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Revision of the genus *Evansula* T. Scott, 1906 (Copepoda, Harpacticoida, Cylindropsyllidae) with a description of three new species

RONY HUYS FLS* and SOPHIE CONROY-DALTON

Department of Zoology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

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A revision of the marine mesopsammic genus *Evansula* T. Scott (Copepoda, Harpacticoida, Cylindropsyllidae) is presented. Analysis of type and newly collected material, using both light and scanning electron microscopy, revealed that the genus consists of a complex of morphologically similar species, which frequently occur sympatrically. Redescriptions are provided for *E. incerta* T. Scott (type), *E. pygmaea* T. Scott and *E. arenicola* Nicholls, and published records are reviewed. Three new species, previously confused with either *E. incerta* (***E. polaris* sp. nov.**, ***E. spinosa* sp. nov.**) or *E. pygmaea* (***E. cumbraensis* sp. nov.**) are described from north-western European waters. Scanning electron microscopy revealed that the reported plumosity of certain setae on the P5 is, in reality, a biofouling artefact caused by site-specific, epibiotic, filamentous bacteria. *Evansula* is the only cylindropsyllid genus that has retained inner setae on the P4 endopod and exhibits the ancestral complement of seven setae on the male P5. Its early divergence within the family is further evidenced by the absence of two sexually dimorphic structures in the male, the apomorphic presence of which supports the monophyly of the residual genera: (1) the spinous process on the P2 basis, and (2) the secretory pore on the anterior surface of the male P3 exp-2. The Cylindropsyllidae has recently been relegated to subfamilial status, and as a result was subsumed within the Canthocamptidae. The evidence employed to justify this course of action is critically evaluated and proven essentially unsound. Consequently, the Cylindropsyllidae is reinstated here as a valid taxon. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean* Society, 2006, **147**, 419–472.

ADDITIONAL KEYWORDS: biofouling – Canthocamptidae – *Evansula cumbraensis* sp. nov. – *Evansula polaris* sp. nov. – *Evansula spinosa* sp. nov. – phylogeny – scanning electron microscopy – taxonomy.

INTRODUCTION

In 1906, T. Scott (1906a) established the new genus *Evansia* for two species he had described from the Firth of Forth (Scott, 1892, 1903a) and provisionally assigned to the genus *Tetragoniceps* Brady: *T. incertus* and *T. pygmaeus*. In the same year, Scott (1906b) proposed the replacement name *Evansula*, as Pickard-Cambridge (1900) had already used *Evansia* for a genus of spiders, a course of action that escaped Sars' (1911) attention when he redescribed *E. incerta*. Scott (1906a) designated *T. incerta* as the type species of *Evansia*, but did not do so for *Evansula*. According to the *International Code of Zoological Nomenclature* Art. 67.8 (4th edition), both the prior nominal taxon and its replacement must have the same type species and, therefore, type fixation, for either also applies to the other.

A third *Tetragoniceps* species, *T. trispinosus* A. Scott, 1896, was placed with great reservations as *species incerta* in *Evansula* by Lang (1948). Willems & Claeys (1982) removed this species to their newly established genus *Syrticola*, which was subsequently placed in the Leptopontiidae (Huys & Ohtsuka, 1993). Bodin's (1964) single male specimen from Marseilles, identified as *Evansula* sp.?, is not a cylindropsyllid, but proven upon re-examination to belong to *Parevansula mediterranea* Guille & Soyer (Ameiridae), a conspecificity already hinted at by Guille & Soyer (1966).

With the addition of *E. arenicola* Nicholls, 1939 from the St. Lawrence River (Canada) (Nicholls,

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*Corresponding author. E-mail: rjh@nhm.ac.uk

1939), the number of valid species currently stands at three. However, several authors have expressed difficulties in identifying and separating these species, whereas others have reported on the considerable intraspecific variability, hampering the construction of a reliable species key (Klie, 1929; Kunz, 1938; Nicholls, 1939; Scheibel, 1972; Mielke, 1975). A re-examination of material from a wide range of localities has shown that this alleged variability is largely attributable to a failure to discriminate morphologically similar species, which may or may not occur sympatrically. The aims of this paper are to: (1) provide redescriptions and review published records of *E. incerta*, *E. pygmaea* (female only) and *E. arenicola*; (2) describe three new species previously confused with *E. pygmaea* or *E. incerta*; and (3) discuss the phylogenetic relationships of the genus *Evansula* within the Cylindropsyllidae.

MATERIAL AND METHODS

Before dissection, the habitus was drawn from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid and the parts individually mounted in lactophenol under coverslips, which were subsequently sealed with transparent nail varnish. All drawings were prepared using a camera lucida on a Leica Diaplan or Leica DMR differential interference contrast microscope. The terminology follows that of Huys & Boxshall (1991) for body and appendage morphology and that of Huys *et al*. (1996) for swimming leg formula notations. The setal notation on the female P5 follows Figure 36. The following abbreviations have been used: P1–P6, swimming legs 1–6; exp (enp)-1 (-2-3), proximal (middle, distal) segment of a ramus; ae, aesthetasc. Body length was measured along the dorsal curvature in lateral aspect, from the anterior margin of the rostrum to the posterior margin of the caudal rami. Scale bars in illustrations are in µm.

Females and males of *E. cumbraensis* sp. nov. were examined with a Philips XL 30 scanning electron microscope. Specimens were prepared by dehydration through graded acetone, critical-point dried, mounted on stubs and sputter-coated with palladium.

Type and other material has been deposited in the Natural History Museum, London (NHM). Material termed 'cotypes' by Norman (1912) are specimens given to Norman by the nominal author of a particular species, but were not designated types as recognized by the *International Code of Zoological Nomenclature*. These 'cotypes' often represent the only existing specimens recognized by the nominal author as identical with his species and are extremely valuable for this reason.

SYSTEMATICS

FAMILY CYLINDROPSYLLIDAE SARS, 1909

Various authors (Huys, 1992; Huys & Conroy-Dalton, 1993; Martínez Arbizu & Moura, 1994) have remarked on the polyphyletic status of the family Cylindropsyllidae *sensu* Lang (1948) and the artificiality of its subfamilial division. These problems were partly resolved by upgrading the Leptastacinae to family level (Huys, 1992). In a controversial paper on the phylogenetic position of the Cylindropsyllinae and the systematic status of the Leptopontiinae, Martínez Arbizu & Moura (1994) elevated the latter to the family level and subsumed the Cylindropsyllinae within the Canthocamptidae on the basis of the similarity in the male P3 endopod and the female genital field – two characters they regarded as synapomorphies for the Canthocamptidae. If this is to be adopted as a measure leading to a more natural phylogenetic system, their subsequent failure to find any characters supporting a sister-group relationship between both taxa is, in view of the monophyletic status of the Cylindropsyllinae, a real contradiction in terms. The authors arrived at their conclusions by employing the outmoded character sets selected by Lang (1948) to define the Cylindropsyllinae and the Canthocamptidae. No new phylogenetically informative characters were identified, nor was a detailed analysis of the genera in each family group taxon undertaken. Martínez Arbizu & Moura (1994) used the following two characters to support the incorporation of the Cylindropsyllinae into the Canthocamptidae:

1. Homology of apophysis on the three-segmented P3 endopod in the male. Although the derivation of this apophysis in the Cylindropsyllidae and at least the freshwater component of the Canthocamptidae is now fully understood and proven homologous (Martínez Arbizu & Moura, 1994; R. Huys & S. Conroy-Dalton, unpubl. data), it needs to be stressed that this modification is not a synapomorphy for the Canthocamptidae, as it is found in a wider group of families, including the Louriniidae, Huntemanniidae, Rhizothrichidae, and in all probability also the Cletodidae. Therefore, it cannot be used as evidence for the allocation of the Cylindropsyllinae to the Canthocamptidae.
2. Similarity in structure of the female genital field with a posteriorly displaced copulatory pore. The authors claim that this posterior position is displayed by all genera of the Canthocamptidae, and that they also observed this character in a number of cylindropsyllid genera such as *Evansula*, *Cylindropsyllus* Brady and *Stenocaris* Sars. In reality, the copulatory pore is not posteriorly displaced in the primitive genus *Evansula* (see below) or the more derived *Stenocaris*

(R. Huys, pers. observ.), and does not represent the ancestral state for the family, but has evolved secondarily only in the *Cylindropsyllus*–*Cylinula* Coull lineage. Therefore, the similarity found in both families is a result of convergence.

Moura & Pottek (1998) regarded the pore patterns on the female genital somite (in particular the pore clusters or 'sieves') as an additional synapomorphy supporting a relationship between the Canthocamptinae and Cylindropsyllinae, but this evidence is not convincing. Pore triplets flanking the copulatory pore have been recorded in other families of the canthocamptoid complex, such as the Ancorabolidae (e.g. Conroy-Dalton, 2001), Cletodidae (e.g. Gee, 1994, 1999; Gee & Huys, 1996) and Huntemanniidae (Dahms & Pottek, 1992). In addition to their evolutionary labile nature within families, the phylogenetic significance of genital pore clusters is further limited by their presence in taxa that are not related to the Canthocamptidae and its allies, such as the Miraciidae (Huys & Böttger-Schnack, 1994) and Clytemnestridae (Huys & Conroy-Dalton, 2000).

There is as yet no evidence questioning the monophyly of the Cylindropsyllidae. The unique sexual dimorphism on the male P2 exopod, the structure of the P4, and the composite seta V of the caudal ramus are distinctive synapomorphies for the family. Conversely, it is at present not clear at all what characters define the Canthocamptidae. Martínez Arbizu & Moura's (1994) proposal to amalgamate the Cylindropsyllinae within the Canthocamptidae is also an unwise one for pragmatic reasons. Currently, three subfamilies exclusively containing freshwater genera are recognized in the Canthocamptidae: Canthocamptinae, Morariinae and Epactophaninae. Pesta (1932) lumped all the marine and brackish-water canthocamptids in the catch-all taxon 'Halocanthocamptinae', a family group name that, for nomenclatural reasons, is unavailable as it was not based on the stem of an available genus (in fact the genus name *Halocanthocamptus* has never been proposed). Lang (1948) argued strongly against the recognition of this subfamily and finally abandoned it. The marine genera, however, have never been placed satisfactorily and are still floating in the system of the Canthocamptidae. This state of affairs has inspired other people to include even more marine genera in this family and, in one instance, an entire subfamily was transferred (Por, 1986). The Canthocamptidae, once a morphologically homogeneous, primarily freshwater-inhabiting family, currently contains 55 genera, 18 of which are found in fully marine or estuarine habitats (Boxshall & Halsey, 2004; Karanovic, 2004; Karaytuğ & Huys, 2004). Paradoxically, subsuming the Cylindropsyllidae within this family would increase this number to 27, half of the total number of genera.

Transferring a monophyletic group to a larger polyphyletic group without considering the possible implications this may have is generally regarded as bad practice. The systematic arrangement of the Canthocamptidae has not reached any stability and cannot be expected to do so within the foreseeable future. The Cylindropsyllinae, on the other hand, is a sharply delimited group with definite characteristics that deserves separate family rank. It is not even at all established that the Canthocamptidae, or any subgroup currently contained in it, is the sister taxon of the Cylindropsyllidae, as the characters that would support such a relationship are found in other taxa as well. It is the misapplication of the shared presence of very few characters that has caused the Canthocamptidae to become a repository for anything that could not fit the diagnoses of the other families contained in the second volume of Lang's (1948) monograph. A lack of decisive facts permits every taxonomist to have their own opinion about the rank of groups. However, any objective observer cannot fail to notice the unfortunate consequences of amalgamating various cletodid genera with doubtful affiliations in a loosely defined group, assigning this group the rank of subfamily and accommodating it in the Canthocamptidae (Por, 1986). The concept of the 'Halocanthocamptinae' introduced by Pesta (1932) deserves to be abolished, as Lang (1948) suggested. Yet from the recent addition of the marine Hemimesochrinae (Por, 1964), Cylindropsyllinae (Martínez Arbizu & Moura, 1994), and a group of genera formally designated 'Canthocamptidae *incertae sedis*' (Por, 1986), it seems that this unsatisfactory taxonomic practice is being kept alive by certain taxonomists. Pending a full-blown phylogenetic analysis of the canthocamptoid complex and the arrival of molecular sequence data, we retain the Cylindropsyllidae as a valid family comprising the following genera: *Cylindropsyllus* Brady, 1880; *Evansula* T. Scott, 1906b; *Stenocaris* Sars, 1909; *Cylinula* Coull, 1971; *Boreopontia* Willems, 1981; *Stenocaropsis* Apostolov, 1982; *Willemsia* Huys & Conroy-Dalton, 1993; *Navalonia* Huys & Conroy-Dalton, 1993; and *Selenopsyllus* Moura & Pottek, 1998. Of these, the genus *Cylindropsyllus* is possibly paraphyletic and *Stenocaris* undoubtedly polyphyletic (R. Huys & S. Conroy-Dalton, unpubl. data).

GENUS *EVANSULA* T. SCOTT (1906B)

Synonyms: Tetragoniceps Brady, 1880 [partim]; *Evansia* T. Scott, 1906 a *nec* Pickard-Cambridge (1900).

Diagnosis: Cylindropsyllidae. Body slender, cylindrical. Rostrum elongate, defined at base. Genital double-somite female without chitinous traces marking original segmentation. Copulatory pore large, semicircular, positioned slightly posterior to gonopores. Copulatory duct and paired anterior extensions very well chitinized. Caudal ramus of moderate length, conical; with seven setae; seta I vestigial; seta V with defined flexure zone between proximal styliform and distal flagellate parts, fused to seta IV; seta VI vestigial.

Sexual dimorphism in antennule, P2–P3 (exopod and endopod), P5, P6, ventral ornamentation of anal somite, and in genital segmentation. Occasionally, also in P2 basis (slight), P4 endopod and caudal rami.

Antennule with segment 1 approximately as long as segment 2; segment 2 with nine setae; segment 6 with three setae in female; seven-segmented and with aesthetasc on segments 4 and 7 in female; indistinctly nine-segmented, haplocer and with aesthetasc on segments 5 and 9 in male; apical segment in both sexes with terminal acrothek consisting of two long setae fused basally to slender aesthetasc. Antenna with incompletely fused allobasis and bisetose, one-segmented exopod. Mandible with two-segmented, uniramous palp consisting of unisetose basis and endopod bearing one lateral and four distal setae. Maxillule with one claw and one seta on coxa, five setae plus one claw on basis; endopod and exopod represented by a small, trisetose segment and two setae, respectively. Maxillary endopod discrete, one-segmented, with four setae; proximal endite of syncoxa with three setae/spines. Maxillipeds well developed, subchelate, syncoxa with zero to one seta, endopod represented by strong claw.

P1–P4 with three-segmented exopods and one- (P2–P4) or two-segmented (P1) endopods. P1 with outer and inner seta on basis; exopod with outer spine on middle segment and two geniculate setae plus two spines on distal segment; endopod prehensile, proximal segment longer than exopod, with inner seta being plumose proximally and pinnate distally (except *E. arenicola*), distal segment with two geniculate setae (or spines) and one setule. P2–P4 bases with outer seta. P3 endopod of female with two distal spines. Inner distal spine of P3–P4 exp-3 distinctly shorter than outer distal one. Inner setae of P4 exp-3 and endopod serrate. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.112	1.111
P2	0.0.022	110
P3	0.0.022	020
P4	0.0.122	211

P2 male with inner seta of exp-3 transformed into claw; endopod with slight setal modifications. P3 exopod male usually without or with reduced hyaline frill on exp-1; exp-3 with secretory pore and elongate outer distal seta. P3 endopod male two- or three-segmented; enp-1 minute or incorporated in middle segment; enp-2 (enp-1 if ramus two-segmented) with large apophysis and pinnate seta; enp-3 (enp-2 if two-segmented) with one short seta.

P5 baseoendopod and exopod completely fused, forming elongate plate in both sexes; with eight setae/spines in female; drawn out into spinous pinnate process and with six setae/spines in male. P6 asymmetrical in male, with three setae each; represented by small operculum with three setules in female.

Type species: Tetragoniceps incertus T. Scott, 1892 = *Evansula incerta* (Scott, 1892) [by original designation: Scott (1906a)].

Other species: E. pygmaea (T. Scott, 1903a); *E. arenicola* Nicholls, 1939; *E. cumbraensis* sp. nov.; *E. spinosa* sp. nov.; *E. polaris* sp. nov.

Species incertae: Evansula (?) spec. *sensu* Noodt (1955c).

EVANSULA INCERTA (T. SCOTT, 1892)

Synonyms: Tetragoniceps incertus T. Scott, 1892; *Evansia incerta* (T. Scott, 1892) Scott (1906a).

Original description: Scott (1892: 254–255, plate XII, figs 1–17).

Additional descriptions: All subsequent redescriptions are unreliable, as they were based on another species (Sars, 1911; Wilson, 1932) or on an amalgam of several species of which *E. incerta* may or may not have been part of (Klie, 1929; Kunz, 1935; Scheibel, 1972).

Type locality: Scotland, Firth of Forth, not specified by Scott (1892), but according to a later paper (Scott, 1906b) the types were dredged off St. Monans.

Material examined: (1) NHM, reg. nos. 44505–507: Firth of Forth, Scotland; 2 ♀♀, 1 ♂ in alcohol (labelled as 'cotypes'); coll. T. Scott, 9 September 1894; as part of Cannon A. M. Norman collection (1911.11.8); 1 ♀ (on 11 slides) and 1 ♂ (on seven slides) dissected. This vial also contained 1 ♂ of *E. spinosa* sp. nov. (see below); (2) Royal Museum of Scotland, Edinburgh, reg. no. 1955.63.115: Firth of Forth, coll. T. Scott, June 1901 (labelled *Tetragoniceps incertus*): vial empty.

Redescription

Female: Total body length: 695–710 μm (*N* = 2; mean = 702.5 μm). Body slender, cylindrical (Fig. 1A, B), semi-transparent, light brown; no distinct separation between prosome and urosome. Genital double-somite completely fused (Figs 1B, C, 2D, 6A), original

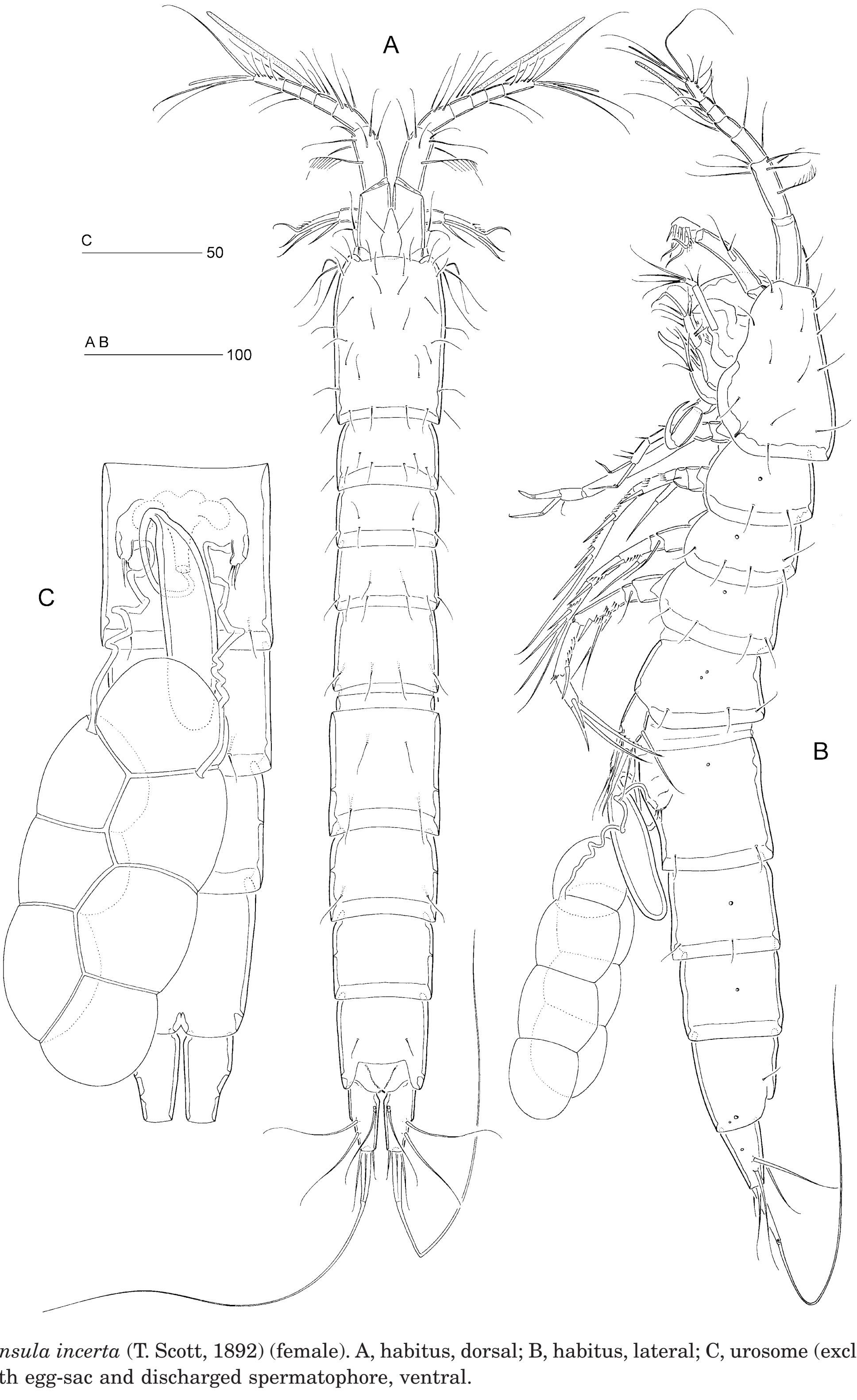

Figure 1. *Evansula incerta* (T. Scott, 1892) (female). A, habitus, dorsal; B, habitus, lateral; C, urosome (excluding P5-bearing somite), with egg-sac and discharged spermatophore, ventral.

