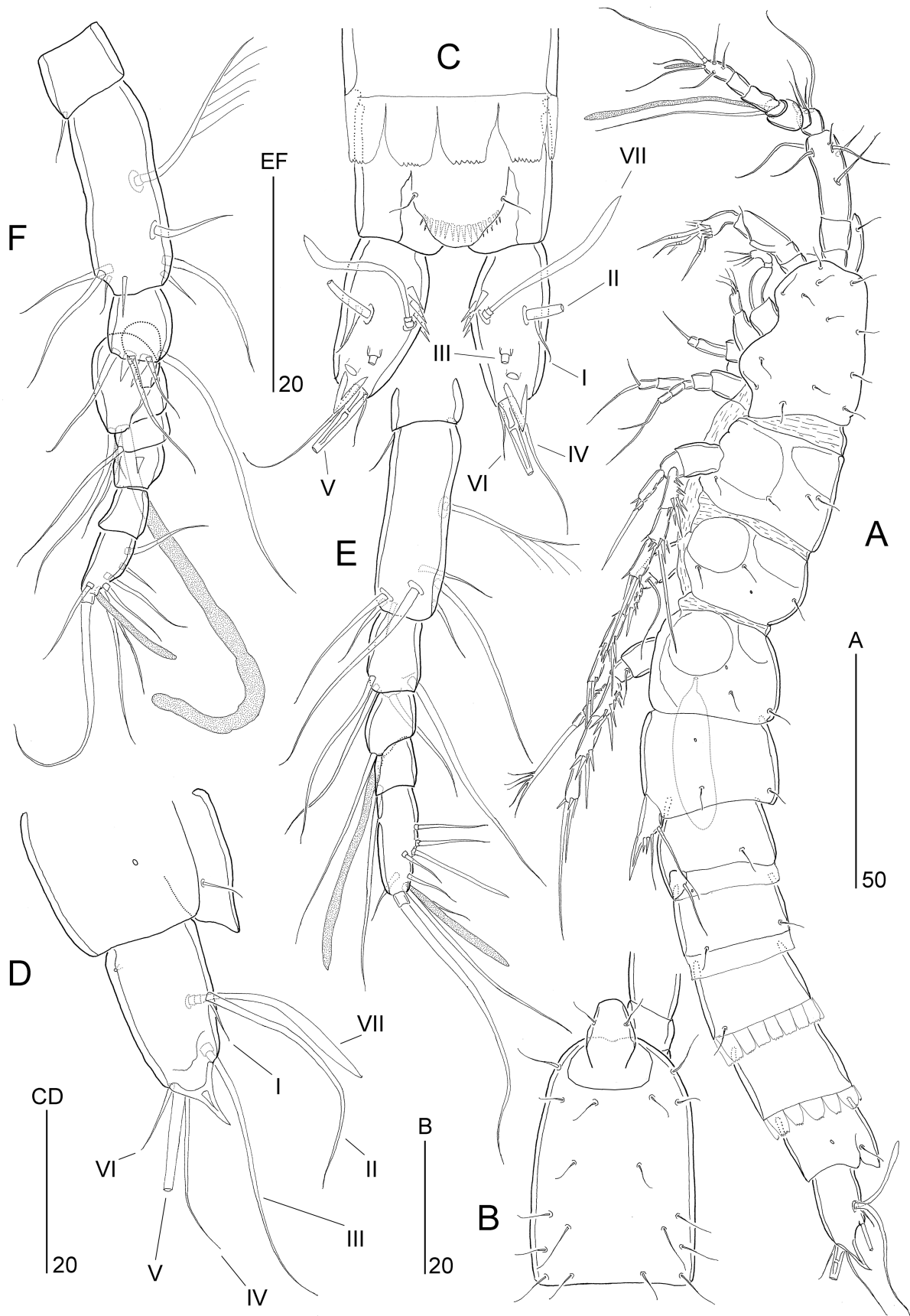


FIGURE 11. *Neoleptastacus supersetosus* sp. nov.: (A) habitus (♂), lateral; (B) rostrum and cephalothorax (♀), dorsal; (C) anal somite and caudal rami (♀), dorsal; (D) anal somite and left caudal ramus (♀), lateral; (E) antennule (♀), dorsal; (F) antennule (♂), dorsal.

Caudal rami (Figs 10A; 11C, D) about 2.2 times longer than wide (measured in lateral view from anterior margin to apex of spinous process), distinctly tapering posteriorly with outer margin almost straight and inner margin distinctly convex; outer distal corner produced into short posteriorly directed, dorsally recurved spinous process; with pore ventrally near proximal margin (Fig. 10A) and dorsally at base of spinous process (Fig. 11C); inner margin with conspicuous spinules near base of seta VII (Fig. 11C). Armature consisting of seven setae; seta I small; setae II and III (displaced to dorsal surface) long and naked; seta IV short, naked, located between seta V and posterior spinous process; seta V long, naked, with proximal fracture plane; seta VI small, naked and located at inner distal corner; seta VII distinctly foliaceous and tri-articulate at base.

Rostrum (Fig. 11B) small, broadly subtriangular, tapering distally; apical part lobate and demarcated by bilateral constrictions; with two delicate sensilla.

Antennule (Fig. 11E) moderately long and slender, 6-segmented. Segment 1 with small seta near anterodistal margin. Segment 2 longest, about three times longer than wide. Segment 4 with long aesthetasc (L: 21 μ m) fused at base with seta. Distal segment with seven setae (none distinctly spatulate) and apical acrothek consisting of short aesthetasc (L: 12 μ m) and two setae. All setal elements naked except for plumose seta on dorsal surface of segment 2. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[7 + acrothek].

Antenna (Fig. 9B, C). Coxa small, without ornamentation (not figured). Basis and proximal endopodal segment forming incompletely fused allobasis, about 2.5 times as long as maximum width; original basis-endopod boundary marked by short transverse surface suture at level of exopodal articulation and by constriction at abexopodal side; proximal part representing original basis with single spinules at distal corner. Exopod one-segmented, unornamented and elongate, with a naked apical seta (about 1.2 times longer than exopod). Free endopodal segment with few lateral spinules proximally and transverse spinular row distally; medial armature consisting of two short spines (indicated by arrows in Fig. 9B); apical armature consisting of two naked spines and three geniculate setae, longest of which with spinules around geniculation and fused basally to naked accessory seta.

Mandible, maxillule, maxilla and maxilliped as in *N. spinicaudatus* (see Sak *et al.* 2008: Figs 16D, E; 17E, F).

P1 (Fig. 9D). Intercoxal sclerite wide and subrectangular. Praecoxa small, triangular and naked. Coxa wider than long, without ornamentation. Basis without spinular ornamentation; anterior surface with small naked seta near medial margin. Exopod two-segmented; segments with several spinules around outer margin; exp-1 unarmed; exp-2 with unipinnate outer spine and two geniculate setae distally. Endopod two-segmented, not prehensile, slightly longer than exopod; enp-1 about 1.4 times longer than enp-2, with a serrate inner seta arising from distal third and four coarse spinules along outer margin; enp-2 without spinules, distal margin with naked outer spine and geniculate inner seta.

P2–P4 (Fig. 9F–G). Intercoxal sclerites rectangular with deeply concave ventral margins. Praecoxae triangular, small and naked. Coxae wider than long and without ornamentation. Bases smaller than coxae; anterior surface with a pore; outer basal seta absent in P2, naked and long (P3) or short (P4) in remaining legs; without ornamentation except for spinular row near base of P4 endopod. Exopods three-segmented; segments with coarse spinular ornamentation along outer margin, as illustrated; outer spine of segments naked (except for P2 exp-2 sparsely unipinnate); exp-3 with an outer unipinnate spine, and two setae distally (both naked in P2, one unipinnate and one bipinnate in P3–P4); outer spine of P2 exp-2 very long, extending far beyond exp-3 and about as long as entire exopod; P4 exp-2 elongate, distinctly longer than exp-1; segments of P4 about equally long, exp-3 with inner serrate seta in distal quarter originating from posterior surface. Endopods one- (P2–P3) or two-segmented (P4); P2–P3 endopods with few coarse spinules along both inner and outer margin; P4 enp-1 elongate, 3.7 times as long as enp-2, with few spinules along outer margin; P4 enp-2 without ornamentation; P2 endopod with long, apically serrate, backwardly directed seta along inner margin and one long unipinnate seta apically; P3 endopod shorter than P2 endopod, with short, naked spine apically; apical margin of P4 enp-2 with long, distally serrate and basally fused, inner seta, and short naked outer seta. Spine and seta formula as follows:

	Exopod	Endopod
P2	0.0.021	110
P3	0.0.021	010
P4	0.0.121	0.020

Fifth legs (Fig. 10A) closely set together, but not touching in ventral midline. Baseoendopod and exopod fused, forming a subrectangular plate; with one pore on anterior surface and two pores along inner margin; inner distal corner with strong, bipinnate, spinous process (homologous to inner spine); distal margin with a minute outer seta, one long naked seta, and two short, subequally long (outer one slightly longer), naked spines; outer basal seta long and naked.

Sixth pair of legs (Fig. 10A) reduced, fused medially forming common genital operculum; armature represented by vestigial spiniform element on either side. Copulatory pore conspicuous (arrowed in Fig. 10A).

Description of male. Total body length from tip of rostrum to posterior margin of caudal rami 235 μm ($n = 1$). Body ornamentation essentially as in female except for internal semicircular reinforcements present only on somites bearing P2–P4 (Fig. 11A). Sexual dimorphism in antennule, genital segmentation and P6. Spermatophore length approximately 33 μm .

Antennule (Fig. 11F) 9-segmented, haplocer; geniculation between segments 7 and 8. Segment 1 with a slender naked seta; segment 2 longest and about 2.4 times longer than wide, with one plumose and seven naked setae; segment 3 with four setae and a spine; segment 4 an incomplete sclerite with one seta and one spiniform element; segment 5 with a long aesthetasc (40 μm) fused basally to slender seta; segment 6 with a seta; segment 7 with a seta and a spine; segment apparently unarmed; distal segment with six setae (none of which spatulate) and apical acrothek consisting of short aesthetasc (10 μm) fused basally to two slender setae. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4 + 1 spine], 4-[(1 + 1 spine)], 5-[1 + (1 + ae)], 6-[1], 7-[1 + 1 spine], 8-[0], 9-[6 + acrothek].

Sixth legs (Fig. 10B) slightly asymmetrical, with smallest P6 closing off functional gonopore; each with a long outer seta and a short inner spine, both elements being naked.

Etymology. The specific epithet is derived from the Latin *super*, meaning over, and *s(a)eta*, *s(a)etosus*, meaning bristle, bristly, and refers to the supernumerary element on the P5 of both sexes.

Remarks. *Neoleptastacus supersetosus* sp. nov. is assigned to the *trisetosus*-group based on (1) the absence of paired spinous processes on the anal somite, (2) a well-developed anal operculum, (3) P1 exp-1 without outer spine and exp-2 with three setae/spines, (4) P2 exp-2 with very long outer setiform element extending far beyond distal margin of exp-3, (5) endopod P2–P3 1-segmented with inner seta and one distal spine on P2 and one distal spine on P3, and (6) outer seta of P4 enp-2 reduced. Within this group it is morphologically closest to *N. trisetosus* and *N. panamensis* sp. nov. with which it shares the 2-segmented condition of the P1 exopod. Characters that differentiate the new species from these two congeners include (1) somites bearing P2–P5, genital double-somite and second abdominal somite with internal semicircular reinforcements in ♀, and on somites bearing P2–P4 in ♂, (2) inner spine of P5 fused to segment, forming spinous process in both sexes (*vs* delimited at base), and (3) male P6 with outer seta and inner spiniform element (*vs* outer seta only). An additional character that differentiates *N. supersetosus* sp. nov. readily from all known species of *Neoleptastacus* (and in fact all other Arenopontiidae) is the presence of a supernumerary setiform element on the P5 of both sexes.

Species inquirendae

Neoleptastacus secundus Krishnaswamy, 1957

Arenopontia secundus (Krishnaswamy, 1957) Lang (1965: 418, 419)

Arenopontia (Neoleptastacus) secundus (Krishnaswamy, 1957): Wells (1967: 324)

Original description. Krishnaswamy (1957): 96–98; Text-Fig. 21.

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

Body length. 410 μm (♀), 323 μm (♂).

Remarks. Krishnaswamy's (1957) vague description has made most authors assume (*e.g.* Lang 1965; Bodiou & Colomines 1986; Karanovic 2000) that the P3 enp-2 carries two setae but this remains to be confirmed since the P3 was not illustrated in the original description. The author only stated that it "... resembled the second one, but the inner seta on the first endopod joint is absent". As pointed out above, the presence of paired anal processes indicates that *N. secundus* belongs in the *acanthus*-group and most likely in the *gussoae*-subgroup. The species shows a remarkable similarity with *N. longiremis* in the length and shape of the P5 (spinous process longest in ♀ in *N.*

secundus, but longest in ♂ in *N. longiremis*) and the elongate caudal rami. Itô (1968) pointed out several deficiencies in Krishnaswamy's (1957) description (P4 endopod refers to exopod; inner seta on P2 enp-1 should insert on enp-2; description of mouthparts unreliable) and recommended a critical re-examination of the type material. Given the inadequate original description *N. secundus* is here placed as a *species inquirenda* in the *gussoae*-subgroup. Krishnaswamy (1957) provides zonation and vertical distribution data.

Neoleptastacus secundus has not been recorded again since its original description, however, it is conceivable that some of the records of *N. indicus* refer to this species [e.g. Mantha *et al.* (2012) who reported it from Chennai, the type region of *N. secundus*] or that the latter is indeed conspecific with *N. secundus*. Evidence in support of such conspecificity is provided by Rao's (1967: fig. 3-28, 29 but not fig. 1-11, 12) illustrations of the P5 in both sexes of *N. indica* which shows a similarly long apical spinous process.

***Neoleptastacus accraensis* (Lang, 1965)**

Arenopontia longiremis Chappuis, 1955 *sensu* Chappuis & Rouch (1961: 608)

Arenopontia accraensis Lang, 1965

Arenopontia (*Neoleptastacus*) *accraensis* Lang, 1965: Wells (1967: 324—spelled *accraensis*)

Arenopontia (*Neoleptastacus*) *acantha accraensis* Lang, 1965: Kunz (1971: 356)

Neoleptastacus accraensis (Lang, 1965) Sak *et al.* (2008: 412)

Original description. Chappuis & Rouch (1961—as *A. longiremis*): 607–608; Figs 9–13 (♀ only).

Type locality. Ghana, Greater Accra Region, Accra; sandy beach in front of the lighthouse.

Body length. Unknown.

Remarks. Chappuis & Rouch (1961: 608, Figs 9–13) recorded two females from a sandy beach in Accra which they assigned to *Arenopontia longiremis* Chappuis, 1955. They considered the differences with the type population as insignificant, being a likely reflection of the disjunct distribution of the species. Lang (1965) considered Chappuis & Rouch's (1961) Ghanaian specimens to fall outside the limits of variability of *A. longiremis* and proposed a new name, *A. accraensis*, for them. Kunz (1971) treated *A. longiremis* and *A. accraensis* as subspecies of *A. acantha* but this was not adopted by subsequent revisers [Itô 1978; Bodiou & Colomines 1986; Wells 2007; Sak *et al.* 2008—but see Bodin (1997) for a dissenting opinion]. The Angolan material identified by Kunz (1971) as *A. (N.) acantha accraensis* belongs to a different species, described here as *N. emendatus* **sp. nov.** (see above).

Although Lang (1965), Bodiou & Colomines (1986) and Wells (2007) claim that P4 exp-3 possesses an inner seta, the setation of this leg has yet to be revealed. Similarly, in the identification keys provided by these authorities and Karanovic (2000) it is assumed that the distal endopod segment of P3 has only one distal element. However, Chappuis & Rouch (1961) show a second short element on enp-2 in their illustration of the P3 endopod. This element is here interpreted as the outer distal spine using the spinule row on enp-1 as a reference point for correct orientation. Note also that Chappuis & Rouch's (1961) illustration of the P1 shows it in an unnatural twisted position and that the terminal spinous process on the caudal ramus was figured as an articulating spine. The latter condition is unlikely since the caudal process in all members of the Arenopontiidae represents a posterior outgrowth of the ramus and not the homologue of an armature element that became secondarily incorporated.

Neoleptastacus accraensis is in need of detailed redescription (including the as yet unknown male) and is treated here as a *species inquirenda* in the genus since it is practically unidentifiable based on the few drawings provided by Chappuis & Rouch (1961). It is tentatively placed in the *spinicaudatus*-group based on the combined absence of paired anal processes and the retention of the plesiomorphic armature formula of P1–P4. The species is only known from the type locality where it occurs sympatrically with *N. africanus*.

Taxa of doubtful identity

***Arenopontia acantha* Chappuis, 1954 *sensu* Božić (1967)**

Original description. Božić (1967): 872–873; Fig. 3(3–4).

Type locality. India, west coast: intertidal locality not specified but probably along the Kerala coast (southwestern India).

Body length. 400 µm (♀).

Remarks. Božić (1967) illustrated the P5 (possibly of the female) and the posterior part of the urosome. From his brief text it appears that identification was made without dissection and based solely on the presence of paired spinous processes on the anal somite and the general morphology of the caudal rami. At that time most currently known species of the *acanthus*-group were still awaiting description and it is conceivable that Božić (1967) compared his material with *N. acanthus* only. No reference was made to the number of elements on P3 exp-2 which is of critical importance in resolving its affinities; should only one seta be present on this segment, Božić's (1967) material may well fall within Wells & Rao's (1987) proposed taxonomic boundaries of *N. indicus*.

Arenopontia ? gussoae Cottarelli, 1973a *sensu* Mielke (1982b) [partim]

Original description. Mielke (1982b: 203; Figs 6B; 7E) [Playa Nueva Gorgona]. Mielke (1982b: 204) [Playa Avenida Balboa].

Body length. 360 µm (♀), 300 µm (♂) [Playa Nueva Gorgona material]; 360 µm (♀) [Playa Avenida Balboa material] (Mielke 1982b).

Remarks. In addition to the material from Isla Melones (here treated as *N. abbreviatus* **sp. nov.**—see above), Mielke (1982b) also reported "*Arenopontia ? gussoae*" from two other localities along the Pacific seaboard of Panamá. Compared to *N. abbreviatus* **sp. nov.**, the specimens (3 ♀♀, 4 ♂♂) from Playa Nueva Gorgona (PNG) display a number of differences: (1) rostrum not tapered to the same extent, (2) P4 exp-2 relatively stouter and exp-3 shorter, (3) inner spinous process of P5 with weak contours, (4) paired lateral spinous processes on anal somite pointed, and (5) caudal rami more square than rectangular. A single female from Playa Avenida Balboa agreed with the PNG material in the morphology of the rostrum, P5 and caudal rami but exhibited a P4 exp-3 that is stouter. It is unlikely that either population belongs to *N. abbreviatus* **sp. nov.** Pending the arrival of new morphological data based on a larger set of specimens both remain as taxa of uncertain status.

Martínez Arbizu & Moura (1994) reported *A. ? gussoae* from Isla Margarita in Venezuela (Nueva Esparta State) and from Lima (Playa S. Bartolo) in Peru but did not make any morphological comparisons.

Arenopontia ? gussoae Cottarelli, 1973a *sensu* Mielke (1987) [2nd form]

Original description. Mielke (1987): 330, 334; Abb. 9C.

Body length. Unknown.

Distribution. Northern Chile, (1) Las Lozas beach, a few km south of Coquimbo and (2) Playa Brava in Iquique.

Remarks. In addition to the "normal form" (here considered as a distinct species, *N. chilensis* **sp. nov.**—see above), Mielke (1987) also distinguished a "2nd form" in his Chilean material that he provisionally identified as *Arenopontia ? gussoae*. According to Mielke (1987), the latter differs from *N. chilensis* **sp. nov.** in (1) rostrum somewhat wider, (2) spinular ornamentation of inner spinous process of P5 more pronounced, (3) caudal ramus without medial spur near insertion site of dorsal seta VII, and (4) position of caudal ramus seta III more distal, originating near base of caudal process. Mielke's (1987) only illustration of the second form depicts the anal somite and caudal ramus in lateral aspect, revealing the elongate, virtually straight, spinous process (50% of caudal ramus length vs 35% and dorsally recurved) and the non-recurved anal processes as additional differences separating it from *N. chilensis* **sp. nov.** (Table 4). Although the sympatric occurrence of both "forms" in the same beach made Mielke (1987) speculate that they may represent different species, he preferred to consider them as morphs of the same species pending the arrival of ecological data. The second form is here treated as distinct from *N. chilensis* **sp. nov.** but assigned uncertain status due to the lack of additional morphological information.

Species incertae sedis

Arenopontia breviarticulata Mielke, 1975

Arenopontia (*Neoleptastacus*) *breviarticulata* Mielke, 1975: Bodin (1979)

Pararenopontia breviarticulata (Mielke, 1975) Bodiou & Colomines (1986)

Arenopontia (*Pararenopontia*) *breviarticulata* Mielke, 1975: Bodin (1997)

Original description. Mielke (1975):110–112; Abb. 74 (♂ only).

Type locality. Germany, Schleswig-Holstein, Isle of Sylt, List; in front of old “Litoralstation List/Sylt”; medium to coarse sandy beach.

Body length. 710 µm (♂).

Remarks. The description of *Arenopontia breviarticulata* is based on a single male that displays a 2-segmented P1 exopod (exp-2 and -3 fused) and a reduced P5 bearing only one spiniform and two setiform elements. As pointed out by Sak *et al.* (2008) it remains unconfirmed whether the inner spine of the male P5 (or spinous process when incorporated in the segment) is genuinely absent or was overlooked. The latter is unlikely given that *A. breviarticulata*, with a recorded male body size of 710 µm, is by far the largest arenopontiid to be described so far. Sak *et al.* (2008) offered an alternative explanation by comparing Mielke’s (1975) illustration with the P5 observed in the copepodid IV stage of *N. indicus* (Rao 1967: fig. 3-22) which shows a similar underdeveloped condition. This may suggest that *A. breviarticulata* has a paedomorphic morphology which is further substantiated by its 2-segmented P1 exopod, a segmentation pattern that is displayed in copepodid II–IV of *N. indicus* before a third segment is added at the next moult (Rao 1967). Conversely, *A. breviarticulata* has retained the plesiomorphic armature pattern on P2 endopod and P4 exopod. Mielke’s (1975) illustration of the P3 is problematic since it shows an inner seta on exp-3 and two very long setae on enp-2. Such features have not been observed in any other arenopontiid, raising the suspicion that Mielke (1975) did not observe the real P3 but duplicated P4 instead. The only difference between his illustrations of P3 and P4 is the extreme disparity in length of the outer basal seta.

Mielke (1975) described the anal operculum with two lateral “Zacken” (jags, sharp projections) which can be regarded as the positional homologues of the paired lateral spinous processes on the anal somite in the *acanthus*-group of *Neoleptastacus*. The very long outer spines on exp-2 of P2 and P4 (and possibly P3) in *A. breviarticulata* differentiates it from all members of this species group.

Bodin (1979) listed *A. breviarticulata* under the subgenus *A. (Neoleptastacus)* while Mielke (1975) considered it a member of the subgenus *A. (Arenopontia)*. Bodiou & Colomines (1986) placed the species in their new genus *Pararenopontia*, the validity of which was dismissed by Martínez Arbizu & Moura (1994) on the grounds that it was an artificial taxon uniting species with reduced leg segmentation. Sak *et al.* (2008) favoured a relationship with the *Mesopontia-Onychopontia-Neoleptastacus* lineage based on the armature formula of P1 enp-2, displaying one geniculate seta and one outer distal spine. Although the morphology of the anal somite suggests that *A. breviarticulata* is probably nested within the *acanthus*-group of the genus *Neoleptastacus*, it is here treated as a *species incertae sedis* in the Arenopontiidae and not in *Neoleptastacus* as proposed by Sak *et al.* (2008).

Key to species

Redefinition of the generic boundaries in the Arenopontiidae (Sak *et al.* 2008) and addition of new species have outdated the keys by Lang (1965), Bodiou & Colomines (1986), Karanovic (2000) and Wells (2007). *Neoleptastacus accraensis* and *N. secundus* (both *species inquirendae*) are included in Table 2 but not in the updated key below. Identifications made with this key must be confirmed by reference to the original descriptions in the literature.

1. Anal somite with paired dorsolateral spinous spurs or processes2.
Anal somite without paired dorsolateral spurs or processes13.
2. Abdominal somites with integumental pattern of rectangular plates dorsally and ventrally; P2 enp-2 without inner seta3.
Abdominal somites without conspicuous surface sculpturing; P2 enp-2 with inner seta4.
3. P3 enp-2 with two distal elements; P5 of both sexes with four articulating setae/spines *N. ornamentus*.
P3 enp-2 with one distal element; P5 of both sexes with three articulating setae/spines. *N. reductaspina*.
4. P3 enp-2 with two distal elements5.

5. P3 enp-2 with one distal element7.
P1 exp-3 with three setae/spines *N. huysi*.
P1 exp-3 with four setae/spines6.
6. P1 endopod clearly longer than exopod; P3 enp-2 about half the length of enp-1; P5 of both sexes with one seta and two short spines between inner spinous process and outer basal seta *N. acanthus*.
P1 endopod as long as exopod; P3 enp-2 only slightly shorter than enp-1; P5 of both sexes with one seta and one spur between inner spinous process and outer basal seta *N. chaufriassei*.
7. Sternal plates of somites bearing P1–P4 with midventral hook-like processes *N. emendatus* **sp. nov.**
Sternal plates of somites bearing P1–P4 without such posteriorly directed processes8.
8. Paired spinous processes on anal somite straight and backwardly directed.9.
Paired spinous processes on anal somite dorsally recurved.10.
9. P1 endopod 1.15 times as long as exopod; P5 elongate in both sexes, length/maximum width ratio 3.0 (♀) and 3.5 (♂), respectively.*N. longiremis*.
P1 endopod 1.30 times as long as exopod; P5 much shorter in both sexes, length/maximum width ratio 1.7 (♀) and 2.25 (♂), respectively. *N. rectus* **sp. nov.**
10. P1 endopod shorter than exopod*N. abbreviatus* **sp. nov.**
P1 endopod at least as long as exopod11.
11. P1 endopod as long as exopod; spinous process on caudal ramus relatively short, about 35% of ramus length.
.....*N. chilensis* **sp. nov.**
P1 endopod 1.25–1.30 times as long as exopod; spinous process on caudal ramus longer, about 45–55% of ramus length ..12.
12. P1 enp-1 1.25 times as long as enp-2; P5 ♀ twice as long as maximum width; terminal process of caudal ramus dorsally recurved*N. gussoae*.
P1 enp-1 1.65 times as long as enp-2; P5 ♀ 2.7 times as long as maximum width; terminal process of caudal ramus not dorsally recurved *N. indicus*.
13. P1 exopod 2-segmented14.
P1 exopod 3-segmented16.
14. P5 inner spine at least partly delimited at base; P6 ♂ with one seta15.
P5 inner spine fused at base, forming spinous process; P6 ♂ with two elements*N. supersetosus* **sp. nov.**
15. P2 exp-2 outer spine shorter than exopod; P2 endopod shorter than exp-1, flask-shaped; P4 exp-3 four times as long as maximum width, with inner seta arising from distal fifth of inner margin*N. trisetosus*.
P2 exp-2 outer spine distinctly longer than exopod; P2 endopod as long as exp-1, subrectangular and slightly tapering in distal third; P4 exp-3 2.75 times as long as maximum width, with inner seta arising from middle third of inner margin
..... *N. panamensis* **sp. nov.**
16. P3 endopod 1-segmented, with one distal element17.
P3 endopod 2-segmented, enp-2 with two elements (outer one fused at base)19.
17. P1 exp-3 with four elements; P2 endopod 2-segmented; P4 exp-3 without inner seta *N. australis*.
P1 exp-3 with three elements; P2 endopod 1-segmented; P4 exp-3 with inner seta18.
18. Inner spinous process of P5 ♀ distinctly curved outwardly (unknown in ♂); terminal process of caudal ramus dorsally recurved *N. angolensis* **comb. nov.**
Inner spinous process of P5 ♀/♂ and terminal process of caudal ramus straight*N. africanus*.
19. P4 exp-3 without inner seta *N. pacificus*.
P4 exp-3 with inner seta20.
21. Urosome (except anal somite) with distinct surface ornamentation consisting of elongate rectangular plates *N. clasingi*.
Urosome without conspicuous surface ornamentation.22.
22. Caudal ramus with dorsolateral spur near base of seta VII23.
Caudal ramus without dorsolateral spur near base of seta VII.24.
23. Lappets of abdominal hyaline frills semi-incised obtusidigitate; inner seta of P2–P3 enp-2 longer than endopod; P5 three 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*.
24. P1 endopod distinctly longer than exopod *N. ishikarianus*.
P1 rami equally long. *N. pseudishikarianus* **sp. nov.**

Genus *Phreatipontia* gen. nov.