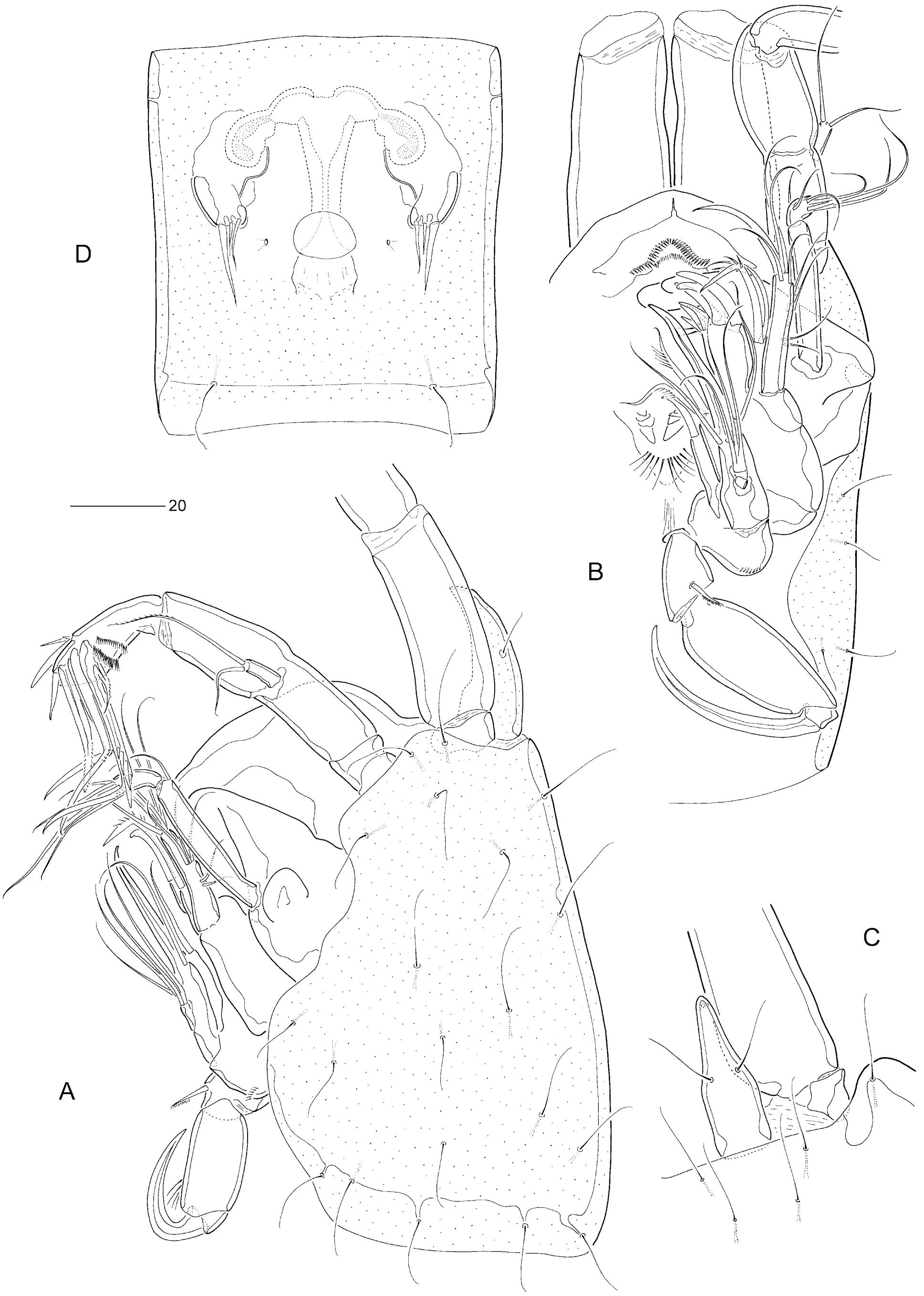

Figure 2. *Evansula incerta* (T. Scott, 1892) (female). A, cephalothorax, lateral (distal antennulary segments and P1 omitted); B, left half of cephalothorax, ventral (P1 and distal segments of antennule and antenna omitted); C, rostral area, dorsal; D, genital double-somite, ventral.

segmentation marked dorsally by paired anterior and posterior sensillae (Fig. 1A). Anal somite only slightly longer than wide (57 × 60 μm), with three pairs of secretory pores laterally (Fig. 6E); posterior margin with two short spinular rows on either side of ventral midline (Fig. 6A, C). Anal operculum weakly developed, unarmed (Fig. 6D).

Caudal ramus conical (Fig. 6A, C), length (measured along the outer margin) approximately 1.9 times the proximal width; dorsal surface without chitinous spur; with seven setae, setae I–VI in distal and seta VII in proximal half (Fig. 1A); seta I diminutive; setae II–III long and bare; seta IV short and bare, approximately half length of styliform part of V (Fig. 6C); seta V long, with distinct flexure zone between styliform part and long distal flagellate part, fused at base with vestigial seta IV; seta VI vestigial; seta VII tri-articulate at base and located along proximal inner margin; ventral surface with one simple and two tube-pores (Fig. 6C), dorsal surface with one tube-pore.

Rostrum elongate (Fig. 2A, C), with parallel margins in proximal half, tapering distally; distinctly shorter than first antennulary segment; demarcated at base; base surrounded by area of flexible integument; with two long sensillae; subapical pore positioned midventrally.

Antennule seven-segmented (Fig. 3A). Segment 1 only slightly shorter than segment 2, with small sclerite around proximal posterior margin, with pattern of spinular rows on anterior surface, as illustrated in Figure 3B; segment 2 longest, without secretory pore; segment 4 with distal cylindrical process bearing large aesthetasc (90 μm). Armature formula: 1-[1], 2-[8 + 1 pinnate], 3-[5], 4-[1 + (1 + ae)], 5-[1], 6-[3], 7-[7 + acrothek]. Apical acrothek consisting of two long setae and one slender aesthetasc (35 μm).

Antenna (Figs 2A, 3C, D) with small unarmed coxa; basis and first endopod segment incompletely fused forming allobasis, abexopodal margin without ornamentation; exopod a narrow segment, with one long, pinnate and one shorter, naked seta apically; endopod with two lateral spines and distal armature consisting of two pinnate spines, two geniculate setae and one large geniculate spine bearing spinules at approximately mid-margin and fused at base with a short, pinnate seta.

Labrum (Fig. 2A, B) a well-developed, ventrally produced extension; distal margin with short, blunt spinules; lateral margins with finer setules.

Mandible (Fig. 4A). Gnathobase well developed; uniramous palp, consisting of basis and one-segmented endopod; basis elongate, with one lateral, pinnate seta; endopod with one outer and four apical setae fused in two clusters.

Maxillule (Fig. 3E). Praecoxal arthrite with ten spines/setae around distal margin and two tubular setae (one long, one rudimentary) on anterior surface. Coxal endite with one geniculate claw and one seta. Basis and rami largely fused into elongate palp; basal armature represented by two lateral setae, and three setae plus a geniculate claw apically. Endopod represented by a small semidiscrete segment with three setae, exopod by two small setae.

Maxilla (Fig. 4B, C). Syncoxa with two endites, proximal endite with three articulating setae, distal endite with one pinnate claw and two setae, all articulating. Allobasis drawn out into a claw-like pinnate endite armed with two additional setae; with a distinct tube-pore. Endopod a discrete segment with four long setae and with a small sclerite around its base (Fig. 4C).

Maxilliped (Figs 2A, B, 3F) well developed, subchelate, directed inwards. Syncoxa well developed, with one pinnate seta and two spinular rows on anterior surface. Basis elongate, with two to three long spinules anteriorly and a spinular row along inner margin posteriorly. Endopod represented by a strong, curved, bare claw.

P1 (Fig. 4D, E). Praecoxa strongly developed. Coxa with three spinular rows. Basis with long, naked, inner seta and short, pinnate, outer seta. Exopod three-segmented; with outer spine on exp-2, with two spines and two geniculate setae on exp-3. P1 endopod prehensile, distinctly longer than exopod; proximal segment approximately ten times as long as average width, with pinnate inner seta being plumose in proximal third; distal segment short, with subdistal setule, and two geniculate spines distally.

Swimming legs P2–P4 (Fig. 5A–F). P4 distinctly longer than P2–P3. Width of intercoxal sclerites decreasing in antero-posterior direction (Fig. 5B, D, E). Praecoxae well developed, with spinular row on anterior surface in P2 and P4. Coxae with pattern of spinules, as in Figure 5A,B,C,D,E,F, with a large tube-pore on anterior surface of P3 and P4. Bases with outer seta (short and pinnate in P2, long and plumose in P3, long and bare in P4); with spinular rows on anterior surface only (Fig. 5A, C, E). Exopods three-segmented, endopods one-segmented. Exopodal spines of P3 minutely serrate; inner distal spine shorter than outer distal one (Fig. 5C). Inner setae of P4 endopod and P4 exp-3 serrate. Inner element of P2 endopod setiform, bare, approximately 0.3 times the length of distal spine. Armature elements of P3 endopod spiniform; inner spine less than half length of outer spine. Seta and spine formulae as for genus.

Fifth pair of legs (Figs 5G, 6A) not fused medially, no distinct intercoxal sclerite. Baseoendopod and exopod fused into a common, elongate plate, tapering distally; apex with strong, articulating spine, distinctly longer than plate and with flagellate tip; outer margin with three sparsely plumose setae (including seta derived from baseoendopod); inner margin with two serrate spines, one pinnate seta and one long, pinnate seta fused to plate; anterior surface with three large tube-pores.

Sixth legs (Fig. 2D) each represented by small operculum closing off gonopore; armature consisting of spiniform outer element and two accessory setules. Genital apertures not fused medially; copulatory pore large, located slightly posterior to gonopores; leading

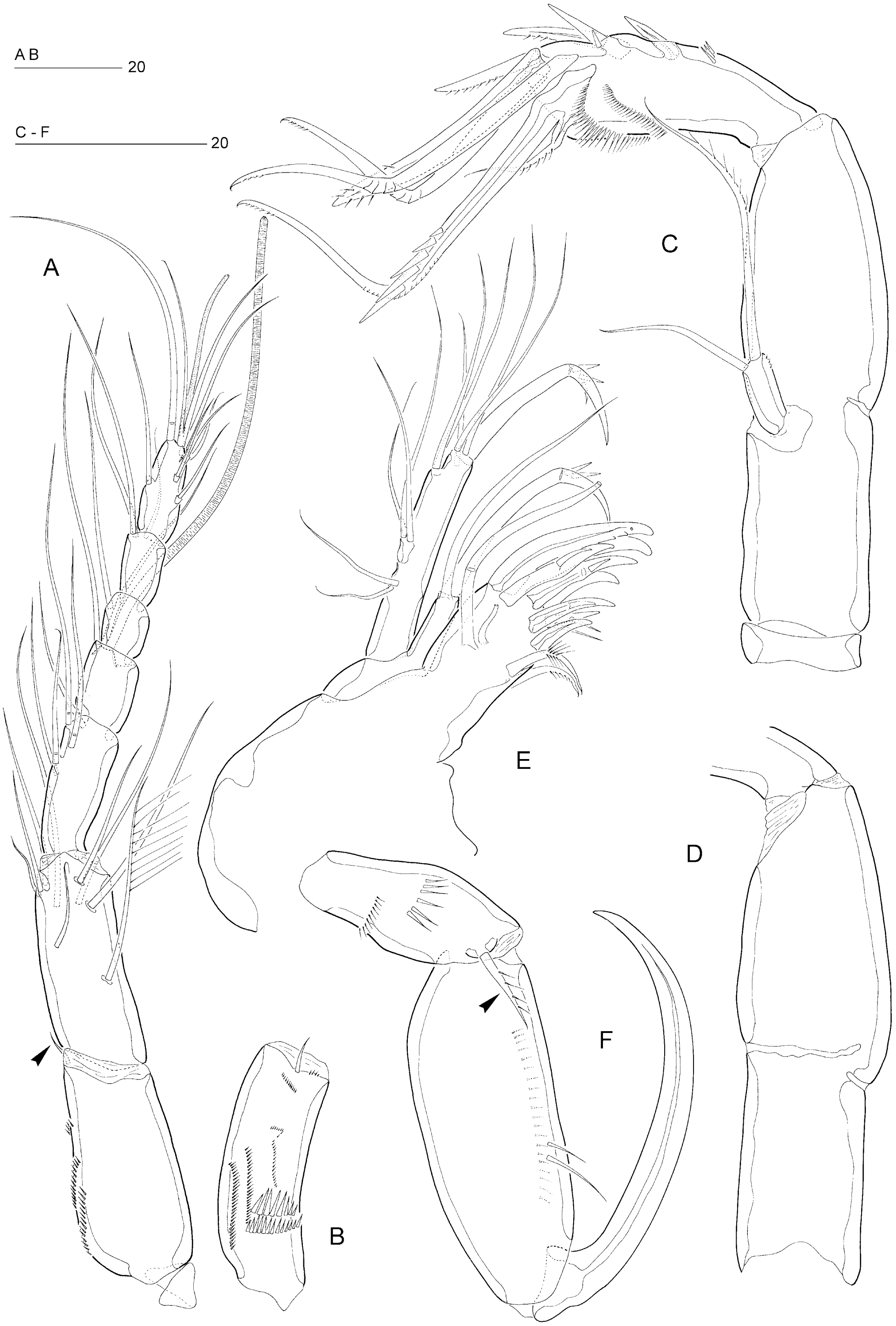

Figure 3. *Evansula incerta* (T. Scott, 1892) (female). A, antennule, dorsal (vestigial seta on segment 1 arrowed); B, first segment of antennule, anterior; C, antenna; D, antennary allobasis, medial; E, maxillule, anterior; F, maxilliped, anterior (syncoxal seta arrowed).

via a short chitinized copulatory duct to paired anterior extensions positioned anterior to genital apertures; copulatory pore flanked by two small secretory pores.

Single egg-sac (Fig. 1B, C) containing approximately seven eggs arranged in a biserial way, enclosed in a common egg-sac membrane; egg-sac connected with each genital aperture via transparent string.

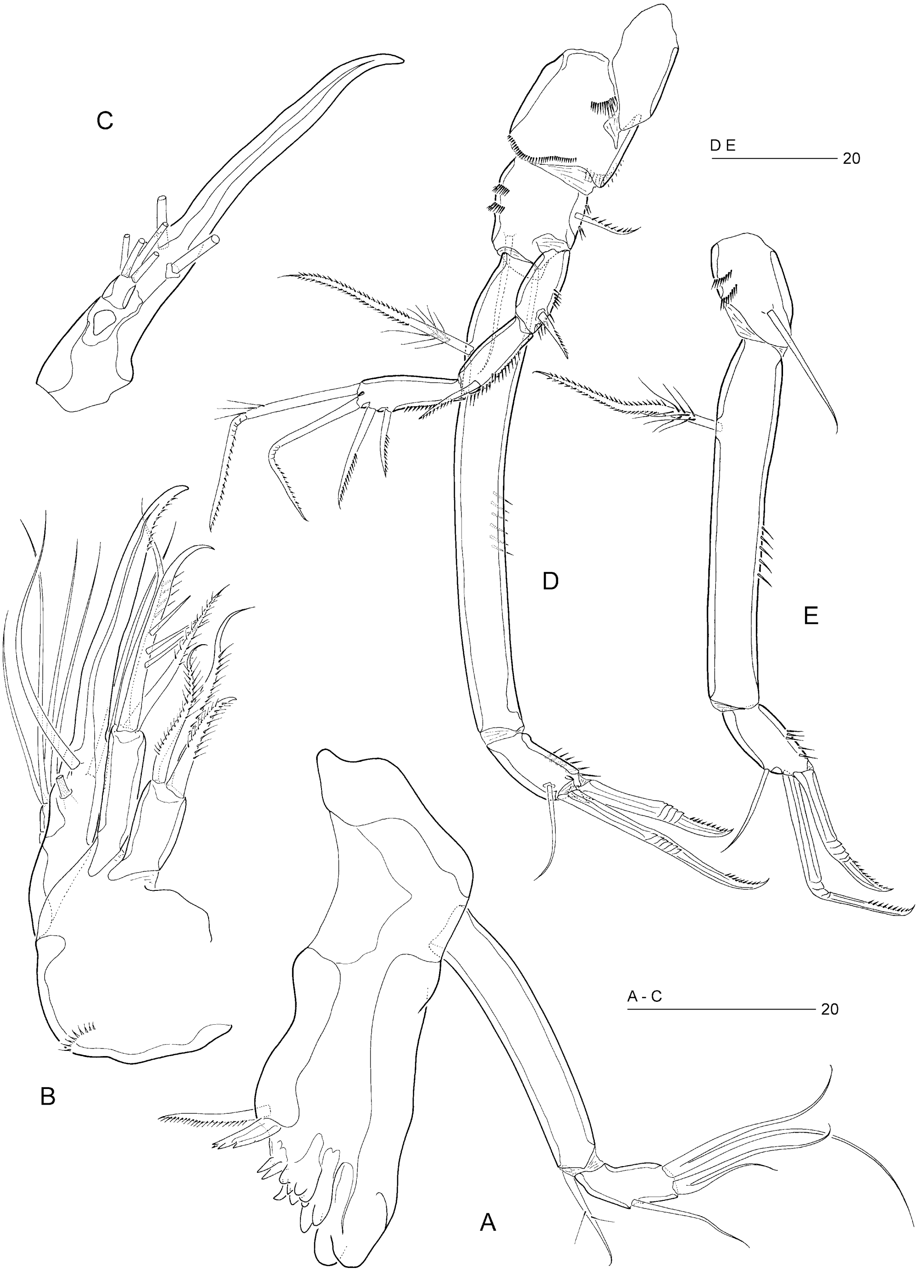

Figure 4. *Evansula incerta* (T. Scott, 1892) (female). A, mandible; B, maxilla; C, maxillary allobasis and endopod, lateral; D, P1, outer lateral; E, P1 basis and endopod, inner lateral (limb foreshortened due to imperfectly flat mounting position on slide).

Male: Body length: 705 µm (Fig. 7A). Spermatophore 110 µm. Anal somite without spinules near ventral anterior (Fig. 6B) and hind margins (Fig. 6B–F).