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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 without dorsolateral spur or raised spinular row near medial margin; seta IV with long setule on outer margin. P1 exopod three-segmented; exp-1 with outer spine; exp-3 with two spines and two

geniculate setae. P1 endopod not prehensile, slightly longer than exopod; enp-2 with two geniculate setae. P2–P4 endopods two-segmented. P2–P3 endopods with one apical seta. P4 endopod with well developed outer distal element. Armature formula as follows:

	Exopod	Endopod
P2	0.0.021	0.110
P3	0.0.021	0.010
P4	0.0.121	0.020

P3 endopod ♂ not sexually dimorphic, two-segmented. P5 with outer basal seta and four discrete elements; innermost element fused to segment forming spinous process; length of process sometimes sexually dimorphic. P6 ♂ with two setae/spines.

Type species. *Arenopontia (Neoleptastacus) speluncae* Cottarelli, Bruno & Venanzetti, 1994 [by original designation].

Other species. *Arenopontia (Neoleptastacus) phreatica* Cottarelli, Bruno & Venanzetti, 1994 = *Phreatipontia phreatica* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.**

Etymology. The genus name is derived from the Greek φρέαρ (phréar), meaning well, spring, and πόντος (póntos), meaning sea, and refers to the low salinity habitat preference of its members. Gender: feminine.

Remarks. The two members included in this genus, *P. phreatica* **comb. nov.** and *P. speluncae* **comb. nov.**, differ from all *Neoleptastacus* species in the presence of two geniculate setae on the distal segment of the P1 endopod (instead of an outer spine and an inner geniculate seta). This character state is shared with two other genera in the Arenopontiidae, *Psammoleptastacus* and *Onychopontia*, both of which display sexual dimorphism on the P3 endopod which is not expressed in *Phreatipontia* **gen. nov.** *Psammoleptastacus* additionally differs from the new genus in (1) the presence of a dorsolateral spur on the inner margin of the caudal ramus, (2) P1 endopod being distinctly shorter than the exopod, (3) the presence of two distal elements on P2–P3 enp-2, and (4) the absence of an inner spinous process on the P5 in both sexes. *Onychopontia* can be differentiated from *Phreatipontia* **gen. nov.** by (1) the characteristic deeply incised hyaline frills on the abdominal somites, (2) the absence of the inner serrate seta on P2 enp-2, (3) the very short P2–P3 enp-2, and (4) the absence of an inner spinous process on the female P5. Both species of *Phreatipontia* **gen. nov.** display a reduced armature on P2–P3 endopods with only one apical seta on the distal segment. This condition is shared with members of the *trisetosus*-group of *Neoleptastacus*, however in this lineage the endopods are only 1-segmented (Table 2). Finally, both *P. phreatica* **comb. nov.** and *P. speluncae* **comb. nov.** exhibit a characteristic caudal ramus seta IV which has a long setule on the outer margin (indicated by arrows in Figs 12C; 16C) which can be considered an autapomorphy for the genus. Current records suggest that, unlike most arenopontiids, both species favour low salinity environments, including phreatic and water table habitats (Cottarelli *et al.* 1994, 1996; Bruno *et al.* 1998; this study).

Within the family, only *Arenopontia* cf. *subterranea* was previously recorded from habitats with a strong freshwater influence in various localities in Abruzzi, Lazio and Tuscany in Italy (Cottarelli 1969; Cottarelli *et al.* 1994; Cottarelli & Venanzetti 1989), representing a second but independent incursion into low salinity environments.

Phreatipontia phreatica* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.*

(Figs 12–15)

Arenopontia (Neoleptastacus) phreatica Cottarelli, Bruno & Venanzetti, 1994

Neoleptastacus phreaticus (Cottarelli, Bruno & Venanzetti, 1994) Sak *et al.* (2008: 412)

Original description. Cottarelli *et al.* (1994): 471–475; Fig. 1 (♂ only).

Type locality. Italy, Sardinia, Sassari Province, Isola della Maddalena, Casale Susini; artesian well, depth 73 m, 53 m above sea level; along road to Cala Spalmatore.

Material examined. Two ♀♀ and one ♂ collected from sandy patch on Islet Melita (Sveta Marija) in Malo Jezero (Small Lake), Isle of Mljet, Dalmatian coast, Croatia; leg. H. Kunz, 06 May 1986.

Body length. 287 µm (♂) [Cottarelli *et al.* 1994]; 383 µm (♀), 325 µm (♂) [present account].

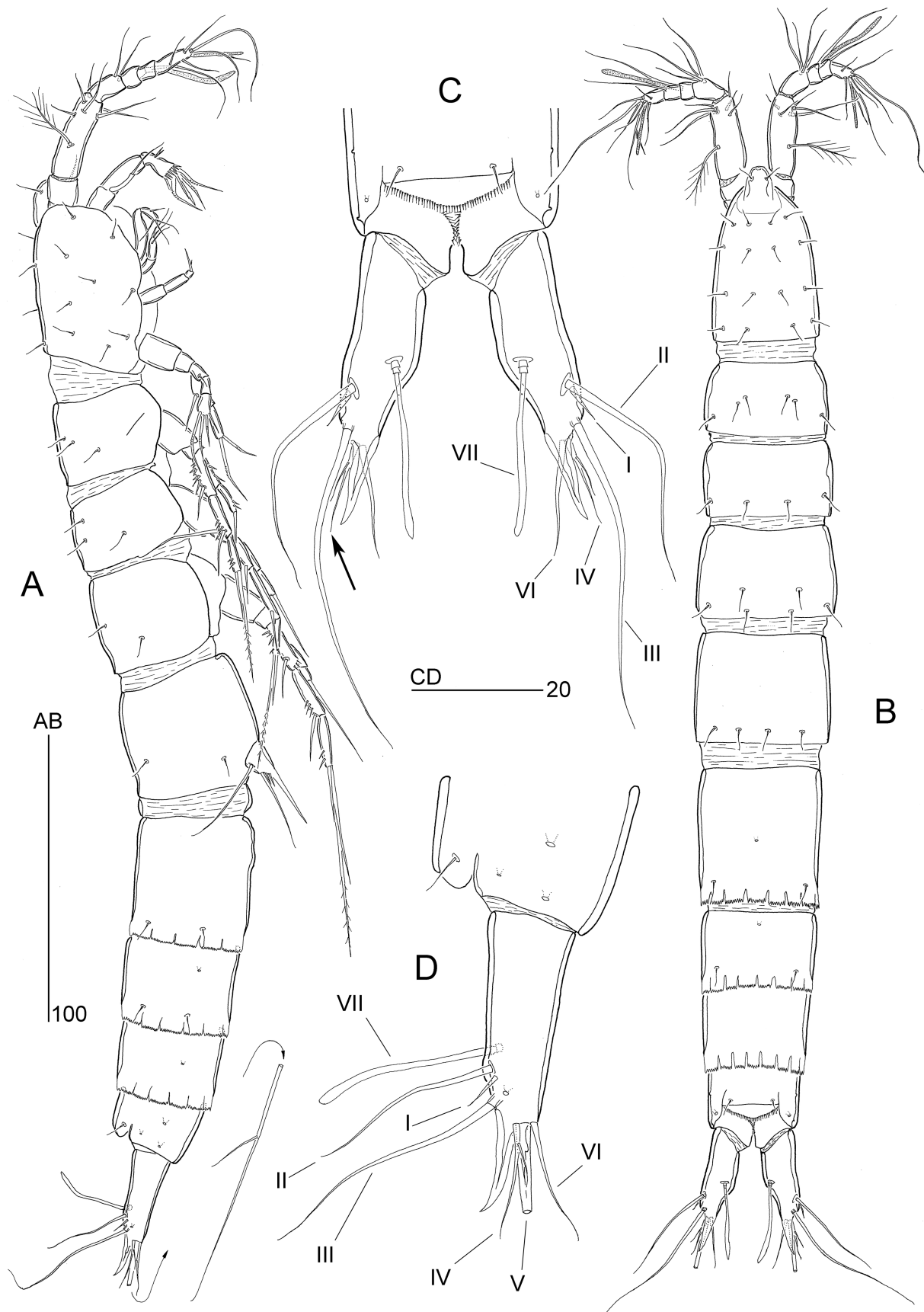


FIGURE 12. *Phreatipontia phreatica* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.** (♀): (A) habitus, lateral; (B) habitus, dorsal; (C) anal somite and caudal rami, dorsal [arrow indicating modified seta IV]; (D) anal somite and right caudal ramus, lateral.

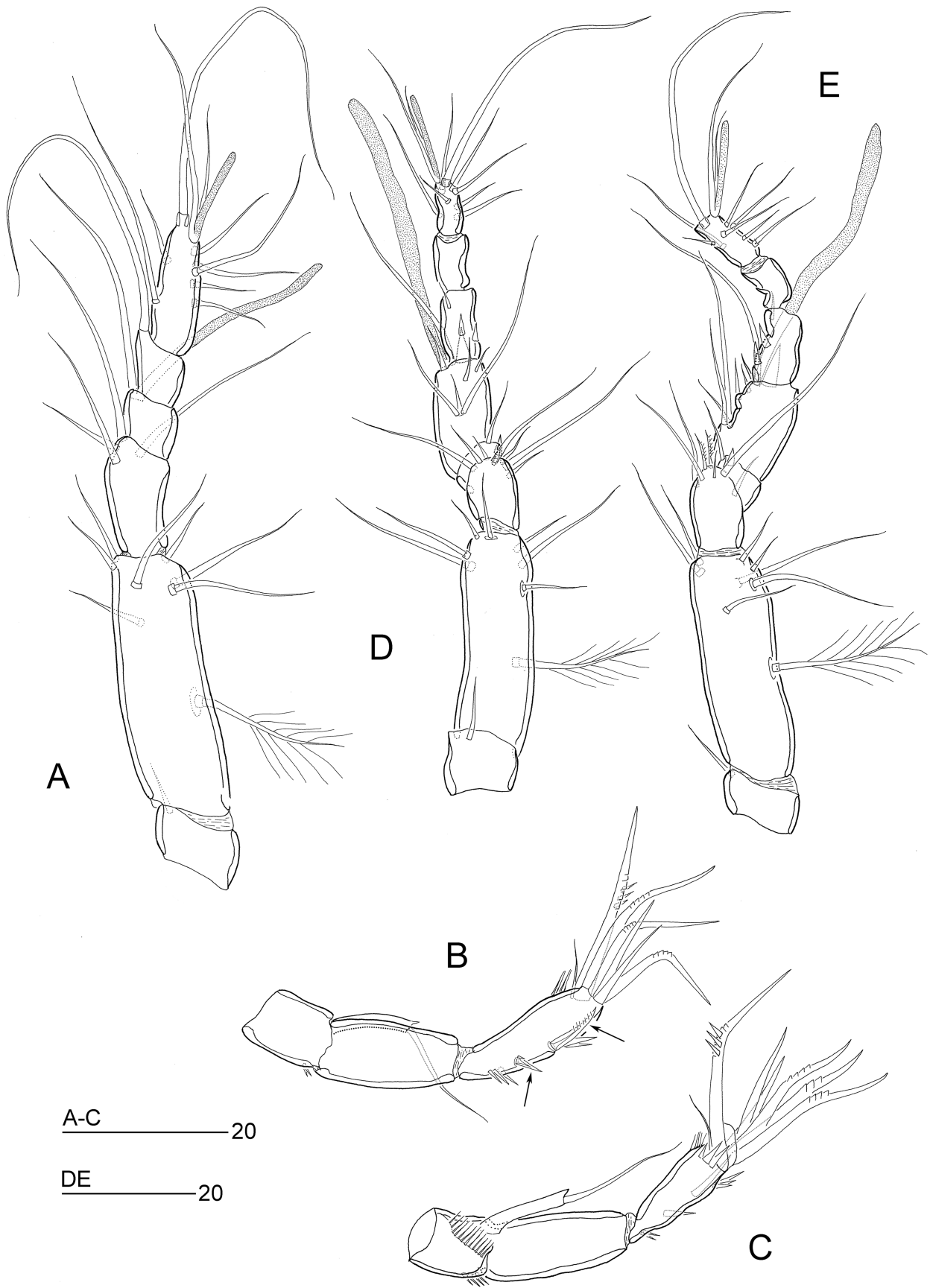


FIGURE 13. *Phreatipontia phreatica* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.**: (A) antennule (♀), dorsal; (B) antenna (♀), medial [lateral endopodal spines indicated by arrows]; (C) antenna (♀), outer; (D) antennule (♂), anterior; (E) antennule (♂), dorsal.