Antennule (Fig. 7B, C) indistinctly nine-segmented; geniculation between segments 7 and 8; segment 1 with one minute seta and spinular pattern as in female; segment 2 longest, with one plumose and eight naked setae; segment 3 with six setae; segment 4 minute, forming an incomplete ring, with two short setae; segment 5 distinctly swollen, with six elements along the anterior margin and with a distal cylindrical process bearing basally fused seta and large, constricted aesthetasc (53 µm); segment 6 with one long seta and one short pinnate spine; segment 7 with

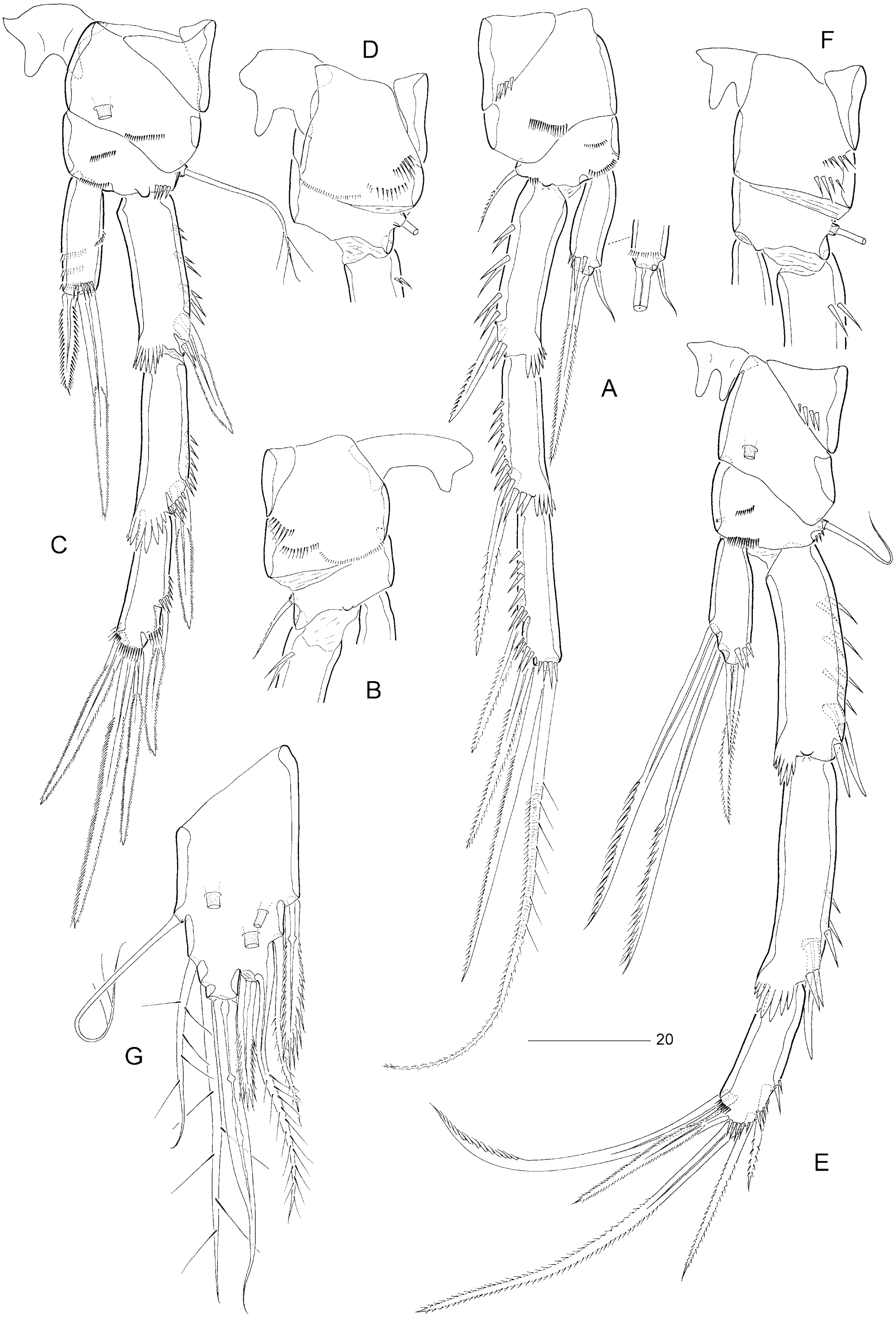

Figure 5. *Evansula incerta* (T. Scott, 1892) (female). A, P2, anterior (inset showing posterior view of distal part of endopod); B, P2 protopod, posterior; C, P3, anterior; D, P3 protopod, posterior; E, P4, anterior; F, P4 protopod, posterior; G, P5, anterior.

three spiniform elements and one seta; segment 8 with one seta and four modified elements (modified as in Figure 24C for *E. cumbraensis*); segment 9 with five posterior setae, one anterior seta and one seta plus an acrothek apically. Apical acrothek consisting of two naked setae and one slender aesthetasc (15 µm).

P2 (Fig. 8A) with inner distal corner of basis not modified into spinous process (as in other cylindrop-

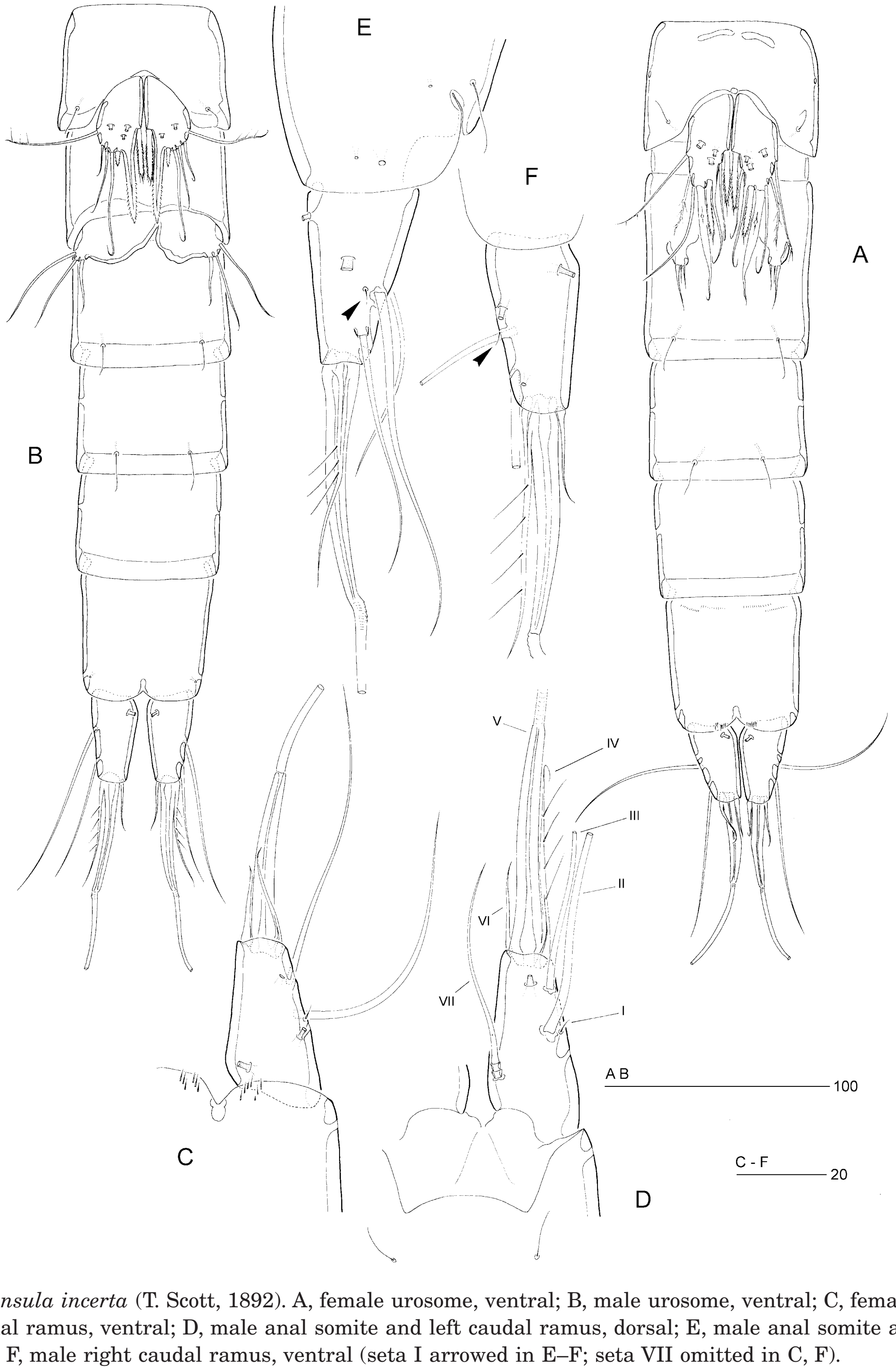

Figure 6. *Evansula incerta* (T. Scott, 1892). A, female urosome, ventral; B, male urosome, ventral; C, female anal somite and right caudal ramus, ventral; D, male anal somite and left caudal ramus, dorsal; E, male anal somite and left caudal ramus, lateral; F, male right caudal ramus, ventral (seta I arrowed in E–F; seta VII omitted in C, F).

syllid genera) but lateral margin more chitinized than in female. Endopod slightly larger than in female; outer margin with more spinules; apical seta distinctly longer, extending beyond distal margin of exp-2, with sparser ornamentation than in female; inner seta larger than in female. Exp-3 modified; outer distal element setiform and distinctly longer than in female; inner distal element transformed into strong claw, directed medially and posteriorly, and with distal half pinnate and tapering to a fine tip.

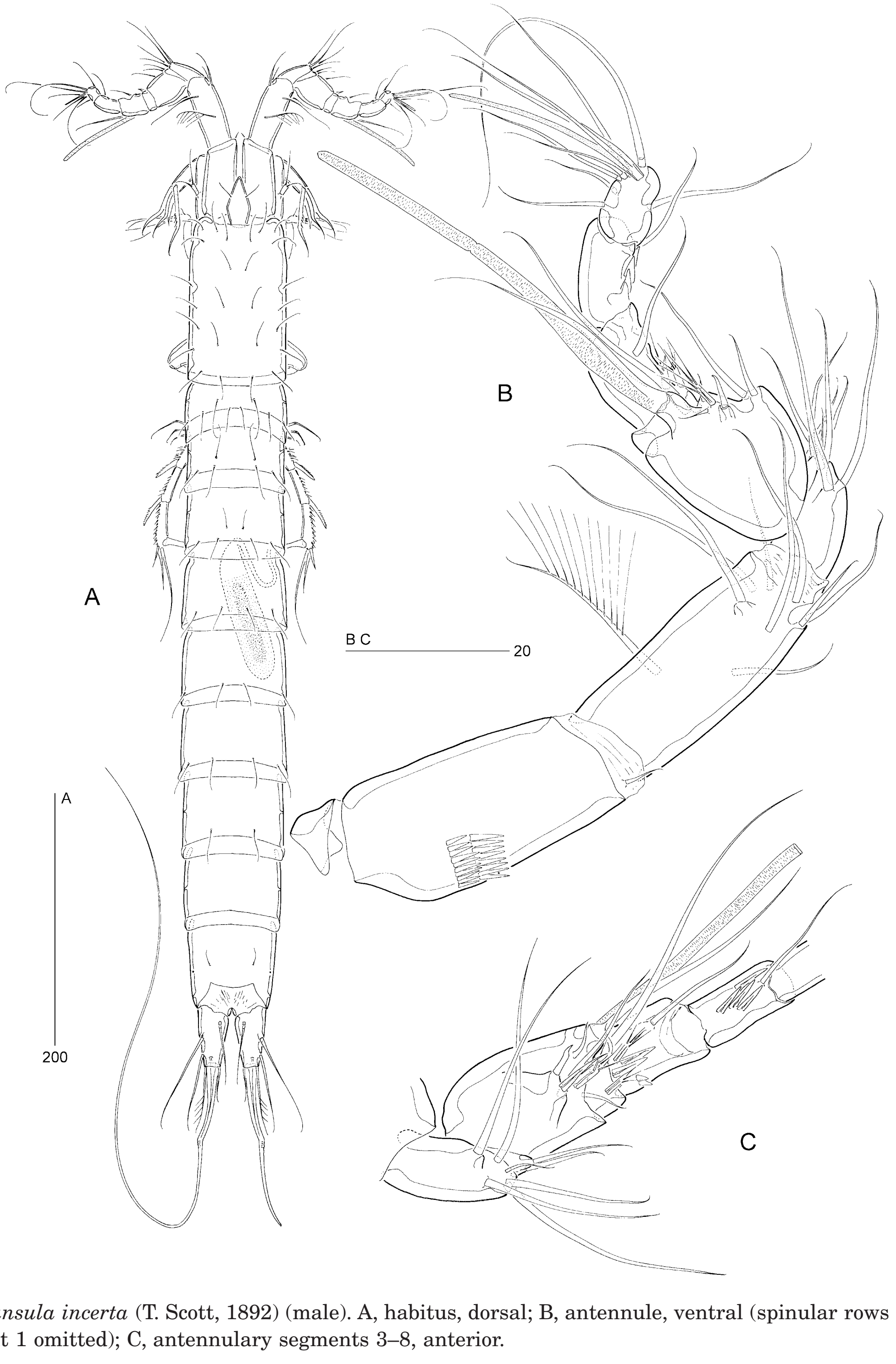

Figure 7. *Evansula incerta* (T. Scott, 1892) (male). A, habitus, dorsal; B, antennule, ventral (spinular rows on dorsal surface of segment 1 omitted); C, antennulary segments 3–8, anterior.

Spines of P3 exopodal segments with pinnate ornamentation (Fig. 8B); exp-1 without hyaline frill; exp-3 with secretory pore on anterior surface near articulation with exp-2; outer distal element of exp-3 setiform and distinctly longer than in female. P3 endopod (Fig. 8B–D) distinctly two-segmented; enp-1 small, with short, serrate, posterior seta and long, rigid apophysis arising from the anterior surface; distal half of apophysis bilaterally compressed (cf. Fig. 8C, D); enp-2 tapering distally, with one short, pinnate seta apically.

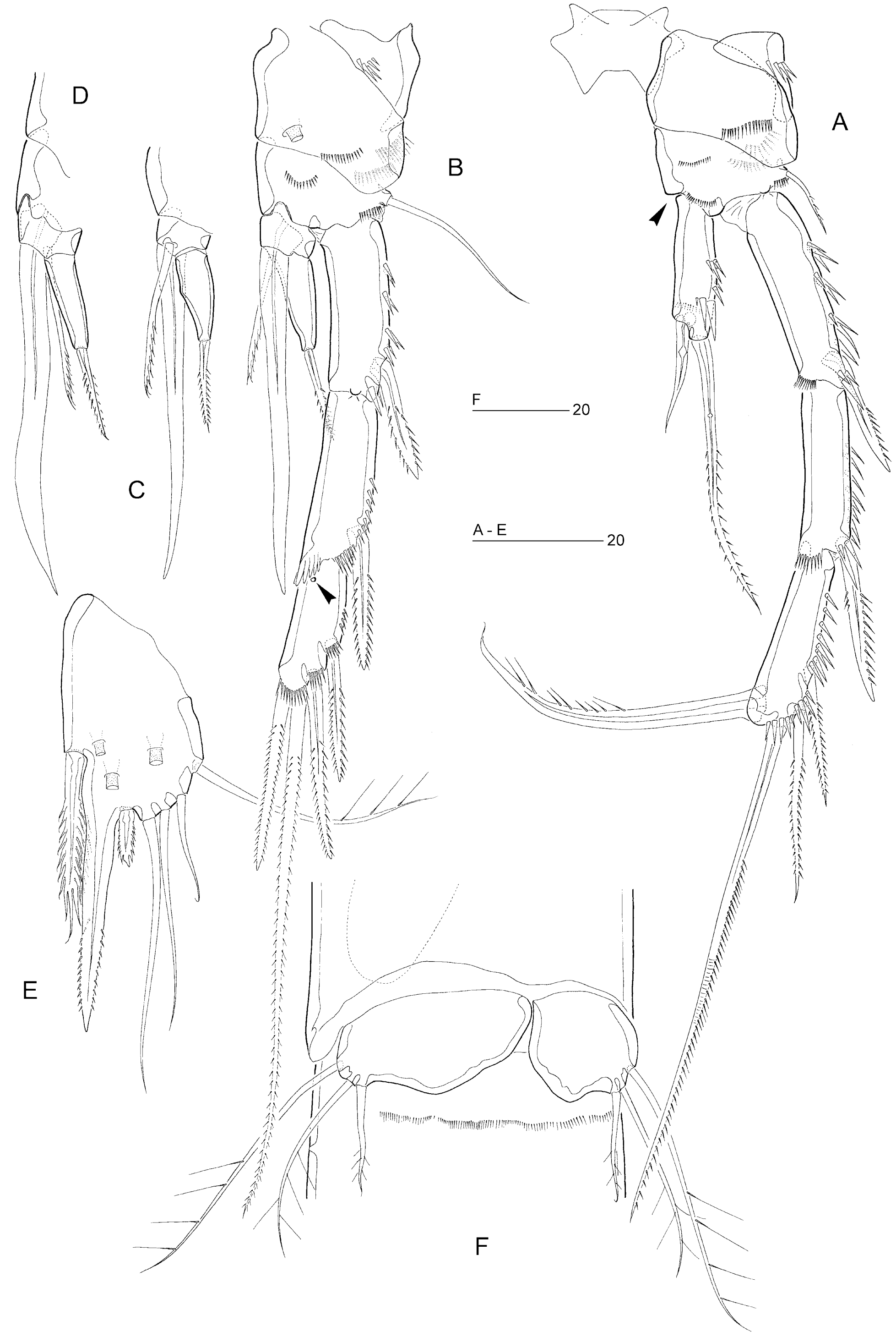

Figure 8. *Evansula incerta* (T. Scott, 1892) (female). A, P2, anterior (position of spinous process in other cylindropsyllid genera arrowed); B, P3, anterior (pore on exp-3 arrowed); C, P3 endopod, posterior; D, P3 endopod, inner lateral; E, P5, anterior; F, sixth pair of legs.

Fifth legs (Figs 6B, 8E) not fused medially, no distinct intercoxal sclerite. Baseoendopod and exopod fused into a common elongate plate, tapering distally towards long, pinnate, spinous process, which is longer than the plate; inner margin with serrate spine; outer margin with small serrate spine, three naked setae and a sparsely plumose seta derived from baseoendopod; anterior surface with three large tube-pores.

Sixth pair of legs (Figs 6B, 8F) asymmetrical, with three sparsely pinnate setae each, decreasing in length medially. Left or right leg articulating according to sinistral or dextral development of testis and vas deferens. First postgenital somite with transverse spinular row near ventral anterior margin (Fig. 8F).

Caudal ramus conical (Fig. 6D–F), slightly longer than in female, length (measured along the outer margin) approximately 2.2 times the proximal width; seta IV long and uniplumose, extending to flexure zone of seta V.

Differential diagnosis: Evansula incerta and *E. arenicola* are the only species in the genus that have retained the syncoxal seta on the maxilliped and that lack the presence of a raised spinular row or spinous process on the dorsal surface of the caudal rami. In both species seta c of the female P5 (cf. Figure 36 for reference position) is fused to the segment. However, this character is also shared by *E. spinosa* sp. nov. Females of *E. incerta* and *E. arenicola* can be differentiated by the general facies of leg 1, the shape of the caudal rami and seta V, the length of the inner distal seta of the P2 endopod, and the presence/absence of ventral anterior spinule rows on the anal somite. Males can be distinguished by the endopodal segmentation of P3 and P4.

Distribution: Scotland: St. Monans in Firth of Forth (Scott, 1892, 1906b).

Although many authors have recorded specimens they attribute to *E. incerta*, there is good reason to believe that in fact they have often mistaken other undescribed species for it. The reasons for this conclusion lie in the frequently repeated statements about the difficulty in differentiating *E. incerta*, *E. pygmaea*, and *E. arenicola*. With the discovery of several new species in the North Sea, the reliability of previously published records from north-western Europe becomes uncertain.

The true state of confusion reigning in the genus is illustrated by the situation in the Firth of Forth – the type locality of both *E. incerta* (St. Monans) and *E. pygmaea* (Musselburgh). Examination of a single, intertidal sandflat sample taken at Elie (near St. Monans) revealed the presence of *E. cumbraensis* sp. nov. (type locality Isle of Cumbrae, and widely distributed in the North Sea) and resulted in the discovery of two other new species, which are currently under study. Surprisingly, the sample did not contain any *E. incerta* or *E. pygmaea*. A re-examination of T. Scott's material of the Forth River produced the second record of *E. spinosa* sp. nov. (type locality Korshavn, Norway), raising the number of *Evansula* species in the Firth of Forth to six.

Evansula incerta of Sars (1911) and at least part of Scheibel's (1972, 1973) material from the Kieler Bucht are in fact *E. spinosa* sp. nov. Scheibel's illustrations of the P5 in different specimens attributed to *E. incerta* raise the suspicion that he was dealing with an amalgam of species. There is no doubt that the American records of *E. incerta* by Wilson (1932) and Coull (1971, 1977) are based on misidentifications and probably all pertain to *E. arenicola*. Scott's (1903b) record from East Finmark (Norway) concerns a different species, here described as *E. polaris* (see below).

All other records provide insufficient information and, consequently, are uncertain at this moment.

Sweden: Hållö (Por, 1964), Isle of Bonden (Por, 1964; Swedmark & Teissier, 1967).

Scotland: River Ythan (Hockin, 1981, 1982a, b, c, 1983, 1984; Hockin & Ollason, 1981).

Wales: Porth-y-Post and Port Swtan (Church Bay), Anglesey (Geddes, 1972).

Germany: Kieler Bucht (Klie, 1929, 1950; Remane, 1933; Kunz, 1935), off Bottsand and Weisenhaus in Kieler Bucht (Noodt, 1956, 1957), Boknis Eck in Kieler Bucht (Scheibel, 1976), Helgoland (Kunz, 1938; Klie, 1950), Isle of Sylt (Noodt, 1952, 1957), Amrum (Noodt, 1957).

Belgium: North Sea coastal zone (Govaere *et al.*, 1980).