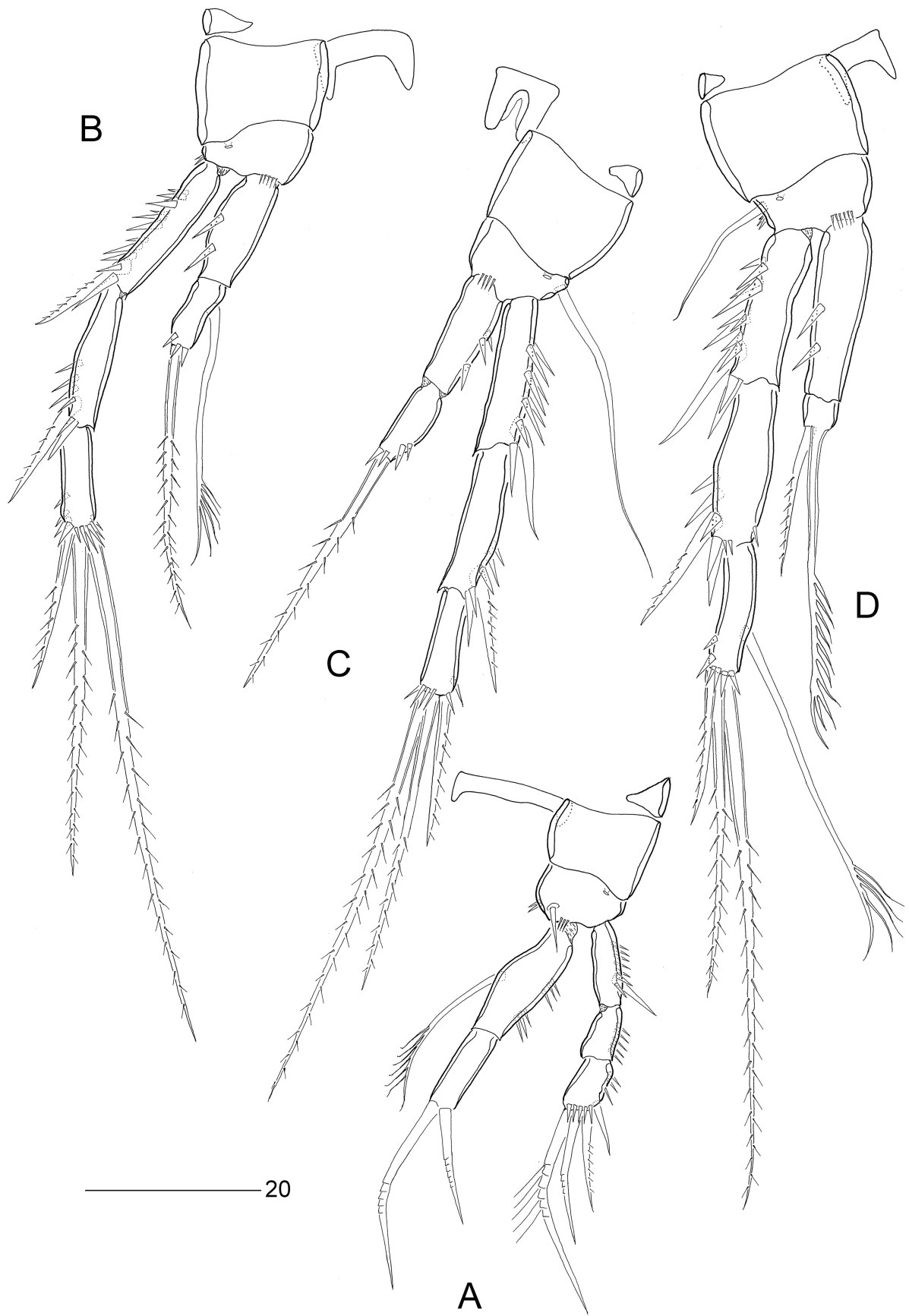


FIGURE 14. *Phreatipontia phreatica* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.** (♀): (A) P1, anterior; (B) P2, anterior; (C) P3, anterior; (D) P4, anterior.

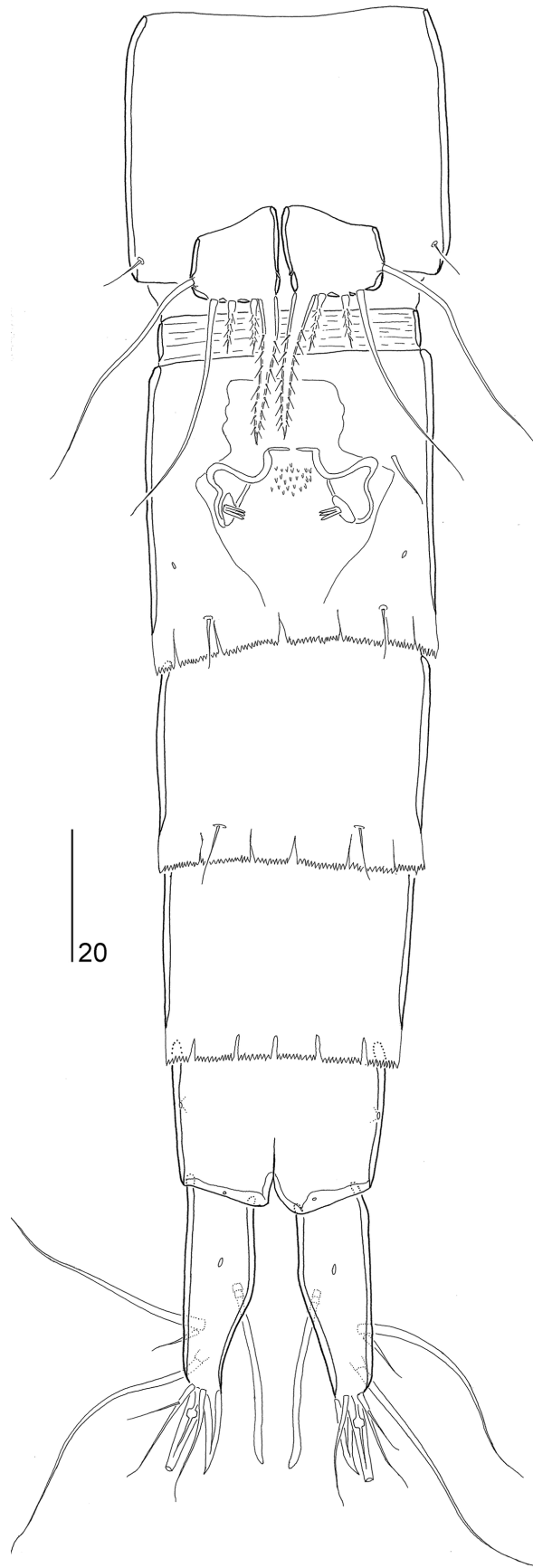


FIGURE 15. *Phreatipontia phreatica* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.:** urosome (♀), ventral.

Redescription of female. Total body length from tip of rostrum to posterior margin of caudal rami 383 μm ($n = 1$). Cephalothorax maximum width 38 μm measured at posterior margin. Maximum body width 46 μm , measured at P5-bearing somite. Body (Fig. 12A, B) slender and cylindrical without clear distinction between prosome and urosome. Sensillar pattern on body as figured. Hyaline frills of thoracic somites weakly developed and plain; those of genital double-somite and free abdominal somites strongly developed and consisting of rectangular digitate lappets (Figs 12A, B; 15). Somites connected by well-developed intersomitic membranes. Genital double-somite slightly longer than wide (measured in dorsal aspect); with one middorsal and four ventrolateral pores (Figs 12B; 15). Anal somite (Figs 12C, D; 15) with two dorsal and six lateral pores. Anal frill triradiate, minutely incised (giving a spinulose appearance); anal operculum virtually straight, without ornamentation.

Caudal rami (Figs 12C, D; 15) about 3.9 times longer than wide (measured in dorsal view from anterior margin to apex of spinous process), distinctly tapering posteriorly; outer margin straight, inner margin with bulge at level of seta VII; with two ventral pores in proximal quarter and lateral pore near insertion of seta III; terminal spinous process slightly recurved dorsally; no spinular ornamentation discernible. Armature consisting of seven setae; seta I small; setae II and III (displaced to dorsal surface) long and naked; seta IV short, located between seta V and posterior spinous process, with long outer spinule; seta V relatively short, with proximal fracture plane and single setule in proximal half (Fig. 12A); seta VI small, naked and located at inner distal corner; seta VII weakly foliaceous and tri-articulate at base.

Rostrum (Fig. 12B) small, broadly subtriangular, tapering distally; apical part lobate and demarcated by bilateral constrictions, with two delicate sensilla.

Antennule (Fig. 13A) long and slender, 6-segmented. Segment 1 with small seta near anterodistal margin. Segment 2 longest, about 2.8 times longer than wide. Segment 4 with long aesthetasc (L: 28 μm) fused at base with seta. Distal segment with eight setae (none of them spatulate) and apical acrothek consisting of short aesthetasc (L: 12 μm) and two setae. All setal elements naked except for plumose seta on dorsal surface of segment 2. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[8 + acrothek].

Antenna (Fig. 13B, C). Coxa small, without ornamentation (not figured). Basis and proximal endopodal segment forming incompletely fused allobasis; original basis-endopod boundary marked by transverse surface suture at level of exopodal articulation; proximal part representing original basis with longitudinal row of small spinules near base of exopod and oblique spinular row on outer surface. Exopod one-segmented, unornamented and elongate, with a naked apical seta (about 1.5 times longer than exopod). Free endopodal segment with few lateral spinules proximally and transverse spinular row distally; medial armature consisting of two short spines (indicated by arrows in Fig. 13B); apical armature consisting of two naked spines and three geniculate setae, longest of which with spinules around geniculation and fused basally to naked accessory seta.

Mandible, maxillule, maxilla and maxilliped as in *Neoleptastacus spinicaudatus* (see Sak *et al.* 2008: Figs 16D, E; 17E, F).

P1 (Fig. 14A). Intercoxal sclerite naked, wide and subrectangular. Praecoxa small, triangular and naked. Coxa wider than long, without ornamentation. Basis with spinular row near base of endopod and few spinules along inner margin; anterior surface with a small setiform spine near medial margin and one pore near articulation with coxa. Exopod three-segmented; all segments with several spinules around outer margin; exp-1 longest and narrowest, with naked outer spine; exp-2 without outer element; exp-3 with short naked outer spine, and a longer unipinnate spine and two geniculate setae (inner one with long setules around geniculation) distally. Endopod two-segmented, not prehensile, slightly longer than exopod; enp-1 expanded medially halfway down its inner margin, about 1.3 times longer than enp-2, with a distally serrate seta arising from halfway down inner margin and two sets of spinules along outer margin; enp-2 without spinules, distal margin with two geniculate setae, outermost of which shortest.

P2–P4 (Fig. 14B–D). Intercoxal sclerite naked (P2–P4), rectangular (P2) or squarish (P3–P4) with deeply concave ventral margins. Praecoxae triangular, small and naked. Coxae wider than long and without ornamentation. Bases smaller than coxae, with a spinular row near base of endopod (P2–P4) and a few spinules around outer corner in P2 and P4; anterior surface with a pore; outer basal seta absent in P2, naked in P3–P4 and extremely long in P3. Exopods three-segmented; segments with coarse spinular ornamentation along outer margin; outer spine of exp-1 unipinnate (P2) or naked (P3–P4); outer spine of exp-2 unipinnate; exp-3 with an outer unipinnate spine and two bipinnate setae distally, P4 exp-3 with additional serrate seta on inner margin; P4 exp-2 only marginally longer than exp-1. Endopods two-segmented; P2–P4 enp-1 unarmed, about 1.6, 1.3, and 5.8 times longer than their respective distal segments, with few coarse spinules along outer margin as figured, but without ornamentation along inner

margin; P2–P3 enp-2 with few spinules around distal margin; P2 enp-2 with long, apically serrate, backwardly directed seta near proximal margin and one bipinnate setae apically; P3 enp-2 with long, bipinnate apically; distal margin of P4 enp-2 with long, distally serrate and basally fused, inner seta, and shorter unipinnate, outer seta. Spine and seta formula as follows:

	Exopod	Endopod
P2	0.0.021	0.110
P3	0.0.021	0.010
P4	0.0.121	0.020

Fifth legs (Fig. 15) closely set together, almost touching medially. Baseoendopod and exopod fused, forming a subrectangular plate with straight distal margin; no pores discernible on anterior surface; inner distal corner with very long, bipinnate, spinous process (homologous to inner spine); distal margin with long naked outer seta and two short equally long, bipinnate setiform spines; outer basal seta long and naked.

Sixth legs (Fig. 15) vestigial, forming opercula closing off genital apertures.

Redescription of male. Total body length from tip of rostrum to posterior margin of caudal rami 325 μm ($n = 1$). Body ornamentation essentially as in female. Sexual dimorphism in antennule, genital segmentation, P5, and P6.

Antennule (Fig. 13D, E) 8-segmented, haplocer; geniculation between segments 6 and 7. Segment 1 with a slender naked seta; segment 2 longest and about three times longer than wide, with one plumose and seven naked setae; segment 3 with seven setae; segment 4 an incomplete sclerite with a seta and a spine; segment 5 with six setae and a long aesthetasc (44 μm) fused basally to a slender seta; segment 6 with one short seta and two spines; no armature discernible on segment 7; distal segment with eight setae (none of which spatulate) and apical acrothek consisting of short aesthetasc (14 μm) fused basally to two slender setae. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[7], 4-[1 + 1 spine], 5-[6 + (1 + ae)], 6-[1 + 2 spines], 7-[0], 8-[8 + acrothek].

P5 essentially as in female except for inner spinous process naked and outer marginal seta shorter.

Sixth legs asymmetrical, with smallest P6 closing off functional gonopore; each with a long outer seta and a short inner spine, both elements being naked.

Remarks. Cottarelli *et al.*'s (1994) original description, which was based on a single male, contains a number of inaccuracies. The report of an outer basal seta on P1 (their Fig. 1–c) is dubious since this element is absent in all other members of the family. The setal formula for P2 exopod (0.0.121) contradicts the text and illustration (their Fig. 1–d) which also gives a distorted view of the distal segment (the outer spine originates from the inner distal corner while the spinular ornamentation is correctly shown on the outer margin). The inner serrate seta shown to originate from P2 enp-1 (their Fig. 1–h) almost certainly inserts on enp-2 as in all other arenopontiids that have this element expressed. The distal segment of the P3 exopod (their Fig. 1–l) has an uncharacteristic armature, showing an extremely long outer distal element and two subequal terminal setae; this condition could not be confirmed in our material. According to Cottarelli *et al.* (1994) the outer distal element of P4 enp-2 (their Fig. 1–m) is absent and the somitic hyaline frills are plain but both observations are contradicted by our study.

The species has been recorded twice from Isola della Maddalena, located opposite the north-eastern coast of Sardinia (Cottarelli *et al.* 1994, 1996). Cottarelli *et al.* (1996) also reported *Arenopontia* cf. *phreatica* from Isola Spargi, another island in the La Maddalena archipelago, but did not specify locality data or why the species deviated from the original description. According to Bruno *et al.* (1998) *P. phreatica* **comb. nov.** is restricted to phreatic habitats, in both superficial (Coghinas River) and deeper waters (Spargi and La Maddalena Islands) in northern Sardinia.

***Phreatipontia spelunca* (Cottarelli, Bruno & Venanzetti, 1994) comb. nov.**
(Figs 16–19)

Arenopontia (*Neoleptastacus*) *spelunca* Cottarelli, Bruno & Venanzetti, 1994

Neoleptastacus turcicus—*nomen nudum* by Sak (2004: 221)

Neoleptastacus spelunca (Cottarelli, Bruno & Venanzetti, 1994) Sak *et al.* (2008: 412)

Original description. Cottarelli *et al.* (1994): 475–480; Figs 2–3.