France: Kersaint, Finistère (Bodin & Boucher, 1981; Bodin, 1988), Charente-Maritime (Bodin, 1976, 1977), Bassin d'Arcachon, Gironde (Renaud-Debyser, 1963a, b), Contis-Plage, Landes (Noodt, 1955a, b; Delamare Deboutteville, Gerlach & Siewing, 1955; Delamare Deboutteville, 1960).

Hockin (1984) recorded the presumed ectocommensal suctorians *Thecacineta inclusa* Meunier, 1903 and *Thecacineta cothurnoides* Collin, 1909 from *E. incerta* in the River Ythan estuary, Aberdeenshire, Scotland.

EVANSULA PYGMAEA (T. SCOTT, 1903A)

Synonyms: Tetragoniceps pygmæus T. Scott, 1903a; *Evansia pygmæa* (T. Scott, 1903a) Scott (1906a); *Evansula pygmæa* (T. Scott, 1903a) Scott (1906b).

Original description: Scott (1903a: 117–118, plate IV, figs 11–19).

Additional descriptions: None. The additional illustrations given by Mielke (1975) and Martínez Arbizu & Moura (1994) are based on specimens of *E. cumbraensis* sp. nov.

Type locality: Scotland, Firth of Forth, near Musselburgh.

Material examined: NHM, reg. nos 45033–035: Firth of Forth, Scotland; 1 ♀ in alcohol (labelled 'cotype'); coll. T. Scott, 1894; as part of Cannon A. M. Norman collection (1911.11.8); dissected on eight slides.

Redescription

Female: Total body length: 475 µm. Body slender, cylindrical (Fig. 9A, B), semitransparent, yellowish; no distinct separation between prosome and urosome. Genital double-somite completely fused (Figs 9A, B, 12C); original segmentation marked dorsally by paired anterior and posterior sensillae (Fig. 9A, B). Anal somite only slightly longer than wide (50×45 µm), with three pairs of secretory pores laterally (Fig. 12D, E); ventral surface with four rows of tiny spinules near anterior border (Fig. 12D); posterior margin with two short spinular rows on either side of ventral midline (Fig. 12D). Anal operculum weakly developed, unarmed (Figs 10E, 12E).

Caudal rami slightly convergent (Figs 9A, 10E, 12E); distinctly constricted around anterior rim resulting in strongly convex contour of proximal inner margin; length (measured along outer margin) approximately 2.8 times proximal width; dorsal surface without chitinous spur but with raised spinular row anterior to seta VII (Fig. 10E) and with blunt dorsal process (discernible in lateral aspect: Fig. 12E); with seven setae, setae I–VI in distal and seta VII in proximal half (Fig. 10D, E); seta I diminutive; setae II–III long and bare; seta IV long and naked, more than twice the length of styliform part of V; seta V long, with distinct flexure zone between styliform part and long distal flagellate part, fused at base with seta IV; seta VI vestigial and spiniform; seta VII triarticulate at base, somewhat flattened near tip (Fig. 10E) and located along proximal inner margin; ventral and dorsal surfaces with one tube-pore each (Fig. 12D, E).

Rostrum elongate (Fig. 12A), with slightly convex margins in proximal half, tapering distally; distinctly shorter than first antennulary segment (Fig. 9A); with two long sensillae; median pore positioned dorsally near apex of rostrum.

Antennule seven-segmented (Fig. 10A). Segment 1 only slightly shorter than segment 2, with small sclerite around proximal posterior margin, anterior surface with pattern of spinular rows, as illustrated in Figure 10B; segment 2 longest, without secretory pore; segment 4 with distal cylindrical process bearing large aesthetasc (55 µm). Armature formula: 1-[1], 2-[8 + 1 pinnate], 3-[5], 4-[1 + (1 + ae)], 5-[1], 6-[3], 7-[7 + acrothek]. Apical acrothek consisting of two long setae and one slender aesthetasc (25 µm).

Antenna, mandible, maxillule, and maxilla as in *E. incerta*.

Maxilliped (Fig. 12B) well developed, subchelate, directed inwards. Syncoxa well developed, with two spinular rows, without seta. Bases elongate, with two to three long spinules on anterior surface and a spinular row along posterior inner margin. Endopod represented by strong, curved, bare claw.

P1 (Fig. 10C, D). Praecoxa strongly developed, unarmed. Coxa with three spinular rows. Basis with long, semiplumose, inner seta and short, pinnate, outer seta. Exopod three-segmented; with two spines and two geniculate setae on exp-3. P1 endopod prehensile, distinctly longer than exopod; proximal segment approximately nine times as long as average width, with pinnate inner seta being plumose in proximal third; distal segment short, with subdistal setule, and two geniculate spines distally.

Swimming legs P2–P4 (Fig. 11A–F) somewhat more robust than in *E. incerta*. Praecoxae well developed, with spinular row on anterior surface (Fig. 11A, C, E). Coxae with pattern of spinules as in Figure 5A–F, with large tube-pore on anterior surface of P3 (but not P4). Bases with outer seta (short and pinnate in P2, long and plumose in P3, long and bare in P4); with spinular rows on anterior surface only (Fig. 11A, C, E). Exopods three-segmented, endopods one-segmented. Exopodal spines of P3 pinnate (Fig. 11C). P2 endopod approximately 0.8 times as long as exp-1; with two spinular rows on anterior and one spinular row on posterior surface; inner element setiform, pinnate, only slightly shorter than distal spine. Armature elements of P3 endopod spiniform; inner spine approximately half length of outer spine. Seta and spine formulae as for genus.

Fifth pair of legs (Fig. 11G) with baseoendopod and exopod fused into a common elongate plate, tapering distally; apex with strong, articulating spine, slightly longer than plate and with flagellate tip; outer margin with three sparsely plumose setae (including seta derived from baseoendopod), middle and distal ones distinctly shorter than in *E. incerta*; inner margin with three pinnate setae (middle one longer than in *E. incerta*) and one short serrate spine (much shorter than in *E. incerta*); none of armature elements fused to plate; anterior surface with three large tube-pores. Inner margin setae sometimes with foreign tubular filaments attached to individual pinnules.

Sixth legs (Fig. 12C) each represented by a small operculum closing off gonopore; armature consisting of setiform outer element and two accessory setules. Genital apertures not fused medially; copulatory pore large, located slightly posterior to gonopores; leading via short chitinized copulatory duct to paired anterior extensions, positioned anterior to genital

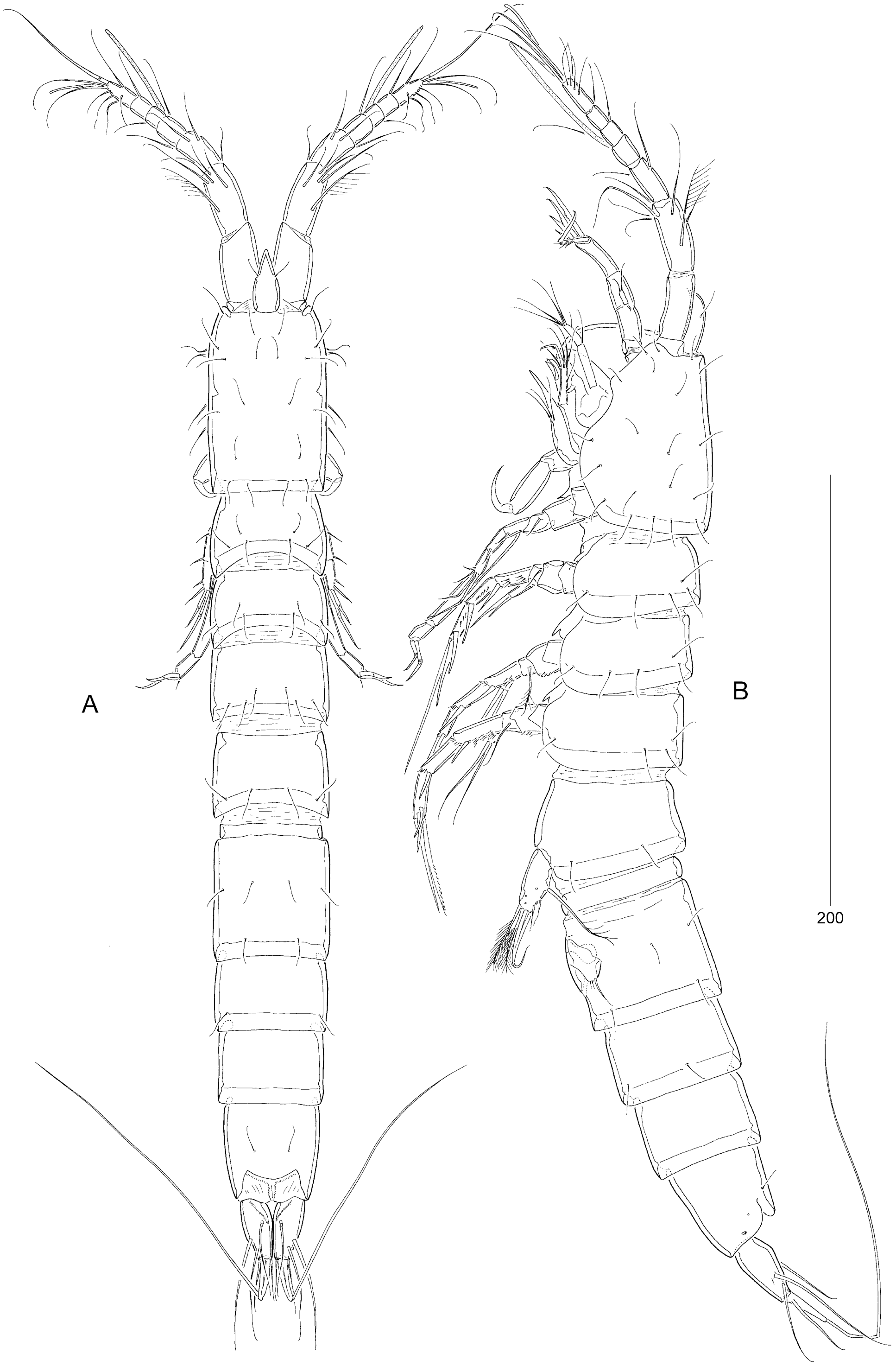

Figure 9. *Evansula pygmaea* (T. Scott, 1903a) (female). A, habitus, dorsal; B, habitus, lateral.

apertures; copulatory pore flanked by two small secretory pores.

Male: Based on Scott's (1903a) original description.

P3 endopod distinctly three-segmented; enp-1 small and unarmed; enp-2 drawn out into long, bent apophysis (the accessory seta on this segment was probably overlooked by T. Scott); enp-3 with one short apical seta.

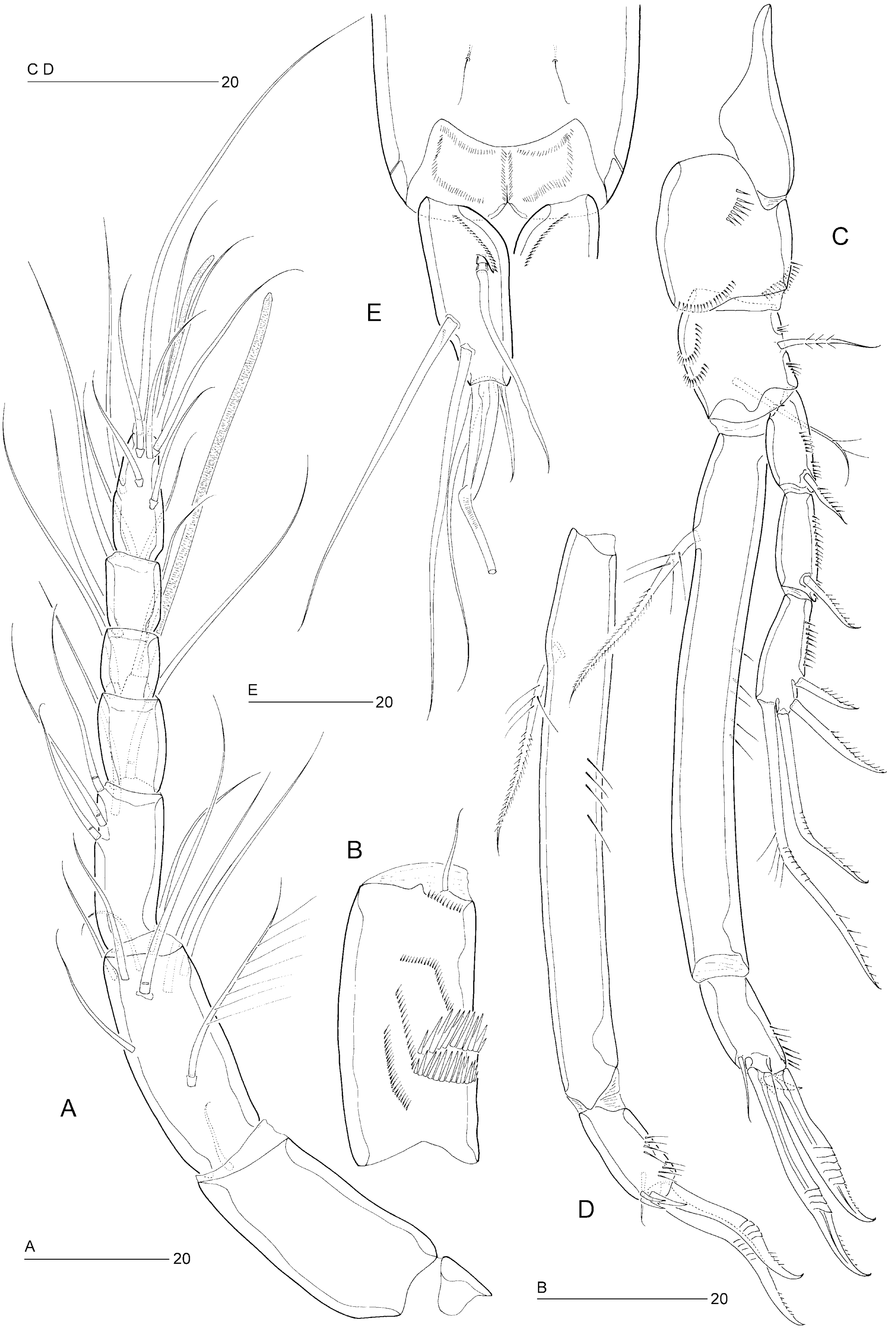

Figure 10. *Evansula pygmaea* (T. Scott, 1903a) (female). A, antennule, dorsal; B, first antennulary segment, anterior; C, P1, anterior; D, P1 endopod, posterior; E, anal somite and caudal rami, dorsal.

P5 baseoendopod and exopod fused into common triangular plate, tapering distally towards curved, naked, spinous process, which is slightly longer than the plate; inner margin with one seta; outer margin with five armature elements, the distalmost one shortest and setiform; no details given about the ornamentation of these elements.

Remark: The plumosity of the long inner setae on the female P5 in Scott's (1903a) original description is an

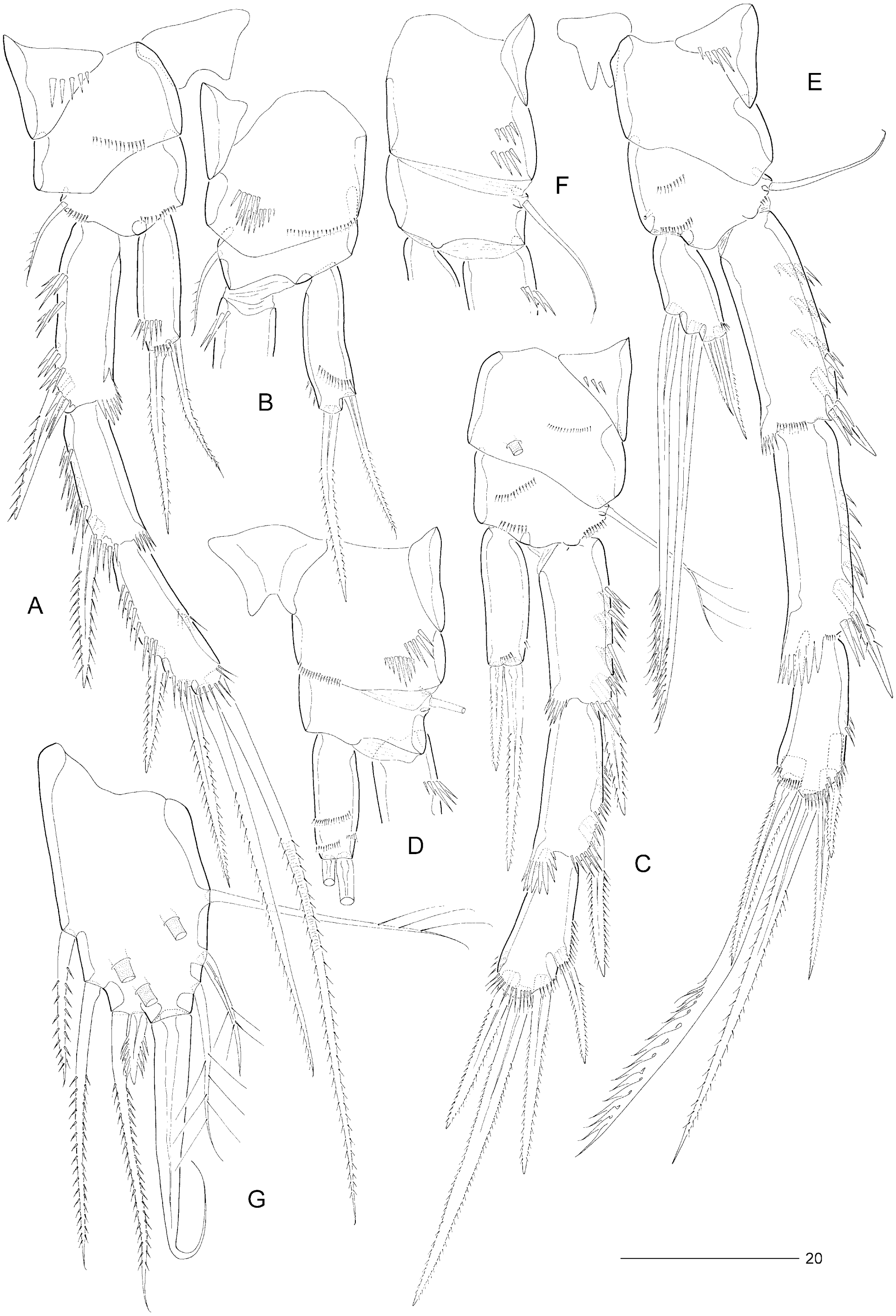

Figure 11. *Evansula pygmaea* (T. Scott, 1903a) (female). A, P2, anterior; B, P2 protopod and endopod, posterior; C, P3, anterior; D, P3 protopod, posterior; E, P4, anterior; F, P4 protopod, posterior; G, P5, anterior.

artefact, being caused by attached filamentous bacterial epibionts.

Differential diagnosis: Perhaps the most characteristic feature of *E. pygmaea* is the peculiar shape of the slightly convergent caudal rami with their strongly convex proximal inner margins. The species is most closely related to *E. cumbraensis* sp. nov. and *E. polaris* sp. nov. with which it shares the raised spinular row on the caudal ramus. *E. pygmaea* differs

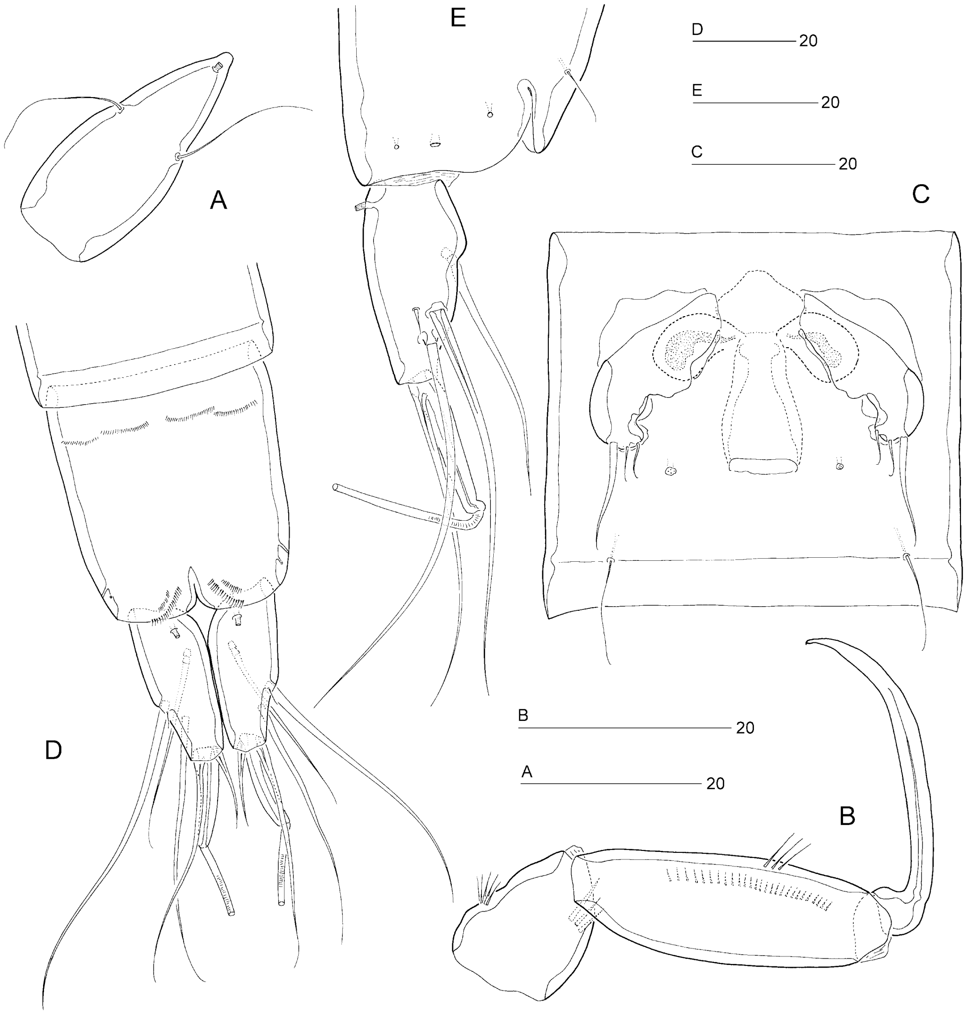

Figure 12. *Evansula pygmaea* (T. Scott, 1903a) (female). A, rostrum, dorsal; B, maxilliped, anterior; C, genital double-somite, ventral; D, anal somite and caudal rami, ventral; E, anal somite and left caudal ramus, lateral.

from *E. cumbraensis* sp. nov. in the length of the outer spines on P2 exp-2 and -3, the size of the copulatory pore, the presence of an anteroventral spinular row on the female anal somite and in both size and ornamentation of the setae on the female P5 (in particular the short inner distal spine). The major discrepancy with the Arctic species is found in the shape and length of the caudal ramus. Provided Scott's (1903a) illustration (plate IV, Fig. 17) is accurate, additional differences can be found in the male P5.

Distribution: Scotland: Musselburgh in Firth of Forth (Scott, 1903a, 1906b).

The following list contains all records attributed to *E. pygmaea* that do not provide enough information for a positive identification to be made.

Scotland: Firemore, Loch Ewe (McIntyre & Murison, 1973), River Ythan (Hockin, 1982c).

Wales: Trearddur Bay, Traeth Lligwy, Traeth Bychan, and Tal-y-Foel, Anglesey (Geddes, 1972).

England: Whitsand Bay, Cornwall (Harris, 1972a, b, c), St. Andrews and St. Agnes, Isles of Scilly (Wells, 1961, 1970), River Exe (Wells, 1963).

Ireland: Silver Strand, Galway (Bodin & Jackson, 1989; Holmes & O'Connor, 1990).

Germany: Isle of Sylt (Noodt, 1952, 1957), Kieler Bucht (Klie, 1929, 1950; Remane, 1933; Kunz, 1935; Scheibel, 1972, 1973; Scheibel & Noodt, 1975; Anger & Scheibel, 1976), Bottsand and Weissenhaus in Kieler Bucht (Noodt, 1956, 1957), Bocknis Eck in Kieler Bucht (Scheibel, 1976), Helgoland (Kunz, 1938; Klie, 1950), Elbe estuary (Riemann, 1966).

The Netherlands: Oosterschelde (Smol *et al.*, 1994), Westerschelde estuary (Van Damme, Heip & Willems, 1984).

Belgium: Sluice Dock, Ostend (Thielemans & Heip, 1984), Kwinte Bank (Willems *et al.*, 1982a, b), coastal zone (Heip, Herman & Vincx, 1984).

EVANSULA ARENICOLA NICHOLLS, 1939

Synonyms: E. incerta (Scott, 1892) *sensu* Wilson (1932).

Original description: Nicholls (1939: 299–302, figs 23, 24).

Additional description: Wilson (1932) (as *E. incerta*).

Type locality: Washings from coarse sand, taken by grab at 8 m depth, at Baie de Mille Vaches on the north shore of the St. Lawrence River, Quebec (Canada).

Material examined: NHM, reg. nos 1940.5.1.73–78: syntypes, 8 ♀♀ and 2 ♂♂ in alcohol; 1 ♀ (on nine slides) and 1 ♂ (on six slides) dissected; leg. A. G. Nicholls, 19 August 1937.

Redescription

Female: Total body length: 710–750 μm ($N = 5$; mean = 730 μm). Body slender, cylindrical (Fig. 13A), semitransparent, yellowish; no distinct separation between prosome and urosome. Genital double-somite completely fused (Figs 13A, 14A); original segmentation marked dorsally by paired anterior and posterior sensillae (Fig. 13A) and ventral chitinous patches (Fig. 14A). Anal somite only slightly longer than wide (84 × 76 μm), with two pairs of secretory pores laterally (Fig. 16D); ventral surface with four rows of tiny spinules near anterior margin (Fig. 14A); posterior margin with two short spinular rows on either side of ventral midline (Fig. 13D). Anal operculum weakly developed, unarmed (Fig. 17E).

Caudal rami slightly divergent, cylindrical except for proximal third, which is swollen both dorsally and medially (Figs 13D, 16D, 17E), length (measured along outer margin) approximately 2.8 times the proximal width; dorsal surface without chitinous spur or raised spinular row; with seven setae, seta VII in proximal third, setae I–II at approximately half ramus length and setae III–VI in distal third (Fig. 17E); seta I diminutive; seta II long and pinnate; seta III long and bare; seta IV relatively long, unipinnate at approximately halfway its length, longer than swollen part of V; seta V long, with distinct flexure zone between short, proximal bulbous part and long, distal flagellate part, fused at base with seta IV (Figs 13D, 17E); seta VI vestigial; seta VII tri-articulate at base and located along proximal inner margin; with three tube-pores, one dorsally, one ventrally, and one laterally (Figs 13D, 16D, 17E).

Rostrum elongate (Fig. 13B), only slightly shorter than first antennulary segment; proximal third with inflated lateral margins, distinctly tapering distally; with two long sensillae; median pore positioned dorsally near apex of rostrum.

Antennule seven-segmented (Fig. 13B). Segment 1 approximately as long as segment 2, with small sclerite around proximal posterior margin, anterior surface with pattern of spinular rows, as illustrated in Figure 13C; segment 2 without secretory pore; segment 4 with distal cylindrical process bearing large aesthetasc (115 μm). Armature formula: 1-[1], 2-[8 + 1 pinnate], 3-[5], 4-[1 + (1 + ae)], 5-[1], 6-[3], 7-[7 + acrothek]. Apical acrothek consisting of two long setae and one slender aesthetasc (40 μm).

Antenna, mandible, maxillule, and maxilla as in *E. incerta*.

Maxilliped (Fig. 14E) well developed, subchelate, directed inwards. Syncoxa well developed, with one pinnate seta and two spinular rows. Basis elongate, with three to four long spinules on anterior surface and a spinular row along posterior inner margin. Endopod represented by strong, curved, sparsely pinnate claw.

P1 (Fig. 15A). Praecoxa strongly developed, with a row of tiny spinules. Coxa with two spinular rows on posterior surface and eight spinular rows on anterior surface. Basis with one posterior and two anterior spinular rows; with long, plumose, inner seta and short, bare, outer seta; anterior surface with secretory pore. Exopod three-segmented; with two spines and two geniculate setae on exp-3. P1 endopod prehensile, distinctly longer than exopod; proximal segment approximately nine times as long as average width, with pinnate inner seta not plumose in proximal third; distal segment short, with three spinular rows, a subdistal pinnate setule, and two geniculate setae distally (both being distinctly longer than in other species).

Swimming legs P2–P4 (Figs 15B, 16A, 17A). P4 distinctly longer than P2–P3. Praecoxae well developed, with spinular row on anterior surface in P2–P4. Coxae with pattern of spinules as in Figures 15B, 16A, 17A; with large tube-pore on anterior surface of P3 and P4. Bases with outer seta (pinnate and spiniform in P2, long and plumose in P3, long and bare in P4); with spinular rows on anterior surface only (Figs 15B, 16A, 17A). Exopods three-segmented, endopods one-segmented. Inner distal spine of P3–P4 exp-3 shorter than outer distal one (Figs 15B, 17A). Inner setae of P4 endopod and exp-3 serrate. Inner element of P2 endopod spiniform, pinnate, less than half length of distal spine. Armature elements of P3 endopod spiniform; of approximately equal length with inner spine, slightly longer than outer. Seta and spine formulae as for genus.

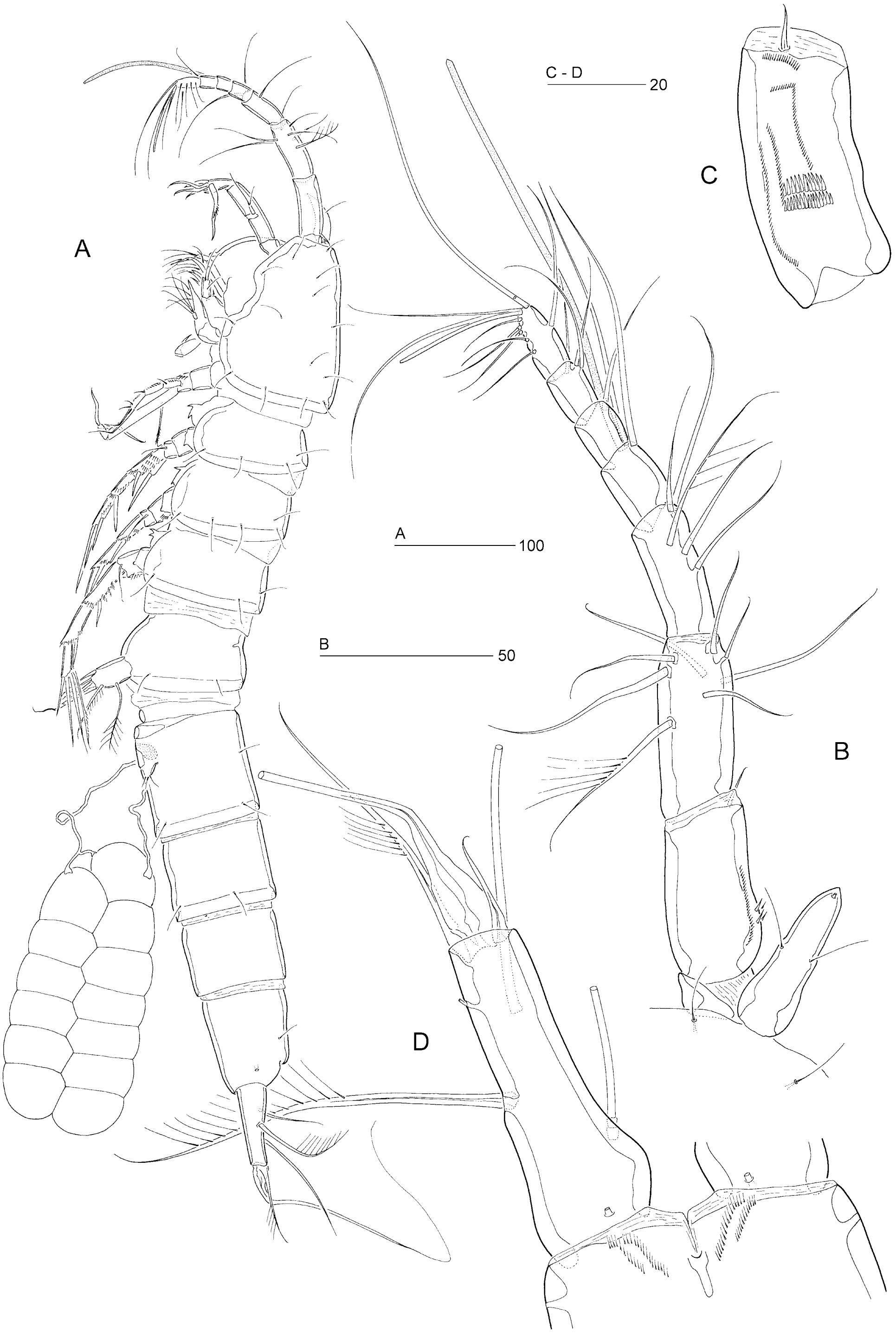

Figure 13. *Evansula arenicola* Nicholls, 1939 (female). A, habitus, ovigerous individual, lateral; B, rostrum and antennule, dorsal; C, first antennulary segment, anterior; D, anal somite and left caudal ramus, ventral.

Fifth pair of legs (Fig. 16C) with baseoendopod and exopod fused into a common elongate plate, tapering distally; apex with strong, articulating spine, approximately as long as the plate and with a flagellate tip; outer margin with three plumose setae (including seta derived from baseoendopod); inner margin with two serrate spines, one plumose seta, and one long, pinnate seta fused to plate and distinctly swollen in proximal half; anterior surface with three large tube-pores.

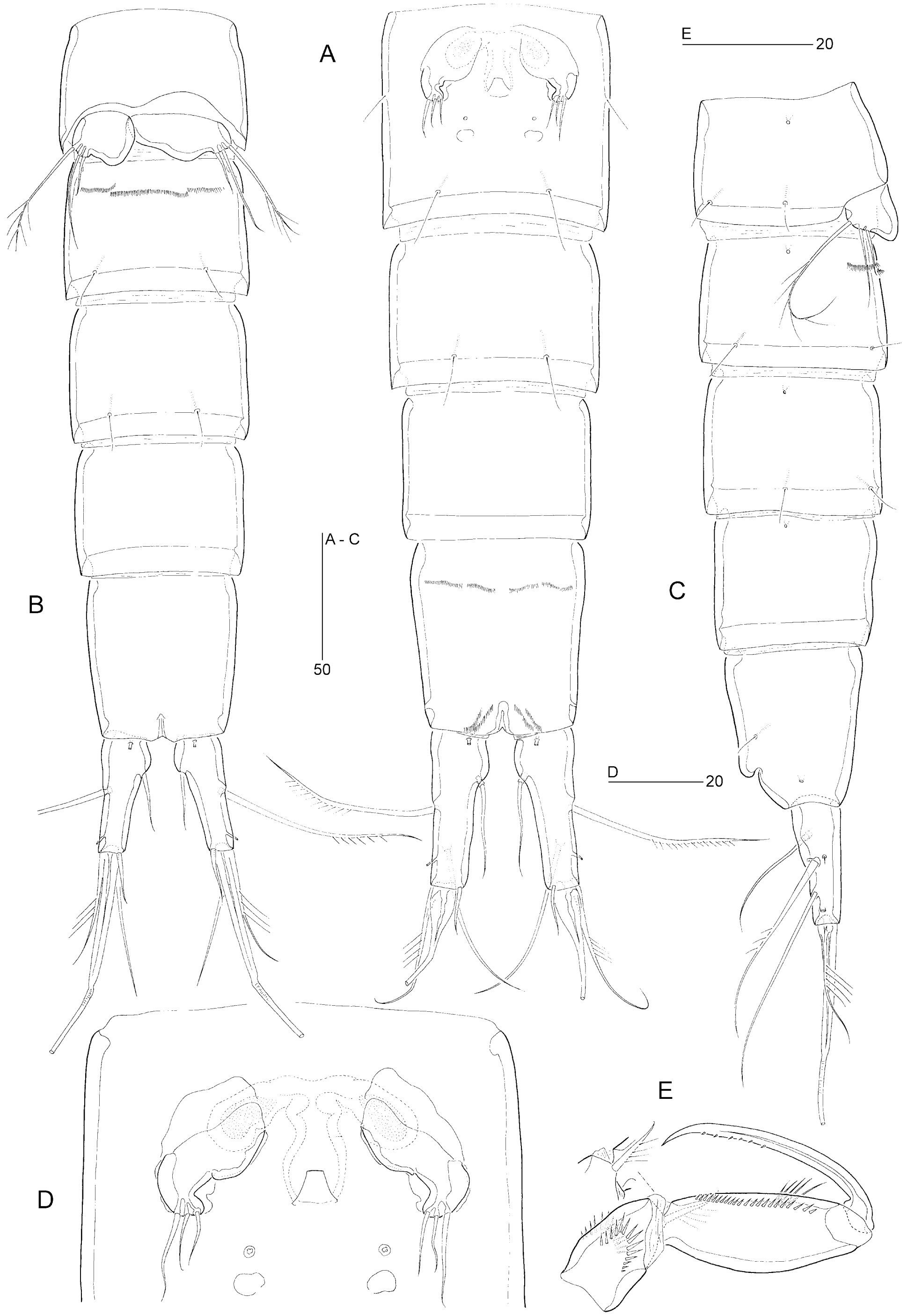

Figure 14. *Evansula arenicola* Nicholls, 1939. A, female urosome (excluding P5-bearing somite), ventral; B, male urosome (excluding P5-bearing somite), ventral; C, male urosome (excluding P5-bearing somite), lateral; D, female genital field, ventral; E, maxilliped, posterior (inset showing syncoxal seta in anterior view).

Sixth legs (Fig. 14A, D) each represented by small operculum closing off gonopore; armature consisting of three setiform elements with outer slightly longer than others. Genital apertures not fused medially; copulatory pore of moderate size, located slightly anterior to gonopores; leading via short chitinized copulatory duct to paired anterior extensions positioned anterior to genital apertures; copulatory pore flanked by two small secretory pores.

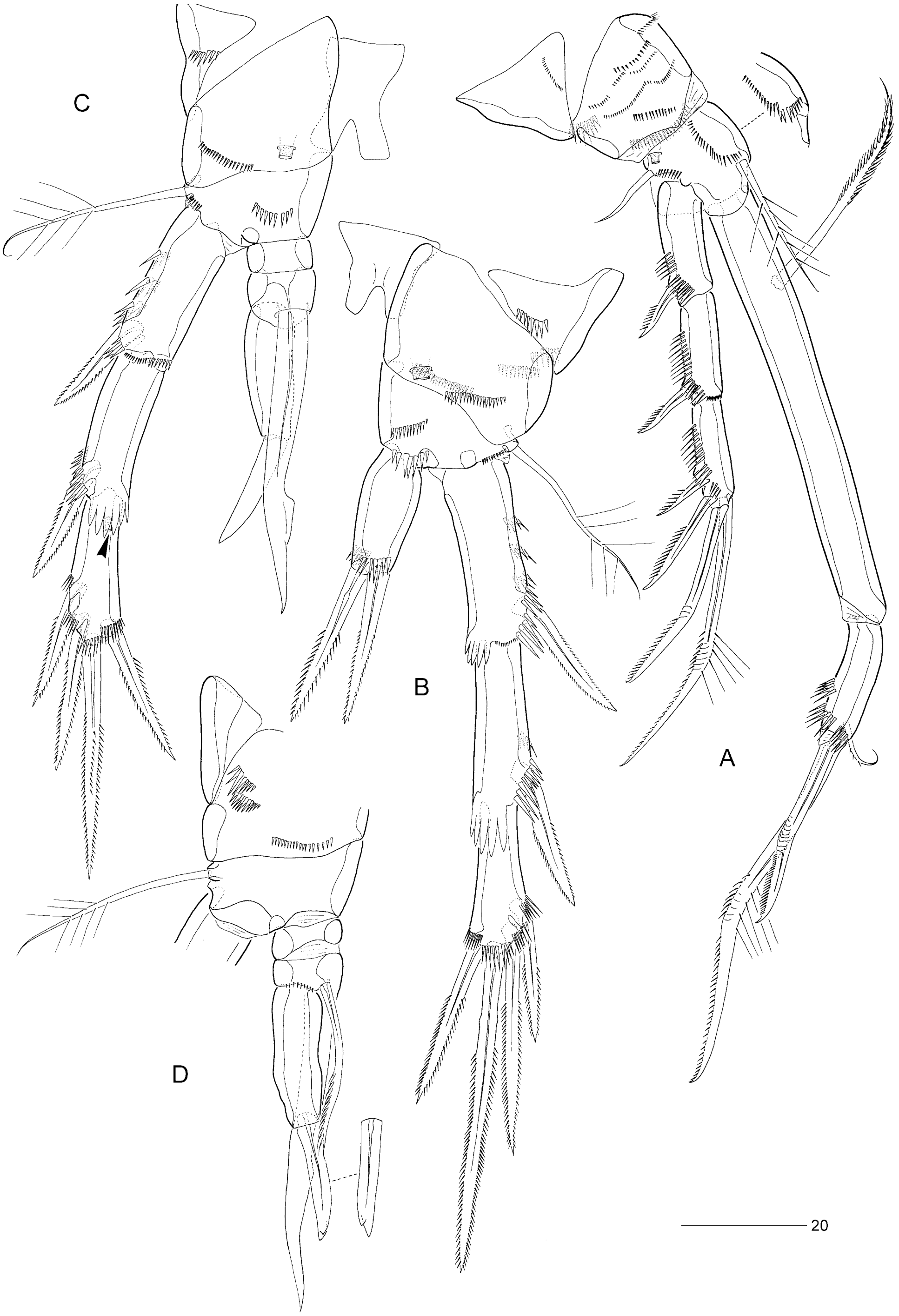

Figure 15. *Evansula arenicola* Nicholls, 1939. A, female P1, anterior (inset showing posterior view of inner basal margin); B, female P3, anterior; C, male P3, anterior (secretory pore on exp-3 arrowed); D, male P3 protopod and endopod, posterior (inset showing lateral view of distal spine).