Type locality. Italy, Lazio, Latina Province, Sperlonga, Tiberio beach; on the banks of a little stream that originates from a spring on the beach; interstitial water. Note that Cottarelli *et al.* (1994) also collected two females from a second locality in the Latina Province (S. Agostino beach in Gaeta) but did not explicitly state where the female holotype originated from. Since they allocated numbers 2–13 to the paratypes (six ♀♀ and five ♂♂ in total were collected from Sperlonga, two ♀♀ from Gaeta) it appears rational to assume that number 1 was given to the holotype and that it came from Sperlonga. The etymology of the species name and the fact that additional drawings (Figs 2–e, 3–g) were presented of an atypical female of S. Agostino beach also seem to suggest that Sperlonga was the intended type locality.

Material examined. One ♀ (dissected on eight slides) and one ♂ (dissected on seven slides); 10 individuals in ethanol. All specimens collected from Ismailbeyli Village beach (41°02.198' N; 38°56.901' E) close to a small stream, Giresun (Giresun Province), northeastern Türkiye (Black Sea region); leg. S. Karaytuğ & S. Sak, 10 September 2002.

Body length. 394 µm (♀), 346 µm (♂) [Cottarelli *et al.* 1994]; 356 µm (♀), 338 µm (♂) [present account].

Redescription of female. Total body length from tip of rostrum to posterior margin of caudal rami 356 µm ($n = 1$). Cephalothorax maximum width 42 µm measured at posterior margin. Maximum body width 47 µm, measured at P5-bearing somite. Body (Fig. 16A, B) slender and cylindrical without clear distinction between prosome and urosome. Sensillar pattern on body as figured. Hyaline frills of thoracic somites weakly developed and plain; those of genital double-somite and free abdominal somites well developed and consisting of rectangular digitate lappets that taper towards their distal margins (Figs 16A–B; 19A). Somites connected by well-developed intersomitic membranes. Genital double-somite slightly longer than wide (measured in dorsal aspect); with two ventral pores (Fig. 19A). Anal somite (Figs 16C, D; 19A) with two dorsal and four lateral pores. Anal frill triradiate, minutely incised (giving a spinulose appearance); anal operculum virtually straight, without ornamentation.

Caudal rami (Figs 16C, D; 19A) about 3.4 times longer than wide (measured in dorsal view from anterior margin to apex of spinous process), distinctly tapering posteriorly; outer and inner margins slightly convex; with two ventral pores in proximal third and two lateral pores near insertion of seta III; terminal spinous process slightly recurved dorsally; no spinular ornamentation discernible. Armature consisting of seven setae; seta I small; setae II and III (displaced to dorsal surface) long and naked; seta IV short, located between seta V and posterior spinous process, with long outer spinule; seta V with proximal fracture plane; seta VI small, naked and located at inner distal corner; seta VII spatulate and tri-articulate at base.

Rostrum (Fig. 16A) small, subtriangular, tapering distally; with two delicate sensilla.

Antennule (Fig. 17C) long and slender, 6-segmented. Segment 1 with small seta near anterodistal margin. Segment 2 longest, about 2.5 times longer than wide. Segment 4 with long aesthetasc (L: 29 µm) fused at base with seta. Distal segment with eight setae (none of them spatulate) and apical acrothek consisting of short aesthetasc (L: 13 µm) and two setae. All setal elements naked except for plumose seta on dorsal surface of segment 2. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[(1 + ae)], 5-[1], 6-[8 + acrothek].

Antenna (Fig. 17D). Coxa small, without ornamentation (not figured). Basis and proximal endopodal segment completely separated. Basis with few spinules along exopodal margin and with oblique spinular row near base of exopod. Exopod one-segmented and elongate, with a naked apical seta (about 1.4 times longer than exopod). Free endopodal segment with transverse spinular row distally; medial armature consisting of two short spines (indicated by arrows in Fig. 17D); apical armature consisting of two naked spines and three geniculate setae, longest of which with spinules around geniculation and fused basally to naked accessory seta.

Mandible, maxillule, maxilla and maxilliped as in *P. phreatica*.

P1 (Fig. 18A). Intercoxal sclerite wide, naked and subrectangular, with concave ventral margin. Praecoxa small, triangular and naked. Coxa wider than long, without ornamentation. Basis with spinular row near base of endopod; anterior surface with a small setiform spine near medial margin and one pore near articulation with coxa. Exopod three-segmented; all segments with several spinules around outer margin; exp-1 about as long as exp-3, with naked outer spine; exp-2 without outer element; exp-3 with short naked outer spine, and a longer naked spine and two geniculate setae distally. Endopod two-segmented, not prehensile, slightly longer than exopod; enp-1 with virtually straight inner margin, about 1.5 times longer than enp-2, with a serrate seta arising from about halfway down inner margin and two sets of two spinules along outer margin; enp-2 without spinules, distal margin with two geniculate setae, outermost of which shortest.

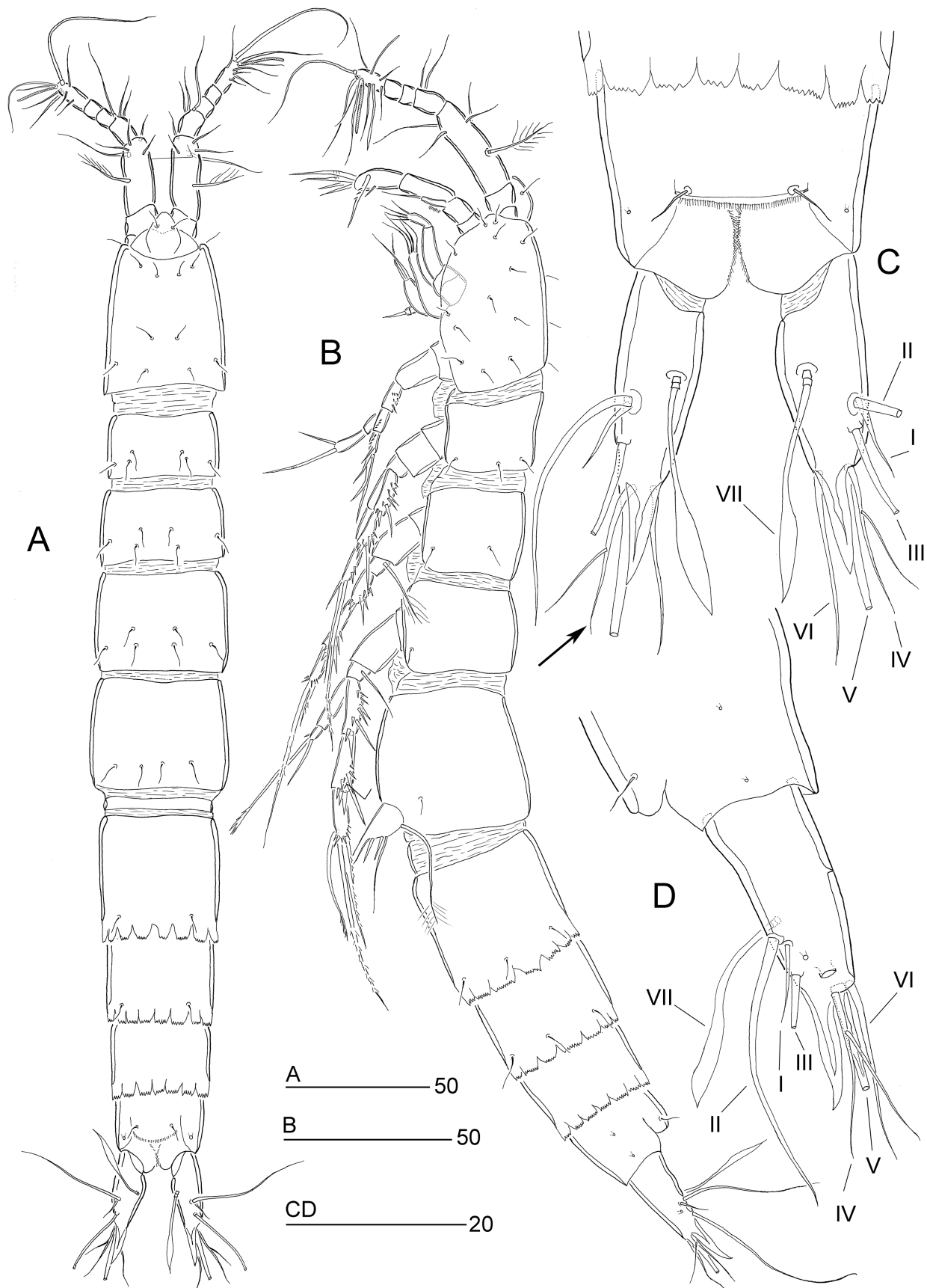


FIGURE 16. *Phreatipontia speluncae* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.** (♀): (A) habitus, dorsal; (B) habitus, lateral; (C) anal somite and caudal rami, dorsal [arrow indicating modified seta IV]; (D) anal somite and right caudal ramus, lateral.

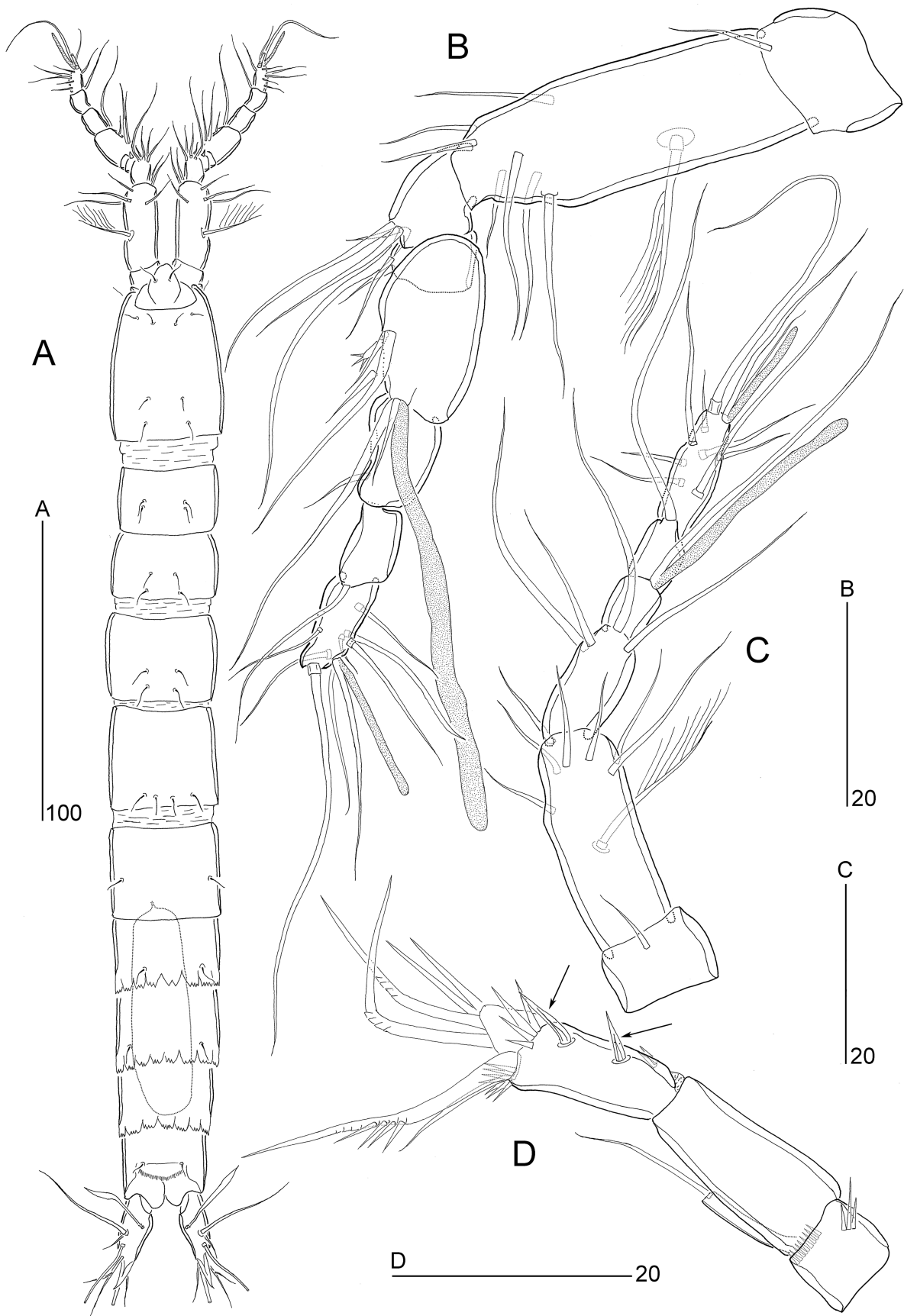


FIGURE 17. *Phreatipontia spelunca* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.:** (A) habitus (♂), dorsal; (B) antennule (♂), ventral; (C) antennule (♀), ventral; (D) antenna (♀), medial [lateral endopodal spines indicated by arrows].