Single egg-sac (Fig. 13A) containing approximately 12–13 eggs arranged biserially, enclosed in a common egg-sac membrane; egg-sac connected with each genital aperture via transparent string.

Male. Body length: 690 µm. Spermatophore 100 µm. Anal somite without spinules on ventral anterior or hind margins (Fig. 14B).

Antennule as in *E. incerta*.

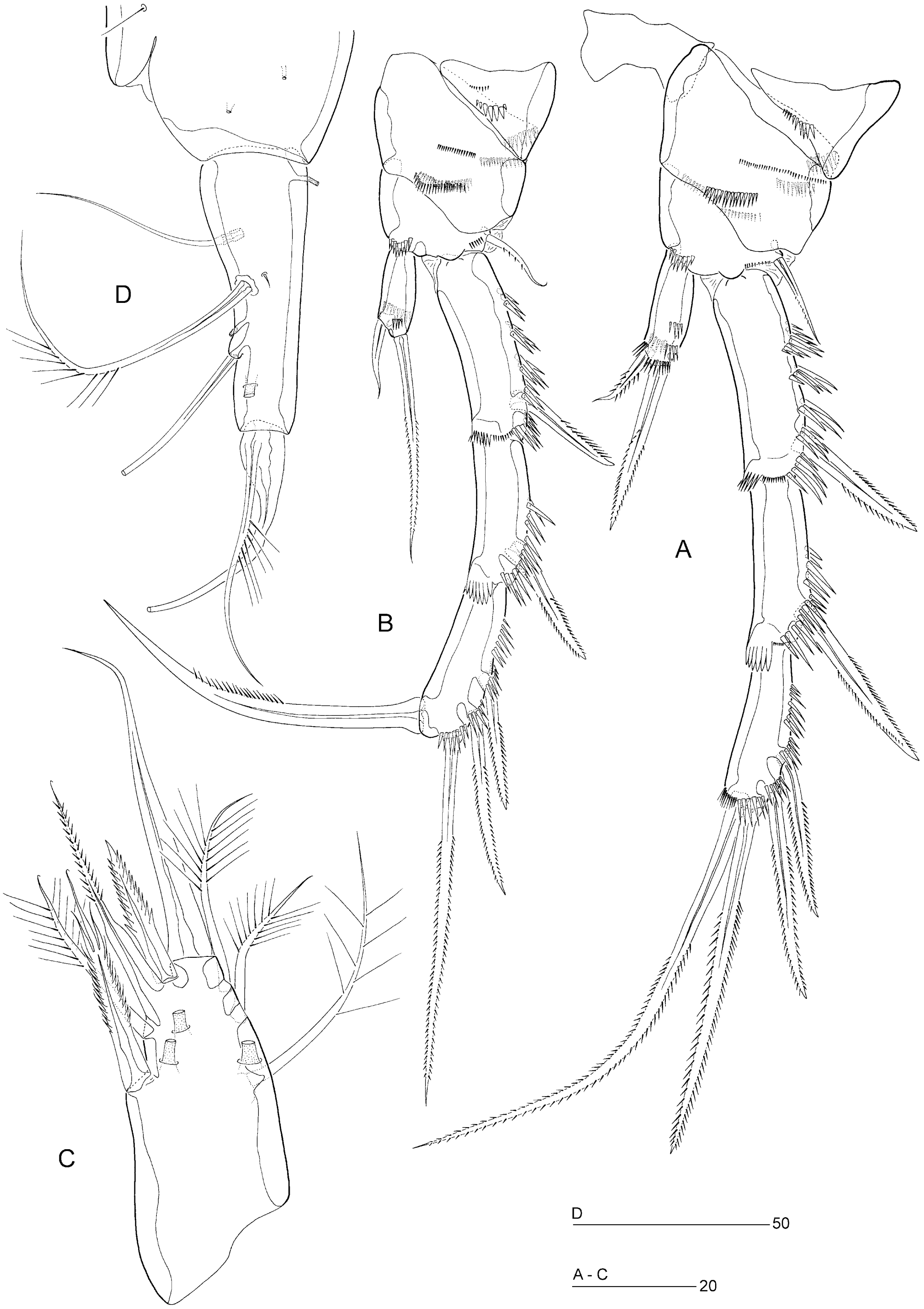

Figure 16. *Evansula arenicola* Nicholls, 1939. A, female P2, anterior; B, male P2, anterior; C, female P5, anterior; D, female anal somite and right caudal ramus, lateral.

P2 (Fig. 16B) with inner distal corner of basis not modified into spinous process. Exp-3 modified; outer distal element more setiform than in female; inner distal element transformed into strong claw, directed medially and posteriorly, pinnate along middle third. Endopod slightly shorter than in female; anterior surface with only one spinular row (four in female); apical spine distinctly longer and more slender than in female; inner spine bare.

P3 (Fig. 15C) exp-1 with reduced hyaline frill; exp-3 with secretory pore on anterior surface near joint with exp-2; outer distal spine of exp-3 distinctly shorter than

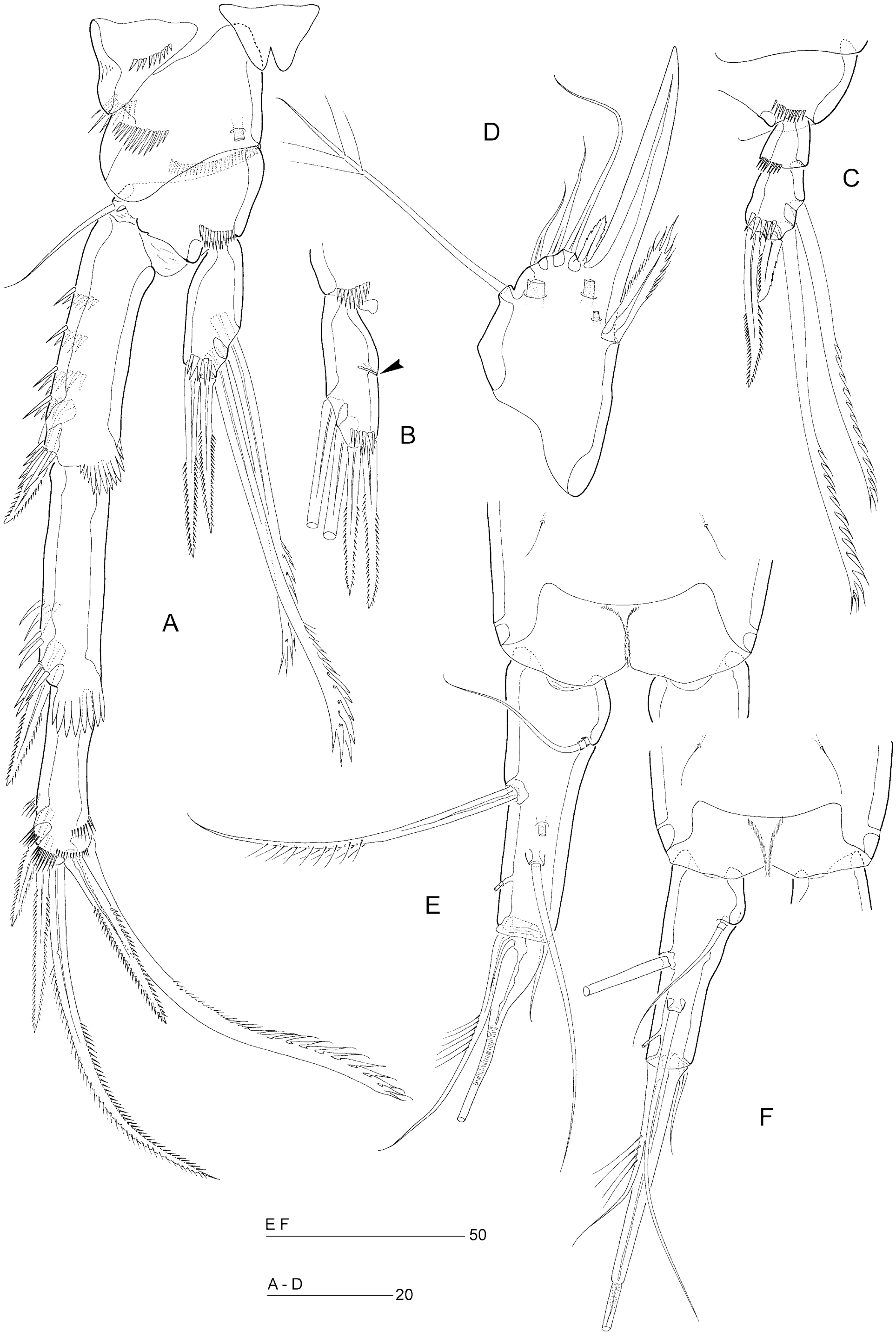

Figure 17. *Evansula arenicola* Nicholls, 1939. A, female P4, anterior; B, female P4, endopod of other side (arrow indicating incomplete suture); C, male P4 endopod, anterior; D, male P5, anterior; E, female anal somite and left caudal ramus, dorsal; F, male anal somite and left caudal ramus, dorsal.

in female. P3 endopod (Fig. 15C, D) distinctly three-segmented, longer than exp-1; enp-1 small, without armature; enp-2 with serrate, posterior seta and long, rigid apophysis arising from anterior surface; distal half of apophysis with flimsy barb; enp-3 tapering distally, with one strong, bare spine apically (bifid at tip).

P4 endopod two-segmented (Fig. 17C); enp-1 with spinular row, without armature; enp-2 with two serrate setae along inner margin and two pinnate spines apically, inner distal spine distinctly shorter than in female.

Fifth legs (Fig. 17D) with baseoendopod and exopod fused into a common, elongate plate, tapering distally towards long, spinous process, which is longer than the plate, slightly curved and bare; inner margin with serrate spine; outer margin with small serrate spine (partly fused to the plate), three naked setae and a sparsely plumose seta derived from baseoendopod; anterior surface with three large tube-pores.

Sixth pair of legs (Fig. 14B, C) asymmetrical, with three setae each, decreasing in length medially; outer seta sparsely plumose. Left or right leg articulating according to sinistral or dextral development of testis and vas deferens. First postgenital somite with transverse spinular row near ventral anterior margin (Fig. 14B).

Caudal ramus (Fig. 17F) as in female, except for length and shape of proximal styliform part of seta V, which is distinctly longer than caudal ramus length.

Variability: Nicholls (1939) described the female P4 endopod as being partly divided into two segments. This partial subdivision, marked by a suture line halfway along the outer margin (Fig. 17B), was found in most female specimens examined. However, in some individuals and sometimes in the same specimen, no such subdivision could be observed (Fig. 17A). Surprisingly, the separation in two distinct segments in the male was overlooked by Nicholls (1939).

Remarks: Nicholls (1939) figures two geniculate setae and only one outer spine on P1 exp-3 of the female, whereas for the male he states '. . . with 3 terminal setae on exopod'. Re-examination of all syntypes revealed that Nicholls' illustration was based on a damaged or aberrant female.

There is little doubt that Wilson's (1932) illustrations of *E. incerta* were based on *E. arenicola*. Evidence for this is found in his illustrations of the male, which show a two-segmented P4 endopod and agree in most other aspects, and in his statement that the female seta V of the caudal ramus '. . . is stout and spiniform proximally and passes abruptly at an angle into a filiform distal portion'. For the male he characterized the latter seta as being enlarged at the base, which conforms to the sexual dimorphism found in *E. arenicola*.

Differential diagnosis: Evansula arenicola clearly occupies an isolated position in the genus by virtue of its two-segmented P4 endopod in the male. It is also the only species that displays sexual dimorphism in the caudal seta V (bulbiform in the female) and the inner distal spine of the P4 endopod (reduced in the male). The male P2 endopod is significantly smaller in comparison with other species. The male P3 endopod, on the contrary, is much larger than in its congeners and differs in the presence of a strong, naked apical spine. The general shape of the caudal rami and the P1 (enp-1 inner seta not plumose in proximal part; enp-2 with much longer geniculate elements) provide additional differentiating characters.

Distribution: Canada: St. Lawrence River, Quebec (Nicholls, 1939).

USA: Katama Bay, Marthas Vineyard, Massachusetts (Wilson, 1932); it is conceivable that Coull's (1971, 1977) records of *E. incerta* from the North Carolina continental shelf also belong to *E. arenicola*.

EVANSULA CUMBRAENSIS SP. NOV.

Synonym: E. pygmaea (T. Scott, 1903) *sensu* Mielke (1975).

Original description: Mielke (1975: 98–100, abb. 66, as *E. pygmaea*: figs 2b, 3a–c).

Additional description: Martínez Arbizu & Moura (1994) (as *E. pygmaea*).

Type locality: Scotland, Isle of Cumbrae, Fintray Bay; exposed sandy beach with a steep profile; coarse sand.

Material examined: (1) From type locality: holotype ♀ (NHM reg. no. 2005.2025) and paratype ♂ (NHM reg. no. 2005.2026) dissected on six and five slides, respectively; other paratypes in alcohol 15 ♀♀ and 7 ♂♂ (NHM reg. nos 2005.2027–48); coll. R. Huys & S. Conroy-Dalton; 27 August 1993; Karaman-Chappuis method (Delamare Deboutteville, 1954); (2) Firth of Forth, Elie Bay (Scotland): 15 ♀♀ and 10 ♂♂ in alcohol; coll. R. Huys & S. Conroy-Dalton; 26 August 1993; sandbank sampled at low tide; clean medium sand; deposited in NHM (reg. nos 2005.2049–58); (3) From Dr W. Mielke: Isle of Sylt; 5 ♀♀ and 5 ♂♂ in alcohol (NHM reg. nos 2005.2059–68).

Etymology: The species is named after the type locality, the Isle of Cumbrae in Scotland.

Description

Female: Total body length: 500–560 µm ($N = 10$; mean = 535 µm). Body slender, cylindrical, semitransparent, colourless; no distinct separation between prosome and urosome. Genital double-somite completely fused (Fig. 18B, C); original segmentation marked dorsally by paired anterior and posterior sensillae. Anal somite longer than wide (60 × 44 µm), with three pairs of secretory pores laterally (Fig. 21C); posterior margin with two short spinular rows on either side of ventral midline (Figs 18B, 21E). Anal operculum weakly developed, unarmed (Fig. 21B).

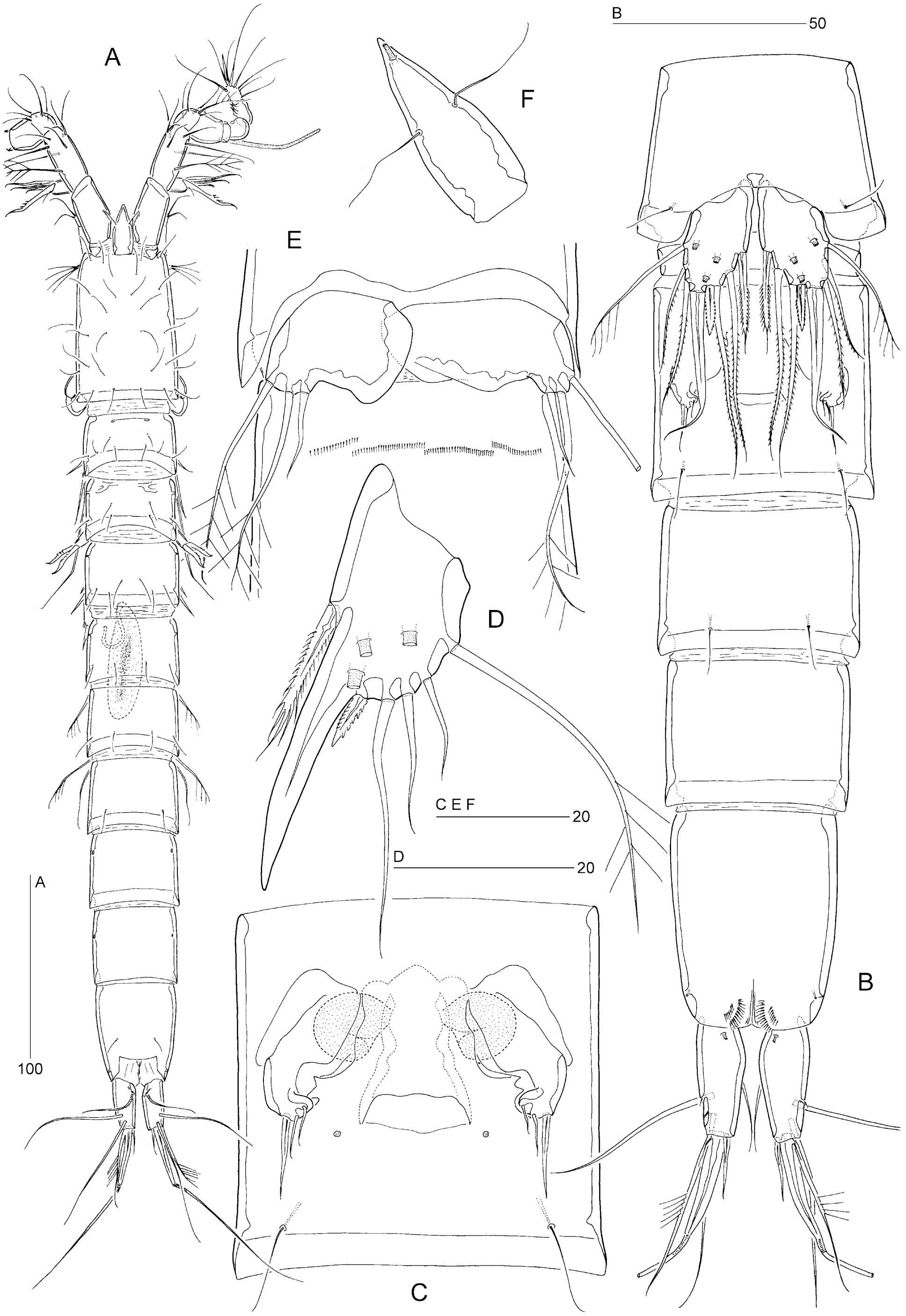

Figure 18. ***Evansula cumbraensis* sp. nov.** A, male habitus, dorsal; B, female urosome, ventral; C, female genital field, ventral; D, male P5, anterior; E, male P6, anterior; F, female rostrum, dorsal.

Caudal ramus slightly conical (Figs 18B, 21B–E), length (measured along outer margin) approximately 2.5 times the proximal width; dorsal surface without chitinous spur but with raised spinular row forming crest covering base of seta VII (Figs 21B, 27C, D); with seven setae, setae I–VI in distal and seta VII in proximal half (Fig. 21B); seta I diminutive, tubular (Fig. 27A, B); setae II–III long and bare; seta IV long, longer than styliform part of V, plumose half its length; seta V long, with distinct flexure zone between styliform basal part and long distal flagellate part, fused at base with seta IV (Fig. 27A); seta VI vestigial; seta VII tri-articulate at base (Fig. 27D) and located along proximal inner margin; ventral surface with one tube-pore near anterior margin (Fig. 21E), lateral surface with two tube-pores (Figs 21C, 27A, B).

Rostrum elongate (Figs 18F, 23A, B), with parallel margins in proximal half, tapering distally; distinctly shorter than first antennulary segment; base surrounded by area of flexible integument (Fig. 23A), with two long sensillae; median pore raised and positioned dorsally near apex of rostrum (Fig. 23A, B).

Antennule seven-segmented; armature formula as in *E. incerta*; segment 1 only slightly shorter than segment 2, with small sclerite around proximal posterior margin (Fig. 23A), with pattern of spinular rows as illustrated in Figure 21A.

Antenna, mandible, maxillule, and maxilla as in *E. incerta*.

Labrum, a massive lobe (Fig. 22A) overlying mouth and mandibular gnathobases; with series of overlapping spinular rows around midventral margin (Figs 22C, 23D).

Paragnaths, well-developed lobes, closely adpressed to gnathobases of mandibles (Fig. 22C); with two rows of spinules each.

Maxilliped (Fig. 22A) as in *E. pygmaea*. Syncoxa without seta. Palmar margin of basis with spinular row posteriorly and patch of longer setules anteriorly. Endopodal claw distinctly curved, bare. Area between maxillipedal syncoxae and intercoxal sclerite of P1 provided with midventral, trifid, spinous process (Figs 22A, 23C).

P1 (Fig. 19A, B). Praecoxa strongly developed. Coxa with three distinct spinular rows. However, scanning electron microscopy (Fig. 23C) revealed additional rows of tiny spinules, which cannot be discerned using differential interference contrast microscopes. This additional ornamentation was observed in *E. arenicola* and it is probable that the same spinular pattern is present in all species. Basis with long, naked, inner seta and short, pinnate, outer seta. Exopod three-segmented; with two spines and two geniculate setae on exp-3. P1 endopod prehensile, distinctly longer than exopod; proximal segment approximately ten times as long as average width, with pinnate inner seta being plumose in proximal third; distal segment short, with two spinular rows, a subdistal setule, and two short, geniculate spines distally.

Swimming legs P2–P4 (Fig. 20A–F). P4 distinctly longer than P2–P3. Width of intercoxal sclerites decreasing in antero-posterior direction (Fig. 20A, D–F). Praecoxae well developed, with spinular row on anterior surface. Coxae with pattern of spinules as in Figures 20A, B, D–F, with a large tube-pore on anterior surface of P3 and P4. Bases with outer seta (short and bare in P2, long and plumose in P3, long and bare in P4); with spinular rows on anterior surface only (Fig. 20A, B, D–F). Exopods three-segmented, endopods one-segmented. Exopodal spines of P2 exp-2 and exp-3 elongate. Inner distal spine of P3–P4 exp-3 shorter than outer distal one. Inner setae of P4 endopod and exp-3 serrate. Inner element of P2 endopod spiniform, pinnate, less than half length of distal spine. Armature elements of P3 endopod spiniform; inner spine longer than half length of outer spine. Seta and spine formulae as for genus.

Fifth pair of legs (Figs 18B, 20G) with baseoendopod and exopod fused into a common elongate plate, tapering distally, with stepped inner and outer margins; apex with strong, articulating spine, distinctly longer than plate and with flagellate tip; outer margin with one bare (seta derived from baseoendopod) and two pinnate setae; inner margin with two serrate spines and two long, pinnate setae (all free at base); anterior surface with three large tube-pores.

Sixth legs (Figs 18C, 26A) each represented by small operculum closing off gonopore; armature consisting of spiniform outer element and two accessory setules. Genital apertures not fused medially; copulatory pore very wide, located at level of gonopores (Fig. 26A); leading via short chitinized copulatory duct to paired anterior extensions positioned anterior to genital apertures; copulatory pore flanked by two complex secretory pores, each consisting of four vents (Fig. 26B).

Male: Body length: 480–525 µm ($N = 5$; mean = 505 µm) (Fig. 18A). Spermatophore 65 µm. Anal somite without spinules on ventral anterior and hind margins (Figs 21F, 25D).

Antennule indistinctly nine-segmented; geniculation between segments 7 and 8 (Fig. 24A); segment 1 with one minute seta and spinular pattern as in female; segment 2 longest, with one plumose and eight naked setae; segment 3 with six setae; segment 4 minute, forming an incomplete ring, with two short setae; segment 5 distinctly swollen, with six elements along the anterior margin and with a distal cylindrical process bearing a basally fused seta and large, constricted aesthetasc; segment 6 with one long seta and one short pinnate spine; segment 7 with three spiniform elements and one seta (Fig. 24D); segment 8 with one seta and three interdigitating modified setae (Fig. 24B, C); segment 9 with five posterior setae, one anterior seta and one seta plus an acrothek apically. Apical acrothek consisting of two naked setae and one slender aesthetasc.

P2 (Fig. 19D, E) with inner distal corner of basis not modified into spinous process. Exp-3 modified; inner distal element transformed into slender claw, directed

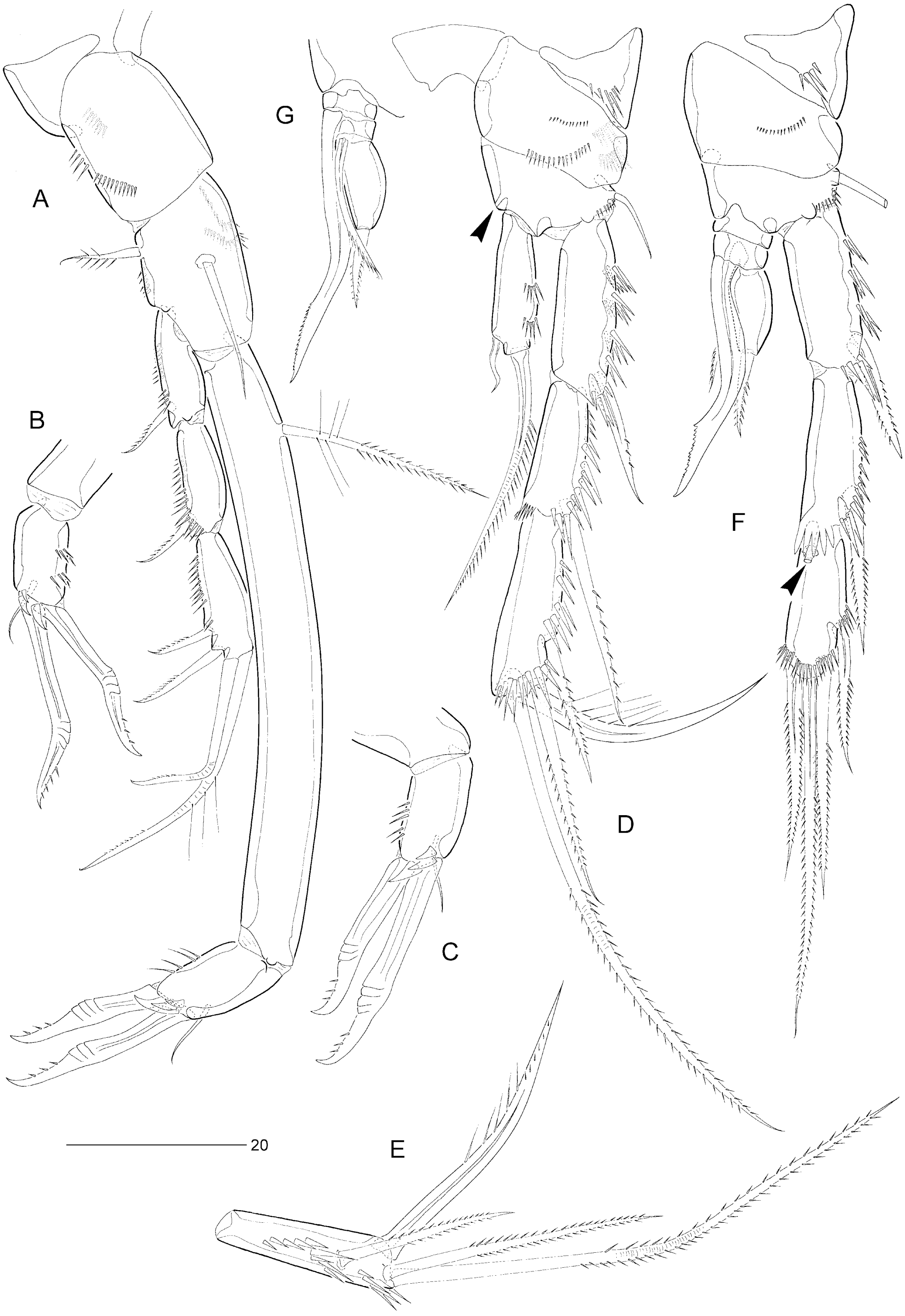

Figure 19. ***Evansula cumbraensis*** **sp. nov.** A, female P1, anterior (holotype); B, female P1 enp-2 of other side (mounted in a more flattened position; holotype, NHM reg. no. 2005.2025); C, female P1 enp-2 (Sylt specimen, NHM reg. no. 2005.2059); D, male P2, anterior (position of sexually dimorphic process in other cylindropsyllid genera arrowed); E, male P2 exp-3, lateral; F, male P3, anterior (sexually dimorphic tube-pore on exp-3 arrowed); G, male P3 endopod, posterior.

medially and posteriorly, and with pinnules in distal half (Fig. 19E). Endopod of approximately the same size as in female; outer margin with two spinular rows; apical seta longer and more slender, extending beyond distal margin of exp-2; inner seta minute, bare.

P3 (Fig. 19F) with reduced hyaline frill on exp-1 (Fig. 25B); exp-3 with secretory pore on anterior

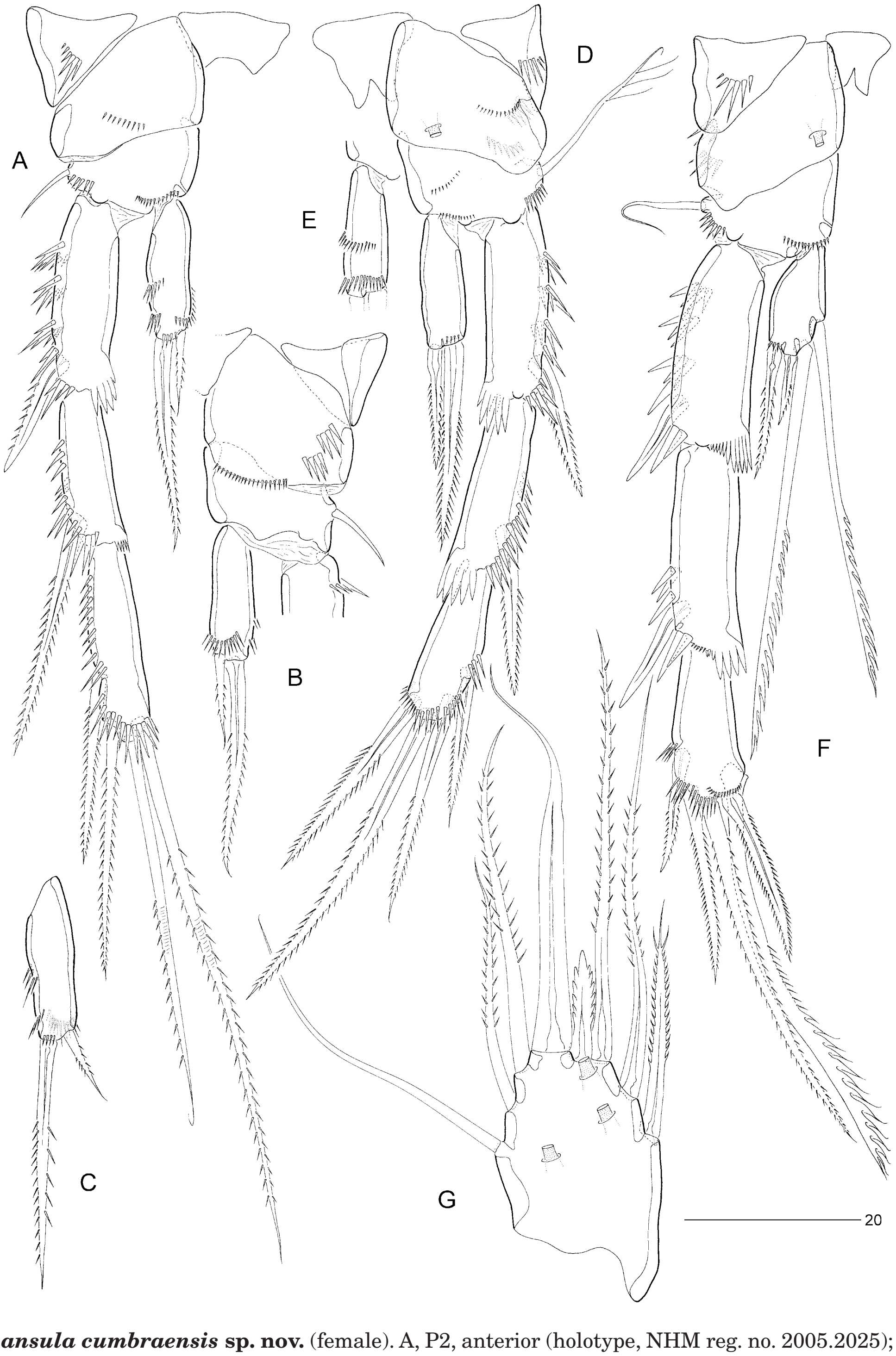

Figure 20. ***Evansula cumbraensis* sp. nov.** (female). A, P2, anterior (holotype, NHM reg. no. 2005.2025); B, P2 protopod and endopod, posterior (holotype, NHM reg. no. 2005.2025); C, P2 endopod, anterior (Sylt specimen, NHM reg. no. 2005.2059); D, P3, anterior; E, P3 endopod, posterior (distal armature omitted); F, P4, anterior; G, P5, anterior.

surface near joint with exp-2 (Fig. 25A). P3 endopod (Fig. 19F, G) distinctly three-segmented; enp-1 small, without ornamentation or armature; enp-2 short, with serrate, posterior seta and rigid, sigmoid apophysis arising from anterior surface; distal third of apophysis with denticulate margin; enp-3 a short bulbous segment, with one short, pinnate seta apically.

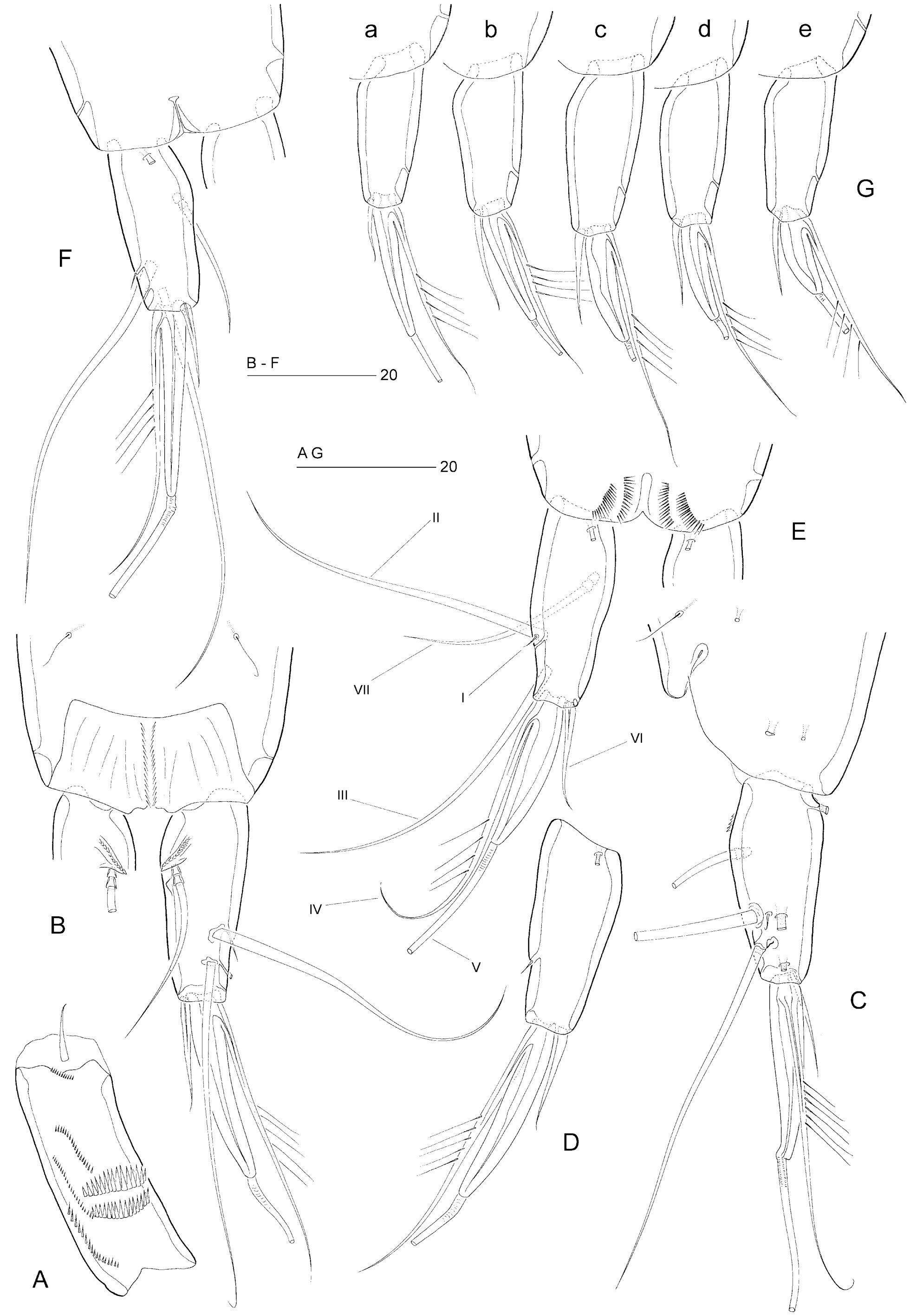

Figure 21. ***Evansula cumbraensis* sp. nov.** A, female antennule, segment 1, anterior; B, female anal somite and right caudal ramus, dorsal (Fintray, NHM reg. no. 2005.2027); C, female anal somite and right caudal ramus, lateral (Fintray, NHM reg. no. 2005.2027); D, female right caudal ramus, ventral (Fintray, NHM reg. no. 2005.2027); E, female anal somite and right caudal ramus, ventral (Sylt, NHM reg. no. 2005.2059); F, male anal somite and right caudal ramus, ventral (Fintray, NHM reg. no. 2005.2042); G, variability encountered in seta V in Elie population [♂♂ (a, b) and ♀♀ (c–e); NHM reg. nos 2005.2049–58].

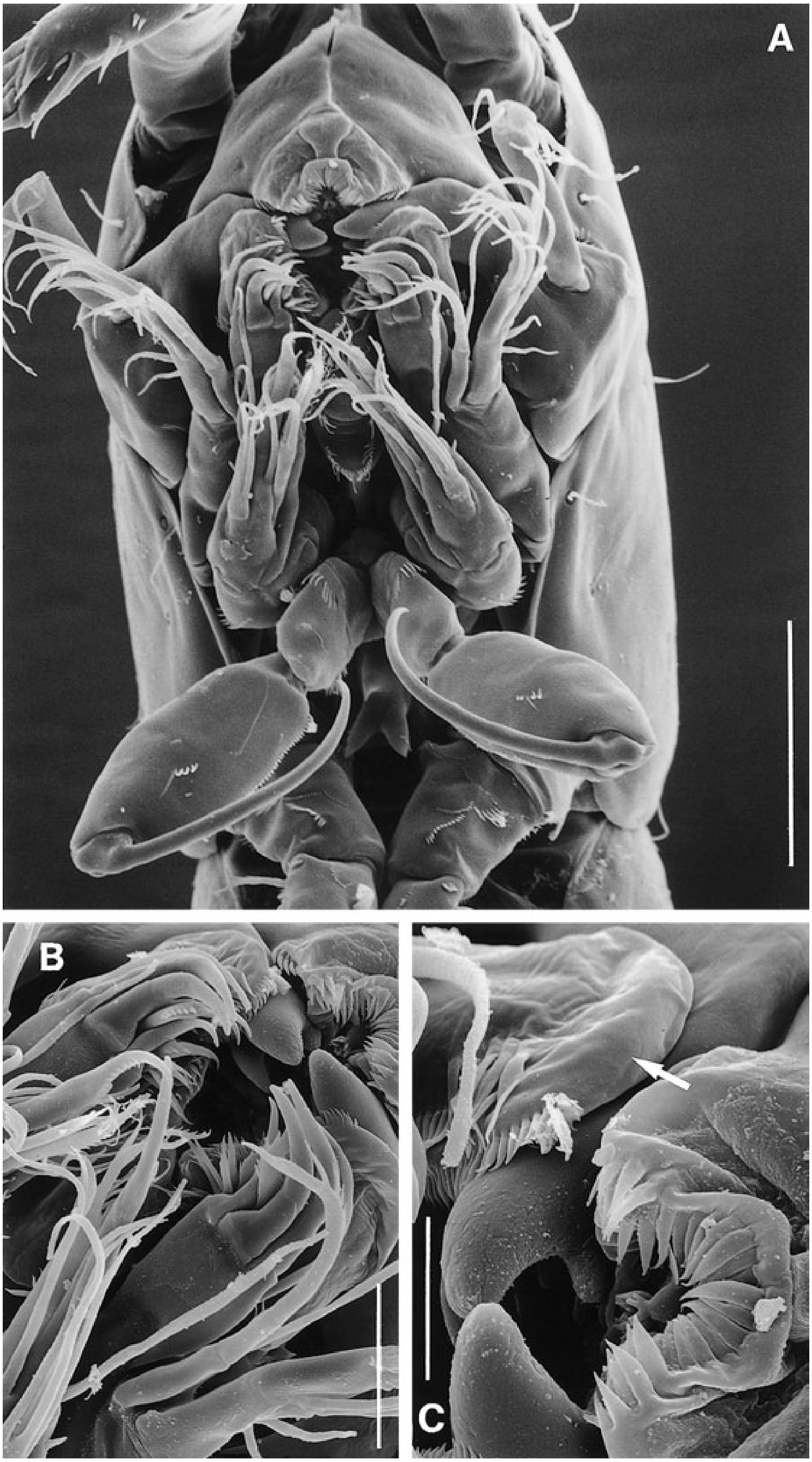

Figure 22. ***Evansula cumbraensis*** **sp. nov.** Scanning electron micrographs (female). A, cephalothorax, ventral; B, oral area showing labrum, paragnaths, and maxillules; C, anterior margin of labrum and paragnath (arrowed), closely adpressed to mandibular gnathobase. Scale bars: 30 µm (A), 10 µm (B), 4.3 µm (C).