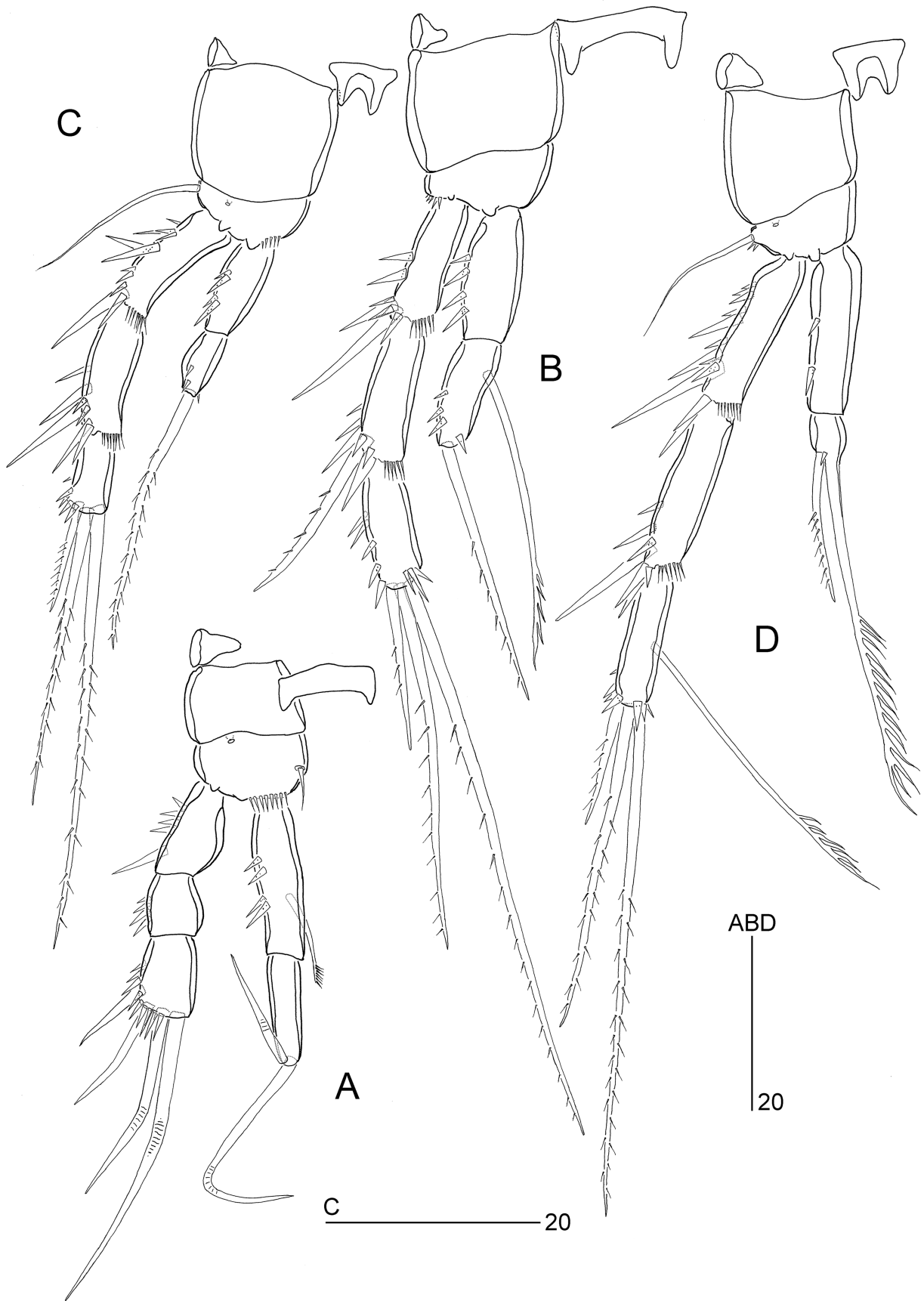


FIGURE 18. *Phreatipontia speluncae* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.** (♀): (A) P1, anterior; (B) P2, anterior; (C) P3, anterior; (D) P4, anterior.

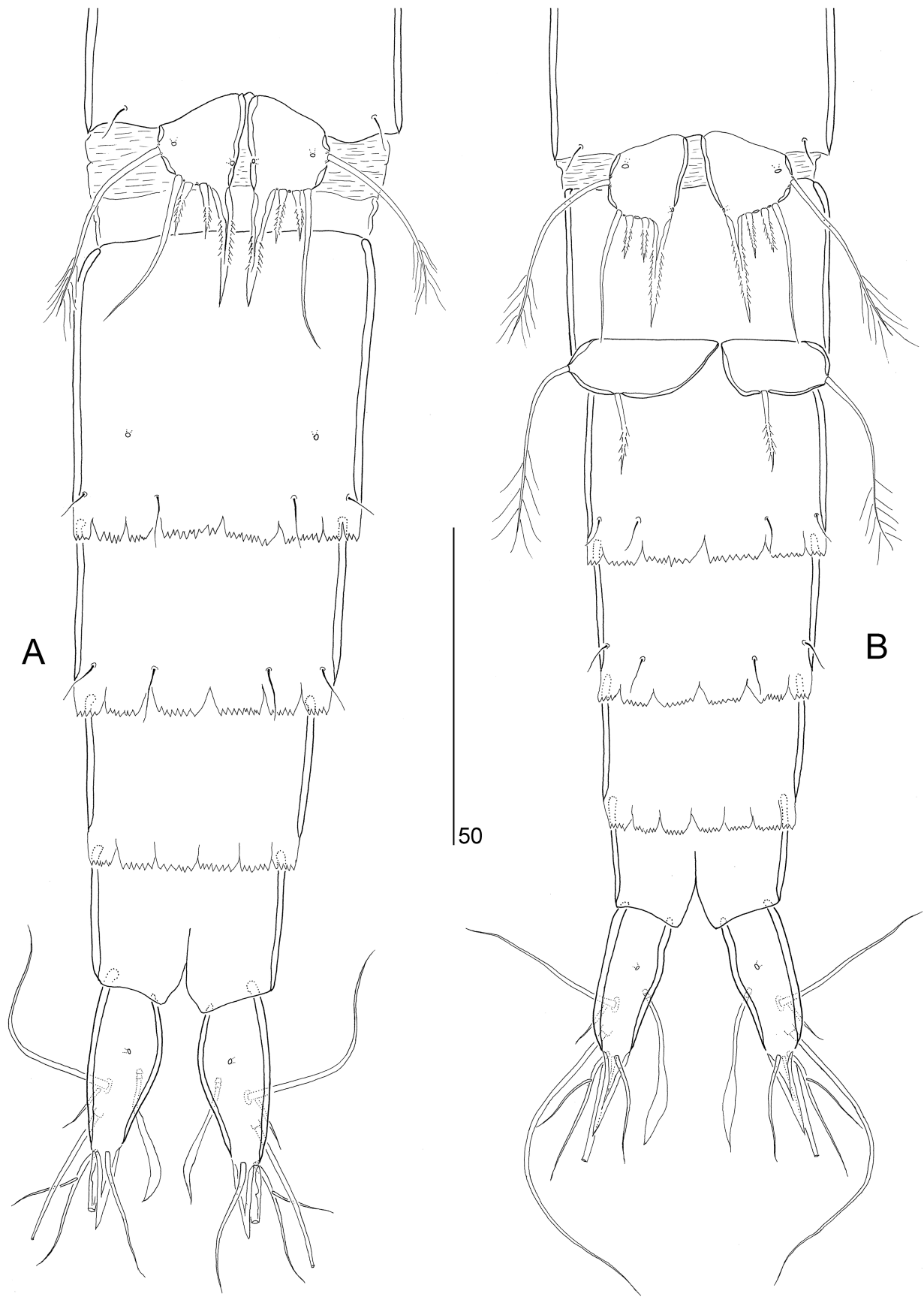


FIGURE 19. *Phreatipontia speluncae* (Cottarelli, Bruno & Venanzetti, 1994) **comb. nov.:** (A) urosome (♀), ventral; (B) urosome (♂), ventral.

P2–P4 (Fig. 18B–D). Intercoxal sclerite naked (P2–P4), rectangular (P2) or squarish (P3–P4) with deeply concave ventral margins. Praecoxae triangular, small and naked. Coxae squarish (P3) or slightly wider than long (P2, P4) and without ornamentation. Bases smaller than coxae, with a spinular row near base of endopod (P2–P3) and a few spinules around outer corner in P2 and P4; anterior surface with a pore in P3–P4; outer basal seta absent in P2, naked in P3–P4. Exopods three-segmented; segments with coarse spinular ornamentation along outer margin; outer spine of exp-1 and exp-2 naked; exp-3 with an outer unipinnate spine and two bipinnate setae distally, P4 exp-3 with additional serrate seta on inner margin; P4 exp-2 only marginally longer than exp-1. Endopods two-segmented; P2–P4 enp-1 unarmed, about 1.2, 1.5, and 4.2 times longer than their respective distal segments, with few coarse spinules along outer margin as figured, but without ornamentation along inner margin; P2–P3 enp-2 with few spinules around distal margin; P2 enp-2 with long, apically serrate, backwardly directed seta near proximal margin and one unipinnate setae apically; P3 enp-2 with long, bipinnate apically; distal margin of P4 enp-2 with long, distally serrate and basally fused, inner seta, and shorter unipinnate, outer seta. Spine and seta formula as follows:

	Exopod	Endopod
P2	0.0.021	0.110
P3	0.0.021	0.010
P4	0.0.121	0.020

Fifth legs (Fig. 19A) closely set together, almost touching medially. Baseoendopod and exopod fused, forming a subrectangular plate with straight distal margin; with one pore on anterior surface; inner distal corner with long, bipinnate spinous process (homologous to inner spine); distal margin with long naked outer seta and two short equally long, bipinnate spines; outer basal seta long and plumose.

Sixth legs vestigial, forming opercula closing off genital apertures.

Redescription of male. Total body length from tip of rostrum to posterior margin of caudal rami 338 μm ($n = 1$). Body ornamentation essentially as in female (Fig. 17A). Sexual dimorphism in antennule, genital segmentation, P5, and P6. Spermatophore length approximately 70 μm .

Antennule (Fig. 17B) 8-segmented, haplocer; geniculation between segments 6 and 7. Segment 1 with a naked seta; segment 2 longest and about 2.7 times longer than wide, with one plumose and seven naked setae; segment 3 with four setae; segment 4 an incomplete sclerite with two setae; segment 5 with four setae, one pinnate spine and a long aesthetasc (43 μm) fused basally to a slender seta; segments 6–7 with one seta each; distal segment with seven setae (none of which spatulate) and apical acrothek consisting of short aesthetasc (16 μm) fused basally to two slender setae. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[4], 4-[2], 5-[4 + (1 + ae)], 6-[1], 7-[1], 8-[7 + acrothek].

P5 (Fig. 19B) essentially as in female but inner spinous process slightly more slender.

Sixth legs (Fig. 19B) asymmetrical, with smallest P6 closing off functional gonopore; each with a long outer plumose seta and a shorter inner bipinnate seta.

Remarks. The report of an inner seta on P3 exp-2 by Cottarelli *et al.* (1994) is extremely doubtful and requires confirmation. No other member in the family Arenopontiidae displays an inner seta on this segment. Our specimens from the Black Sea agree in virtually all other morphological aspects with Cottarelli *et al.*'s (1994) original description, adding further credence to the notion that their illustration of P3 is based on an observational error. The presence of an outer basal seta on P2 (their Fig. 3–e), their statement that the somitic hyaline frills are plain, and the absence of spinular ornamentation on the spinous process of P5 are also questionable and require further examination.

Cottarelli *et al.* (1994) did not observe any variability among the individuals from Sperlonga but illustrated the P5 and caudal ramus of a female from S. Agostino beach without further comment. The fifth leg of the latter deviates from that of the holotype in the shorter spinous process, the longer outer marginal seta (extending well beyond the process) and the general appearance of the two medial elements which are unequal in length and setiform in shape. The dorsal view of the caudal ramus is difficult to compare with the holotype since it was only illustrated in lateral aspect for the latter.

The two described species of *Phreatipontia* **gen. nov.** are morphologically very similar. The type species, *P. speluncae* **comb. nov.**, can primarily be differentiated from *P. phreatica* **comb. nov.** by morphometric differences

in the caudal rami and swimming legs. The exopodal segments of P2–P3 are distinctly more slender and longer in the latter, P2 enp-2 is markedly shorter (enp-1:enp-2 length ratio 1.6 vs 1.2) while P4 enp-1 is longer (enp-1:enp-2 length ratio 5.8 vs 4.2). The caudal rami are generally more slender and longer (L:W ratio 3.9 vs 3.4) in *P. phreatica* **comb. nov.** while the dorsal seta VII is more foliaceous in *P. spelunca* **comb. nov.**

In addition to the type locality, *P. spelunca* **comb. nov.** was also obtained in interstitial freshwater of S. Agostino beach (Gaeta, Latina Province, Lazio) on the banks of a little stream fed by a spring in Grotta del Serpente (Cottarelli *et al.* 1994) and from the mouths of the Fiora River and Valfragida Stream, in the Viterbo Province (Lazio) (Cottarelli *et al.* 1998; Berera 2000). Cottarelli & Berera (2004) also recorded it from the banks of the Fiora River near Montalto di Castro. Our material extends its distribution further into the Black Sea basin. Cottarelli *et al.* (1994) suggested that the species may be restricted to fresh or slightly brackish water but admitted that more data are needed before this can be corroborated. It is conceivable that *P. spelunca* **comb. nov.** (and *P. phreatica* **comb. nov.**) is in the process of colonizing continental subterranean waters (Bruno *et al.* 1998). A third species, apparently close to *P. spelunca* **comb. nov.** and still under study, was discovered in freshwater habitats in Greece (Bruno *et al.* 1998; Bruno & Cottarelli 1999).

Concluding remarks

Neoleptastacus is by far the most speciose genus in the family Arenopontiidae, currently including 24 valid species. Species identification is hampered by the fact that many members are only known from the type locality or a single record, have not been adequately described, or are part of cryptic species complexes (*e.g.* *gussoae*-subgroup) which are difficult to unravel. There is little doubt that some species have repeatedly been misidentified (*e.g.* *N. secundus* and *N. indicus*) while others have mistakenly been treated as conspecific, leading to the misconception that they assume amphi-Pacific or amphi-Panamanian distribution patterns. Although the present review has identified a number of close-knit species groups in *Neoleptastacus*, the relationships between them are as yet not fully understood. A forthcoming phylogenetic analysis including all arenopontiid taxa will assess whether some or all of these groups may be accorded generic status or merely reflect diversification within the genus. This analysis will necessarily assess the phylogenetic significance of previously underrated characters such as male antennule morphology (position of geniculation), presence/absence of a middorsal process on the anal operculum and spinulation patterns on the caudal ramus. Some characters may turn out to be potential apomorphies for particular species-(sub)groups such as the presence of a medial spur on caudal ramus in the *gussoae*-subgroup, the presence of paired processes on the anal somite (*acanthus*-group) or the fusion of the outer distal spine of P3 enp-2 (*spinicaudatus*-group and others?). Others such as the presence of abdominal integumental patterns (*ornamentus*-subgroup and *N. clasingi*) or the shortening of the inner subdistal seta of P4 exp-3 (*N. chaufriassei* and *N. africanus*) are clearly the result of convergence that further complicate analysis of character state evolution in the genus and the family.

Key to genera of Arenopontiidae

1. P1 endopod prehensile, enp-1 distinctly longer than exopod; innermost element of P1 exp-3 penicillate *Arenopontia* Kunz, 1937.
P1 endopod not prehensile, enp-1 not longer than exopod; innermost element of P1 exp-3 geniculate 2.
2. P5 of both sexes with innermost element forming a distinct spinous process which is incorporated in the segment 3.
P5 of both sexes with innermost element not modified (occasionally fused at base) 7.
3. Distal margin of P1 enp-2 with two geniculate setae *Phreatipontia* **gen. nov.**
Distal margin of P1 enp-2 with outer naked spine and inner geniculate seta *Neoleptastacus* Nicholls, 1945 4.
4. Anal somite with paired spinous processes either side of anal operculum *acanthus*-group.
Anal somite without paired spinous processes either side of anal operculum 5.
5. P1 exp-1 without outer spine; distal segment of P1 exopod with three elements; P2 endopod 1-segmented *trisetosus*-group.
P1 exp-1 with outer spine; distal segment of P1 exopod with four elements; P2 endopod 2-segmented 6.
6. Distal segment of P3 endopod with one apical element *australis*-group.
Distal segment of P3 endopod with two apical elements *spinicaudatus*-group.
7. P1 enp-2 with one geniculate seta and one spine; P3 endopod not modified in ♂ *Mesopontia* Sak, Huys & Karaytuğ, 2008.
P1 enp-2 with two geniculate setae; P3 endopod sexually dimorphic 8.
8. P2 enp-2 with inner serrate seta; P3 endopod ♂ two-segmented *Psammoleptastacus* Pennak, 1942.
P2 enp-2 without inner serrate seta; P3 endopod ♂ one-segmented *Onychopontia* Sak, Huys & Karaytuğ, 2008.

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References

- Alper, A. (2009) *Datça-Bozburun özel çevre koruma bölgesi (Muğla, Türkiye) sahillerinin kumiçi ve fital Harpacticoida (Crustacea, Copepoda) faunasının belirlenmesi. Determination of the interstitial and phytal Harpacticoida (Crustacea, Copepoda) fauna of the coast of Datça-Bozburun (Muğla, Turkey) specially protected area*. PhD dissertation, University of Balıkesir, Türkiye, 150 pp. [in Turkish with English summary]
- Alper, A., Karaytuğ, S. & Sak, S. (2010) Interstitial and phytal Harpacticoida (Crustacea: Copepoda) inhabiting the mediolittoral zone of the Datça-Bozburun Peninsulas (Muğla, Turkey). *SDU Journal of Science*, 5, 16–28.
- Alper, A., Sönmez, S., Sak, S. & Karaytuğ, S. (2015) Marine harpacticoid (Copepoda, Harpacticoida) fauna of the Dilek Peninsula (Aydın, Turkey). *Turkish Journal of Zoology*, 39, 580–586.
<https://doi.org/10.3906/zoo-1405-67>
- Berera, R. (2000) *Gli Psammopsyllinae Krishnaswamy 1956 (Copepoda, Harpacticoida) come esempio di colonizzazione delle acque continentali: osservazioni sugli aspetti biologici, ecologici ed evolutivi*. PhD dissertation, Università degli Studi della Tuscia, Viterbo, 121 pp.
- Block, W. (1992) *An Annotated Bibliography of Antarctic Invertebrates (Terrestrial and Freshwater)*. British Antarctic Survey, Cambridge, v + 263 pp.
- Bodin, P. (1967) Catalogue des nouveaux Copépodes Harpacticoides marins. *Mémoires du Muséum national d'Histoire naturelle de Paris*, Nouvelle Série, Series A, 50 (1), 1–76.
- Bodin, P. (1976) Catalogue des nouveaux Copépodes Harpacticoides marins. Additif no. 2. *Téthys*, 7 (2–3), 265–278.
- Bodin, P. (1979) *Catalogue des nouveaux Copépodes Harpacticoides marins (Nouvelle édition)*. Université de Bretagne Occidentale, Brest, 228 pp.
- Bodin, P. (1988) *Catalogue des nouveaux Copépodes Harpacticoides marins (Édition 1988)*. Université de Bretagne Occidentale, Laboratoire d'Océanographie biologique, Brest, 288 pp.
- Bodin, P. (1997) Catalogue of the new marine harpacticoid copepods (1997 Edition). *Studiedocumenten van het K.B.I.N./ Documents de Travail de l'I.R.Sc.N.B.*, 89, 1–304.
- Bodiou, J.-Y. & Colomines, J.-C. (1986) Harpacticoides (Copépodes) des Iles Crozet I. – Description d'une espèce nouvelle du genre *Arenopontia* Kunz. Harpacticoids (Crustacea, Copepoda) from the Crozet Islands. Description of a new species of the genus *Arenopontia* Kunz. *Vie et Milieu*, 36, 55–64.
- Božić, B. (1967) Deux Copépodes Harpacticoides de l'Inde. *Bulletin du Muséum national d'Histoire naturelle, Paris*, Series 2, 38, 869–873.
- Bruno, M.C. & V. Cottarelli, V. (1999) New records of harpacticoids (Crustacea, Copepoda) from subterranean fresh and brackish waters of Greece. *Contributions to the Zoogeography and Ecology of the Eastern Mediterranean Region*, 1, 305–315.
- Bruno, M.C., Cottarelli, V. & Berrera, R. (1998) Preliminary remarks on the cladistic systematics in some taxa of Leptopontiidae and Parastenocarididae (Copepoda, Harpacticoida). *Bolletino. Museo Civico di Storia naturale di Verona*, 2° Serie, 13, 69–79.
- Chappuis, P.-A. (1953) Copépodes Harpacticoides psammiques de Madagascar. *Mémoires de l'Institut scientifique de Madagascar*, Series A, 7, 145–160.
- Chappuis, P.-A. (1954) Harpacticoides psammiques récoltés par Cl. Delamare Deboutteville en Méditerranée. *Vie et Milieu*, 4, 254–276.
- Chappuis P.-A. (1955) Recherches sur la faune interstitielle des sédiments marins et d'eau douce à Madagascar. IV. Copépodes Harpacticoides psammiques de Madagascar. *Mémoires de l'Institut scientifique de Madagascar*, Series A, 9, 45–73.
- Chappuis P.-A. (1958) Harpacticoides psammiques marins des environs de Seattle (Washington, U.S.A.). *Vie et Milieu*, 8, 409–422.

- Chappuis, P.-A. & Delamare Deboutteville, C. (1956) Étude sur la faune interstitielle des îles Bahamas récoltée par Madame Renaud-Debyser. I. Copépodes et Isopodes. *Vie et Milieu*, 7, 373–396.
- Chappuis, P.-A. & Rouch, R. (1961) Harpacticoides psammiques d'une plage près d'Accra (Ghana). *Vie et Milieu*, 11, 605–614.
- Chertoprud, E.S., Frenkel, S.E., Kim, K. & Lee, W. (2015) Harpacticoida (Copepoda) of the northern East Sea (the Sea of Japan) and the southern Sea of Okhotsk: diversity, taxocenes, and biogeographical aspects. *Journal of natural History*, 49, 2869–2890.
<https://doi.org/10.1080/00222933.2015.1056268>
- Cottarelli, V. (1969) Un nuovo Crostaceo di acque interstiziali Italiane: *Psammopsyllus pasquinii* n. sp. –(Harpacticoida, Cylindropsyllidae). *Rendiconti dell'Istituto Lombardo di Scienze e Lettere*, (B) 103, 8–21.
- Cottarelli, V. (1971) Nuove *Parastenocaris* (Copepoda, Harpacticoida) dell'Italia centro-meridionale. Some new species of *Parastenocaris* (Copepoda, Harpacticoida) of the central and southern Italy. *Rivista di Idrobiologia*, 8 (1), 105–132.
- Cottarelli V. (1973a) *Arenopontia gussoae* n. sp., nuovo arpacticoida di acque interstiziali litorali dell'isola di Cuba (Crustacea, Copepoda). *Fragmenta entomologica*, 9, 49–59.
- Cottarelli, V. (1973b) Paramesochridae (Copepoda, Harpacticoida) di acque interstiziali litorali Italiana. *Rivista di Idrobiologia*, 10 (1–2), 19–30.
- Cottarelli, V. (1975) Una nuova *Arenopontia* di acque interstiziali litorali della Sardegna (Crustacea, Copepoda, Harpacticoida). *Fragmenta entomologica*, 11, 65–72.
- Cottarelli, V. & Berera, R. (2004) Il fiume sotto il fiume: ricerche sul popolamento iporreico a crostacei del Fiume Fiora (Italia Centrale). [The river under the river: researches on the hyporheic crustacean community of the Fiora River (Central Italia).] *Studi trentini di Scienze naturali, Acta biologica*, 80, 27–30.
- Cottarelli, V., Bruno, M.C. & Berera, R. (1998) Remarks on the genus *Ichnusella* (Crustacea, Copepoda, Harpacticoida) and description of two new species from subterranean freshwater habitats in Latium and Sardinia, Italy. *Vie et Milieu*, 49, 129–143.
- Cottarelli, V., Bruno, M.C. & Forniz, C. (1996) Copepodi Arpacticoidi e Sincarida (Crustacea) di acque sotterranee delle isole circumsarde. *Biogeographia*, 18, 261–272.
<https://doi.org/10.21426/B618110418>
- Cottarelli, V., Bruno, M.C. & Venanzetti, F. (1994) Ricerche zoologiche della nave oceanografica “Minerva” (C.N.R.) sulle isole circumsarde. XVIII. First record in phreatic freshwater of harpacticoids belonging to the genus *Arenopontia* (Crustacea, Copepoda) and description of two new species. *Annali del Museo Civico di Storia Naturale “Giacomo Doria”*, 90, 471–485.
- Cottarelli, V. & Venanzetti, F. (1989) Ricerche zoologiche della nave oceanografica «Minerva» (C.N.R.) sulle isole circumsarde. II. Cylindropsyllidae del meiobenthos di Montecristo e delle isole circumsarde (Crustacea, Copepoda, Harpacticoida). *Annali del Museo Civico di Storia Naturale “Giacomo Doria”*, 87, 183–235.
- Delamare Deboutteville, C. (1953a) La faune des eaux souterraines littorales des plages de Tunisie. *Vie et Milieu*, 4, 141–170.
- Delamare Deboutteville, C. (1953b) Recherches sur l'écologie et la répartition du Mystacocaride *Derocheilocaris remanei* Delamare et Chappuis, en Méditerranée. *Vie et Milieu*, 4, 321–380.
- Delamare Deboutteville, C. (1953c) La faune des eaux souterraines littorales en Algérie. *Vie et Milieu*, 4, 470–503.
- Delamare Deboutteville, C. (1960) Biologie des eaux souterraines littorales et continentales. *Vie et Milieu*, Supplement 9, 1–740.
- Fricke, A.H., Hennig, H.F.-K.O. & Orren, M.J. (1981) Relationship between oil pollution and psammolittoral meiofauna density of two South African beaches. *Marine environmental Research*, 5, 59–77.
[https://doi.org/10.1016/0141-1136\(81\)90023-4](https://doi.org/10.1016/0141-1136(81)90023-4)
- Hennig, H.F.-K.O., Eagle, G.A., Fielder, L., Fricke, A.H., Gledhill, W.J., Greenwood, P.J. & Orren, M.J. (1983) Ratio and population density of psammolittoral meiofauna as a perturbation indicator of sandy beaches in South Africa. *Environmental Monitoring and Assessment*, 3, 45–60.
<https://doi.org/10.1007/BF00394031>
- Huys, R. (1992) The amphiatlantic distribution of *Leptastacus macronyx* (T. Scott, 1892) (Copepoda: Harpacticoida): a paradigm of taxonomic confusion; and, a cladistic approach to the classification of the Leptastacidae Lang, 1948. *Mededelingen van de Koninklijke Academie voor Wetenschappen, Letteren en schone Kunsten van België*, 54 (4), 21–196.
- Huys, R. (1995) A new genus of Paramesochridae (Copepoda: Harpacticoida) from amphioxus-sand, Elat, Israel. *Journal of natural History*, 29, 673–684.
<https://doi.org/10.1080/00222939500770231>
- Huys, R., Bodiou, J.-Y. & Bodin, P. (1996a) A revision of *Psamthea* (Harpacticoida: Leptastacidae) with description of *P. britannica* sp. nov. *Vie et Milieu*, 46, 7–19.
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468 pp.
- Huys, R., Gee, J.M., Moore, C.G. & Hamond, R. (1996b) Marine and Brackish Water Harpacticoid Copepods. Part 1. In: Barnes, R.S.K. & Crothers, J.H. (Eds.), *Synopses of the British Fauna (New Series)*, 51, Field Studies Council, Shrewsbury, pp. i–viii + 1–352.
- Huys, R. & Iliffe, T.M. (1998) Novocriniidae, a new family of harpacticoid copepods from anchihaline caves in Belize. *Zoologica Scripta*, 27, 1–15.
<https://doi.org/10.1111/j.1463-6409.1998.tb00425.x>

- ICZN [International Commission on Zoological Nomenclature] (1999) *International Code of Zoological Nomenclature*. 4th Edition. The International Trust for Zoological Nomenclature, London, xxx + 306 pp.
- Itô, T. (1968) Descriptions and records of marine harpacticoid copepods from Hokkaido. I. *Journal of the Faculty of Sciences, Hokkaido University, Zoology*, 16, 369–381.
- Itô, T. (1973) The significance of life history study in the benthos research, from the viewpoint of the harpacticoids. *Kaiyo-Kagaku (Marine Sciences Monthly)*, 5 (3), 34–40. [in Japanese with English summary]
- Itô, T. (1978) A new species of marine interstitial harpacticoid copepod of the genus *Arenopontia* from the Bonin Islands, southern Japan. *Annotationes zoologicae japonenses*, 51, 47–55.
- Itô, T. (1984) Studies on the interstitial animals in the Ishikari beach, Hokkaido, northern Japan – a preliminary report. *Benthos Research*, 26, 1–14. [in Japanese with English summary]
- Jayabarathi, R., Padmavati, G. & Anandavelu, I. (2012) Abundance and species composition of harpacticoid copepods from a sea grass patch of South Andaman, India. *Current Research Journal of biological Sciences*, 4, 717–724.
- Kajihara, H., Ikoma, M., Yamasaki, H. & Hiruta, S.F. (2015) *Trilobodrilus itoi* sp. nov., with a re-description of *T. nipponicus* (Annelida: Dinophilidae) and a molecular phylogeny of the genus. *Zoological Science*, 32, 405–417. <https://doi.org/10.2108/zs140251>
- Karanovic, T. (2000) *Arenopontia (Neoleptastacus) huysi*, sp. nov. (Crustacea, Copepoda, Harpacticoida) from marine interstitial of Montenegro (S.E. Europe). *Helgoland marine Research*, 54, 33–38. <https://doi.org/10.1007/s101520050033>
- Karanovic, T. (2008) Marine interstitial Poecilostomatoida and Cyclopoida (Copepoda) of Australia. *Crustaceana Monographs*, 9, 1–336. <https://doi.org/10.1163/ej.9789004164598.i-332>
- Karaytuğ, S. & Sak, S. (2005) A new record of *Psammopsyllus* Nicholls, 1945 (Copepoda, Harpacticoida, Leptopontiidae), with a description of a new species from the Black Sea. *Israel Journal of Zoology*, 51, 135–146. <https://doi.org/10.1560/97VR-LFM4-8YDH-AF9P>
- Kazmi, Q.B. & Naushaba, R. (2000) A survey of coastal marine interstitial arthropods from sandy area of Karachi. In: Ahmed, V.U. (Ed.), *Proceedings of the National ONR Symposium on Arabian Sea as a Resource of Biological Diversity, 18–20 September 2000*. Karachi University Press, Karachi, pp. 129–143.
- Krishnaswamy, S. (1957) *Studies on the Copepoda of Madras*. PhD dissertation, University of Madras, Chennai, Tamil Nadu, 168 pp.
- Kunz, H. (1937) Zur Kenntnis der Harpacticoiden des Küstengrundwassers der Kieler Förde. (Studien an marinen Copepoden I.). *Kieler Meeresforschungen*, 2, 95–115.
- Kunz, H. (1954) Beitrag zur Kenntnis der Harpacticoiden der Deutschen Bucht. *Kieler Meeresforschungen*, 10, 224–228, pls. 27–29.
- Kunz, H. (1971) Harpacticoiden (Crustacea Copepoda) von einem Sandstrand Angolas. *Zoologischer Anzeiger*, 186, 348–357.
- Lang, K. (1948) *Monographie der Harpacticiden. Vols. I & II*. Håkan Ohlsson, Lund, 1682 pp. [pp. 1–896 & pp. 897–1682]
- Lang, K. (1965) Copepoda Harpacticoida from the Californian Pacific coast. *Kungliga Svenska vetenskapsakademiens Handlingar*, Series 4, 10 (2), 1–560.
- Lindgren, E.W. (1972) *Systematics and ecology of North Carolina marine Sandy-beach Harpacticoida (Copepoda: Crustacea)*. PhD dissertation, University of North Carolina, Chapel Hill, North Carolina, 212 pp.
- Lindgren, E.W. (1976) Five species of *Arenopontia* (Copepoda, Harpacticoida) from a North Carolina beach, U.S.A. *Crustaceana*, 30, 229–240. <https://doi.org/10.1163/156854076X00611>
- McLachlan, A. (1980) Intertidal zonation of macrofauna and stratification of meiofauna on high energy sandy beaches in the Eastern Cape, South Africa. *Transactions of the Royal Society of South Africa*, 44, 213–223. <https://doi.org/10.1080/00359198009520563>
- McLachlan, A. & Furstenberg, J.P. (1977) Studies on the psammolittoral meiofauna of Algoa Bay. III. A quantitative analysis of the nematode and crustacean communities. *Zoologica africana*, 12, 61–71. <https://doi.org/10.1080/00445096.1977.11447549>
- Mantha, G., Moorthy, M.S.N., Altaff, K., Dahms, H.-U., Sivakumar, K. & Hwang, J.-S. (2012) Community structure of the Harpacticoida (Crustacea: Copepoda) on the coast of Chennai, India. *Zoological Studies*, 51, 463–475.
- Martínez Arbizu, P. & Moura, G. (1994) The phylogenetic position of the Cyliindropsyllinae Sars (Copepoda, Harpacticoida) and the systematic status of the Leptopontiinae Lang. *Zoologische Beiträge, Neue Folge*, 35, 55–77.
- Masry, D. (1970) Ecological study of some sandy beaches along the Israeli Mediterranean coast, with a description of the interstitial harpacticoids (Crustacea, Copepoda). *Cahiers de Biologie marine*, 11, 229–258. <https://doi.org/10.21411/CBM.A.4943D377>
- Mielke, W. (1975) Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt. *Mikrofauna des Meeresbodens*, 52, 1–134.
- Mielke, W. (1982a) Interstitielle Fauna von Galapagos. XXIX. Darcythompsoniidae, Cyliindropsyllidae (Harpacticoida). *Mikrofauna des Meeresbodens*, 87, 1–52.
- Mielke, W. (1982b) Three variable *Arenopontia* species (Crustacea, Copepoda) from Panamá. *Zoologica Scripta*, 11, 199–207. <https://doi.org/10.1111/j.1463-6409.1982.tb00533.x>

- Mielke, W. (1983) Two new *Psammpsyllus* species (Copepoda) from the Caribbean coast of Panamá. *Studies on neotropical Fauna and Environment*, 18, 101–109.
<https://doi.org/10.1080/01650528309360623>
- Mielke, W. (1985) Interstitielle Copepoda aus dem zentralen Landesteil von Chile: Cylindropsyllidae, Laophontidae, Ancorabolidae. *Microfauna marina*, 2, 181–270.
- Mielke, W. (1987) Interstitielle Copepoda von Nord- und Süd-Chile. *Microfauna marina*, 3, 309–361.
- Mielke, W. (1988) *Apodopsyllus cubensis* n. sp., a new interstitial copepod (Paramesochridae) from Cuba. *Stygologia*, 4, 155–165.
- Munro, A.L.S., Wells, J.B.J. & McIntyre, A.D. (1978) Energy flow in the flora and meiofauna of sandy beaches. *Proceedings of the Royal Society of Edinburgh*, 76B, 297–315.
<https://doi.org/10.1017/S0269727000002943>
- Nagabhushanam, A.K. (1972) Studies on the marine intertidal ecology of the Orissa coast. *Proceedings of the national Institute of Sciences of India*, Biological Sciences, Series B, 38, 308–315.
- Nicholls, A.G. (1945) Marine Copepoda from Western Australia. IV.– Psammophilous harpacticoids. *Journal of the Royal Society of Western Australia*, 29, 17–24.
- Noodt, W. (1955a) Marmara denizi Harpacticoid'leri (Crust. Cop.). Marine Harpacticoiden (Crust. Cop.) aus dem Marmara Meer. *Istanbul Üniversitesi Fen Fakültesi Mecmuası*, Series B, 20, 49–94.
- Noodt, W. (1955b) Harpacticiden (Crust. Cop.) aus dem Sandstrand der französischen Biscaya-Küste. *Kieler Meeresforschungen*, 11, 86–109.
- Pati, S.K., Mahapatro, D., Singhsamant, B. & Panigrahy, R.C. (2009) Intertidal benthic fauna of Gopalpur, east coast of India. *Flora and Fauna*, 15 (2), 310–316.
- Pennak, R.W. (1942) Harpacticoid copepods from some intertidal beaches near Woods Hole, Massachusetts. *Transactions of the American microscopical Society*, 61, 274–285.
<https://doi.org/10.2307/3222599>
- Pugh, P.J.A., Dartnall, H.J.G. & McInnes, S.J. (2002) The non-marine Crustacea of Antarctica and the Islands of the Southern Ocean: biodiversity and biogeography. *Journal of natural History*, 36, 1047–1103.
<https://doi.org/10.1080/00222930110039602>
- Rao, G.C. (1967) On the life-history of a new sand dwelling harpacticoid copepod. *Crustaceana*, 13, 129–136.
<https://doi.org/10.1163/156854067X00297>
- Rao, G.C. (1970) The marine interstitial fauna inhabiting the beach sands of Orissa coast. *Journal of the Zoological Society of India*, 21, 89–104.
- Rao, G.C. (1973) *Trilobodrilus indicus* n. sp. (Dinophilidae, Archiannelida) from Andhra coast. *Proceedings of the Indian Academy of Sciences*, Series B, 77 (3), 101–108.
<https://doi.org/10.1007/BF03045383>
- Rao, G.C. (1975) The interstitial fauna in the intertidal sands of Andaman and Nicobar group of islands. *Journal of the marine biological Association of India*, 17, 116–128.
- Rao, G.C. (1980) On the zoogeography of the interstitial meiofauna of the Andaman and Nicobar Islands, Indian Ocean. *Records of the Zoological Survey of India*, 77, 153–178.
<https://doi.org/10.26515/rzsi/v77/i1-4/1979/161851>
- Rao, G.C. (1987) Meiofauna of the Marine National Park, South Andaman. *Journal of the Andaman scientific Association*, 3, 88–97.
- Rao, G.C. (1989a) Intertidal meiofauna. In: Jairajpuri, M.S. (Ed.), *Fauna of Orissa. Part 2. State Fauna Series 1. Zoological Survey of India*, Calcutta, pp. 1–77.
- Rao, G.C. (1989b) Ecology of the meiofauna of sand and mud flats around Port Blair. *Journal of the Andaman Science Association*, 5 (2), 99–107.
- Rao, G.C. (1991) Meiofauna. In: Jairajpuri, M.S. (Ed.), *Fauna of Lakshadweep. State Fauna Series, 2. Zoological Survey of India*, Calcutta, pp. 41–135.
- Rao, G.C. (1993) Littoral meiofauna of Little Andaman. *Records of the Zoological Survey of India, Occasional Papers*, 155, 1–120.
- Rao, G.C. & Clausen, C. (1970) *Planodasys marginalis* gen. et sp. nov. and Planodasyidae fam. nov. (Gastrotricha Macrodasyoidea). *Sarsia*, 42, 73–82.
<https://doi.org/10.1080/00364827.1970.10411164>
- Rao, G.C. & Misra, A. (1983) Meiofauna from Lakshadweep, Indian Ocean. *Cahiers de Biologie marine*, 24, 51–68.
<https://doi.org/10.21411/CBM.A.FAE78DC2>
- Renaud-Debyser, J. (1963) Recherches écologiques sur la faune interstitielle des sables. Bassin d'Arcachon – île de Bimini, Bahamas. *Vie et Milieu*, Supplement 15, 1–157.
- Rouch, R. (1962) Harpacticoides (Crustacés Copépodes) d'Amérique du Sud. *Biologie de l'Amérique Australe*, 1, 237–280.
- Sak, S. (2004) *Arenopontiidae (Copepoda: Harpacticoida) familyasının taksonomi ve filogenisi. [Taxonomy and phylogeny of the family Arenopontiidae (Copepoda: Harpacticoida)]*. PhD dissertation, University of Balıkesir, Balıkesir, 312 pp.
- Sak, S., Huys, R. & Karaytuğ, S. (2008) Disentangling the subgeneric division of *Arenopontia* Kunz, 1937: resurrection of *Psammolectastacus* Pennak, 1942, re-examination of *Neoleptastacus spinicaudatus* Nicholls, 1945, and proposal of two

- new genera and a new generic classification (Copepoda, Harpacticoida, Arenopontiidae). *Zoological Journal of the Linnean Society*, 152, 409–458.
<https://doi.org/10.1111/j.1096-3642.2007.00373.x>
- Sak, S., Karaytuğ, S. & Huys, R. (2024) A revision of the genus *Arenopontia* Kunz, 1937 (Copepoda, Harpacticoida, Arenopontiidae), including the description of five new species. *Zootaxa*, 5433 (1), 1–50.
<https://doi.org/10.11646/zootaxa.5433.1.1>
- Sevastou, K. (2005) *On the ecology of meiofauna of the sandy shores of Crete: distribution patterns of meiobenthic copepods over space and time*. PhD dissertation, University of Crete, Heraklion, 233 pp. [in Greek with English summary]
- Sevastou, K., Lampadariou, N. & Eleftheriou, A. (2011) Meiobenthic diversity in space and time: The case of harpacticoid copepods in two Mediterranean microtidal sandy beaches. *Journal of Sea Research*, 66, 205–214.
<https://doi.org/10.1016/j.seares.2011.06.004>
- Silva, A.P.C. da (2006) *Efeito da maré na distribuição vertical da meiofauna e de Copepoda Harpacticoida na Praia Arenosa de Maracaípa (Pernambuco, Brasil)*. MSc dissertation, Universidade Federal de Pernambuco, Recife, 56 pp., 16 unnumbered appendices (anexos; 16 pp.). [in Portuguese]
- Sugumaran, J. & Padmasai, R. (2019) Meiofaunal diversity and density of Manamelkudi – an intertidal sandy beach of Palk Bay, India. *Research Journal of Life Sciences, Bioinformatics, pharmaceutical and chemical Sciences*, 5 (2), 31–46.
<https://doi.org/10.26479/2019.0502.03>
- Wandeness, A.P. (1998) *Estrutura espaço-temporal dos Copepoda Harpacticoida em um perfil na região de Macaé, RJ. (Spatio-temporal structure of the Copepoda Harpacticoida on a transect in the region of Macaé, RJ.)*. MSc dissertation, Universidade Federal Fluminense, Niterói, Rio de Janeiro, 69 pp. [in Portuguese]
- Wells, J.B.J. (1967) The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. *Transactions of the Royal Society of Edinburgh*, 67 (7), 189–358.
<https://doi.org/10.1017/S0080456800024017>
- Wells, J.B.J. (1986a) Biogeography of benthic harpacticoid copepods of the marine littoral and continental shelf. In: Schriever, G., Schminke, H.K. & Shih, C.-T. (Eds.), Proceedings II. International Conference on Copepoda, Ottawa, Canada, 13–17 August 1984. *Syllogeus*, 58, pp. 126–135.
- Wells, J.B.J. (1986b) Copepoda: Marine-interstitial Harpacticoida. In: Botosaneanu, L. (Ed.), *Stygofauna Mundi, a Faunistic, Distributional, and Ecological Synthesis of the World Fauna inhabiting Subterranean Waters (including the Marine Interstitial)*. E.J. Brill/Dr. W. Backhuys, Leiden, pp. 356–381.
https://doi.org/10.1163/9789004631977_037
- Wells, J.B.J. (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). *Zootaxa*, 1568 (1), 1–872.
<https://doi.org/10.11646/zootaxa.1568.1.1>
- Wells, J.B.J. & Rao, G.C. (1987) Littoral Harpacticoida (Crustacea: Copepoda) from Andaman and Nicobar Islands. *Memoirs of the Zoological Survey of India*, 16 (4), 1–385.