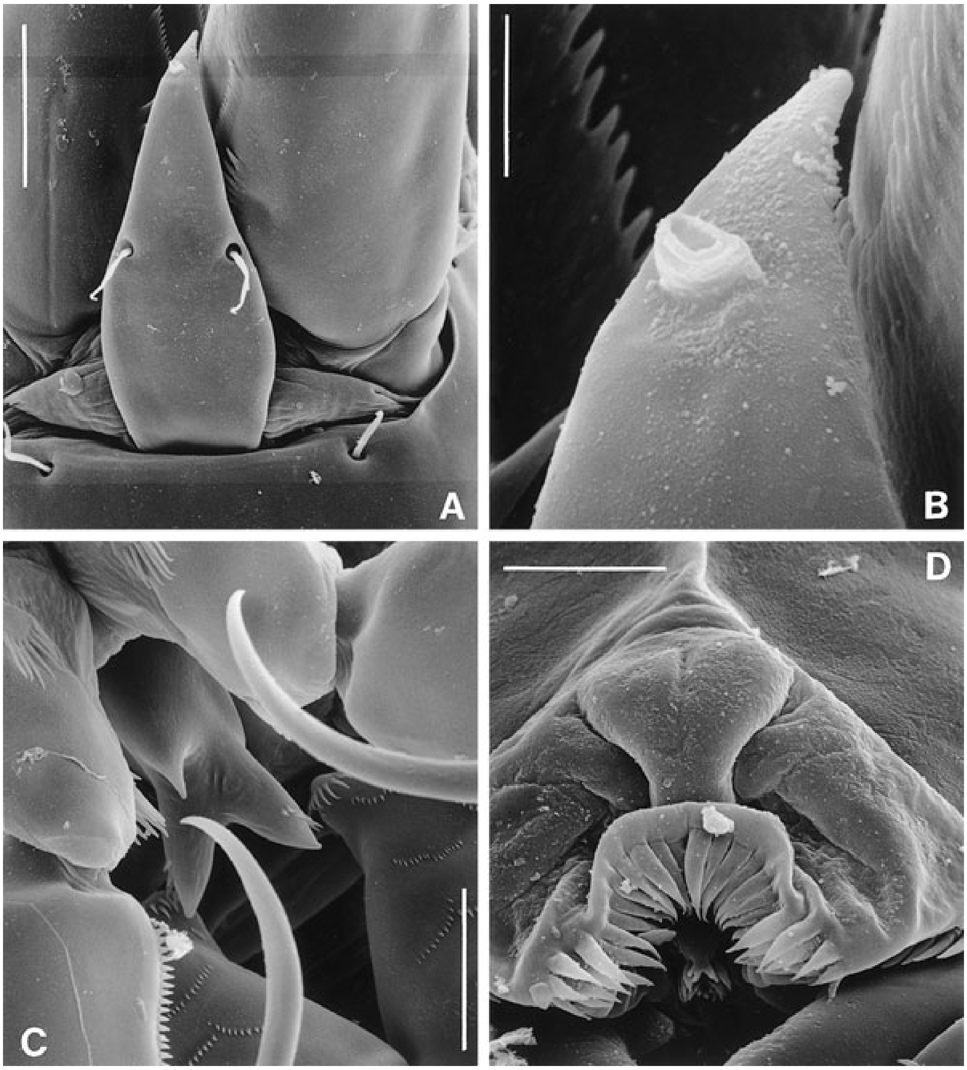

Figure 23. ***Evansula cumbraensis* sp. nov.** Scanning electron micrographs (female). A, rostrum and proximal part of antennules; B, distal part of rostrum, showing mid-dorsal pore; C, trifid process between maxillipeds and intercoxal sclerite of P1; D, labrum. Scale bars: 10 μm (A), 1.5 μm (B), 7.5 μm (C), 4.3 μm (D).

Fifth legs (Fig. 18D) with baseoendopod and exopod fused into a common elongate plate, tapering distally towards a long, bare, spinous process, which is longer than the plate; inner margin with serrate spine; outer margin with small serrate spine, three naked setae and sparsely plumose seta derived from baseoendopod; anterior surface with three large tube-pores.

Sixth pair of legs (Figs 18E, 25C) asymmetrical, with two long, sparsely pinnate setae and one short, bare seta each. Left or right leg articulating according to sinistral or dextral development of testis and vas deferens. First postgenital somite with pattern of transverse spinular rows near ventral anterior margin (Figs 18E, 25C).

Caudal ramus (Fig. 21F) as in female.

Remarks: Mielke (1975) expressed some reservations about the identity of his *Evansula* material from the Isle of Sylt. He decided to attribute his specimens to *E. pygmaea* on the following grounds: (1) body length shorter than in *E. incerta*, (2) distal spines of P1 enp-2 claw-like, and (3) similarity in female P5 with Scott's (1903a) original description. A comparison based on one female and one male from Sylt revealed no differences with the type material of *E. cumbraensis* except for (1) the P2 endopod, which, as well as its distal spine, appears to be slightly longer in the German specimens (Fig. 20C), (2) the shape of the geniculate spines on P1 enp-2, which appear to be slightly more stout (Fig. 19C). However, the precise length and shape of these elements are dependent on their orientation on the slide (cf. Fig. 19A, B), and (3) small differences in

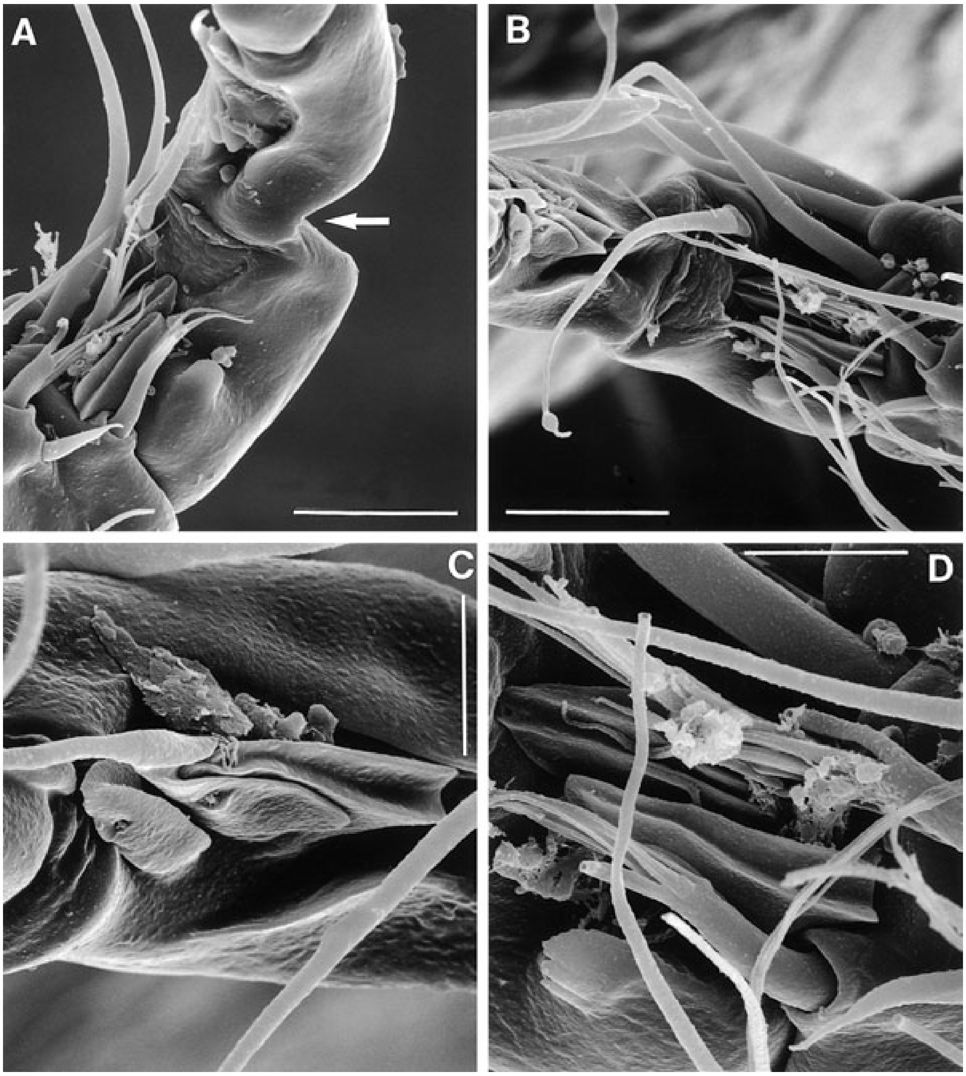

Figure 24. ***Evansula cumbraensis*** **sp. nov.** Scanning electron micrographs (male). A, antennulary segments around geniculation (arrowed), anteriodorsal; B, same, anterior; C, modified setae on segment distal to geniculation; D, modified setae anterior to geniculation. Scale bars: 7.5 μm (A, B), 3 μm (C, D).

caudal ramus contours and length of styliform part of seta V (but see under variability). Mielke seems to have found only *E. cumbraensis*. However, other studies reporting both *E. pygmaea* and *E. incerta* (Noodt, 1952, 1957) potentially indicate the occurrence of other sympatric species on the Isle of Sylt.

Martínez Arbizu & Moura's (1994) drawings of the genital field (cf. position and size of copulatory pore; however, the innermost setule on P6 was overlooked) and the P2 of both sexes (length of exopodal spines, endopod in male) of *E. pygmaea* from Sylt leave no doubt that they were also dealing with *E. cumbraensis*.

Mielke (1975) commented on the structure of the 'plumose' setae found on the female P5. He described the pinnules as composed of '. . . einem kurzen, verstärkten Basalteil und einem langen Endteil, der leicht abbrechen kan. Bei Verlust einer größeren Anzahl von Fiederendstücken werde kurz behaarte Borsten vorgetäuscht'. Scanning electron microscopy revealed that these plumose setae are clearly pinnate (Fig. 26D) and the plumosity is an artefact created by epibiotic filamentous bacteria attached at and around the short pinnules (Fig. 26C: distal part of second innermost seta). McAllen & Hannah (1999) observed similar biofouling by filamentous bacteria on the exoskeleton of the high-shore rockpool harpacticoid *Tigriopus brevicornis* (O.F. Müller). In this species, the major biofoulant is *Leucothrix mucor* Œrsted, which tends to colonize between the body tergites where the

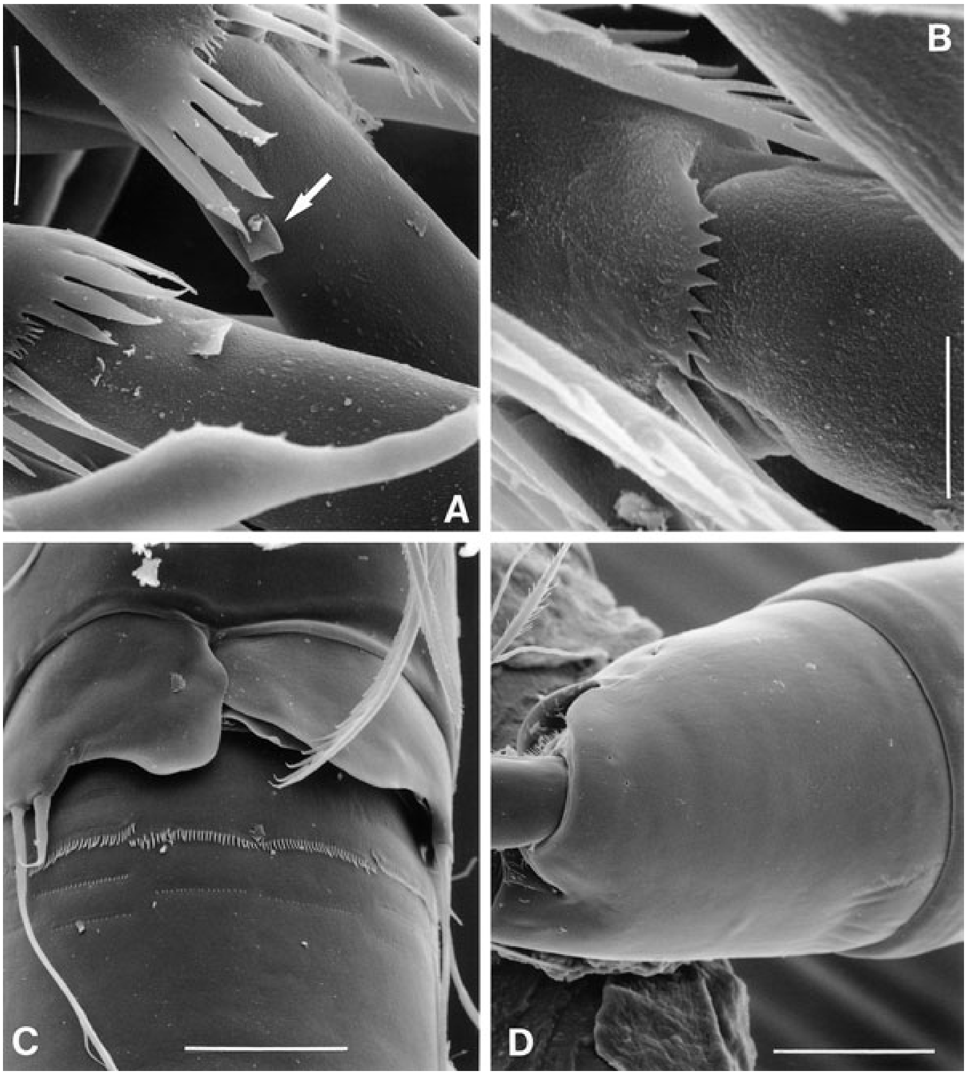

Figure 25. ***Evansula cumbraensis* sp. nov.** Scanning electron micrographs (male). A, P3 exp-3, anterior (secretory pore arrowed); B, reduced hyaline frill of P3 exp-1, anterior; C, P6 and first abdominal somite, ventral; D, anal somite, ventrolateral. Scale bars: 4.3 μm (A), 2.5 μm (B), 15 μm (C), 20 μm (D).

exoskeleton is at its thinnest for the action of chitinolytic enzymes. The filamentous bacteria found in *E. pygmaea*, *E. cumbraensis*, and *E. arenicola* appear to show a high site specificity, attaching themselves only to the long setae of the P5 (usually the female).

Variability: Found only in the proximal styliform part of seta V, the length and shape of which can vary considerably within a population. Figure 21G illustrates the intraspecific variation found in the Elie population. The Sylt population clearly fits within this range (Fig. 21E; Mielke, 1975: abb. 66B).

Differential diagnosis: The most important diagnostic features of female *E. cumbraensis* are the elongated exopodal spines on the middle and distal segments of P2 and the very large copulatory pore. It shares with *E. incerta* the absence of ventral spinular rows near the anterior margin of the anal somite in the female. Males of the closely related *E. cumbraensis* and *E. polaris* can be distinguished by the detailed morphology of the P3 endopod (segmentation, shape of enp-3) and P5 (spinous process smooth vs. pinnate).

Distribution: Scotland: Fintray Bay, Isle of Cumbrae (present account); Elie in Firth of Forth (present account).

Germany: Isle of Sylt (Mielke, 1975, 1976; Martínez Arbizu & Moura, 1994).

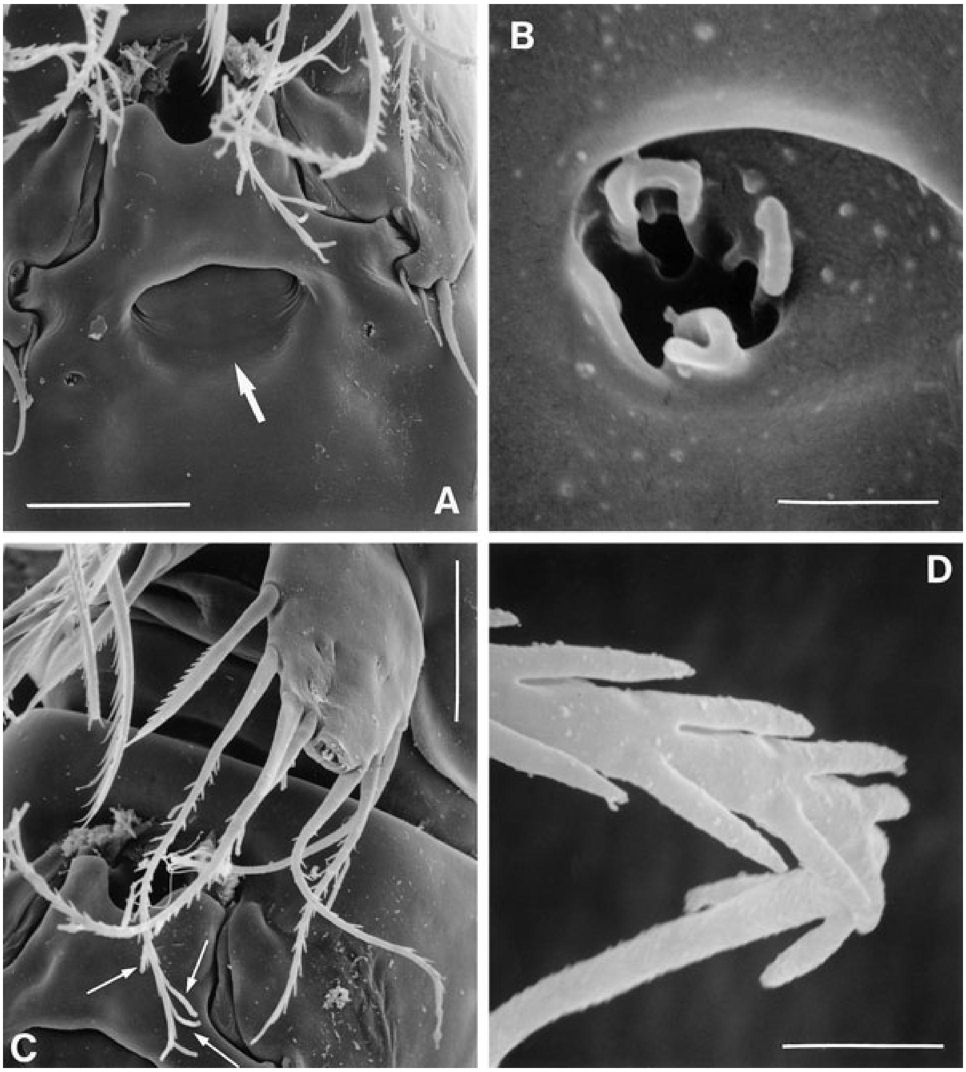

Figure 26. ***Evansula cumbraensis* sp. nov.** Scanning electron micrographs (female). A, genital field, ventral (copulatory pore arrowed); B, secretory pore located lateral to copulatory pore, showing separate vents; C, P5, showing filamentous bacteria attached to setae (arrowed); D, P5 seta without bacterial epibionts attached, revealing pinnate ornamentation. Scale bars: 15 µm (A), 0.75 µm (B), 15 µm (C), 1 µm (D).

EVANSULA SPINOSA SP. NOV.

Synonym: Evansula incerta (T. Scott, 1892) *sensu* Sars (1911).

Original description: Sars (1911: 415–416, suppl., plate 39).

Additional description: Scheibel (1972).

Type locality: Norway, Korshavn, near Lindesnes; at 30–50 fathoms.

Material examined: (1) From type locality: holotype ♀ dissected on eight slides; found among spirit-preserved specimens of *Neobradya pectinifera* T. Scott, 1892, deposited in Zoologisk Museum, Oslo; coll. G.O. Sars; deposited in NHM (reg. no. 1995.428); (2) NHM, reg. no. 1995.429: Firth of Forth (no further details specified), Scotland; 1 ♂ paratype [found among spirit-preserved 'cotypes' of *E. incerta*: reg. nos 44505–507; as part of Cannon A. M. Norman collection (1911.11.8)]; coll. T. Scott, 9 September 1894; dissected on eight slides; (3) NHM, reg. no. 2005.2069: Southern Bight of North Sea, off Suffolk (UK), 51°57′24′N 2°10′57′E; 42.7m depth; 1 ♀ paratype in alcohol; coll. R. Huys, 30 March 1992.

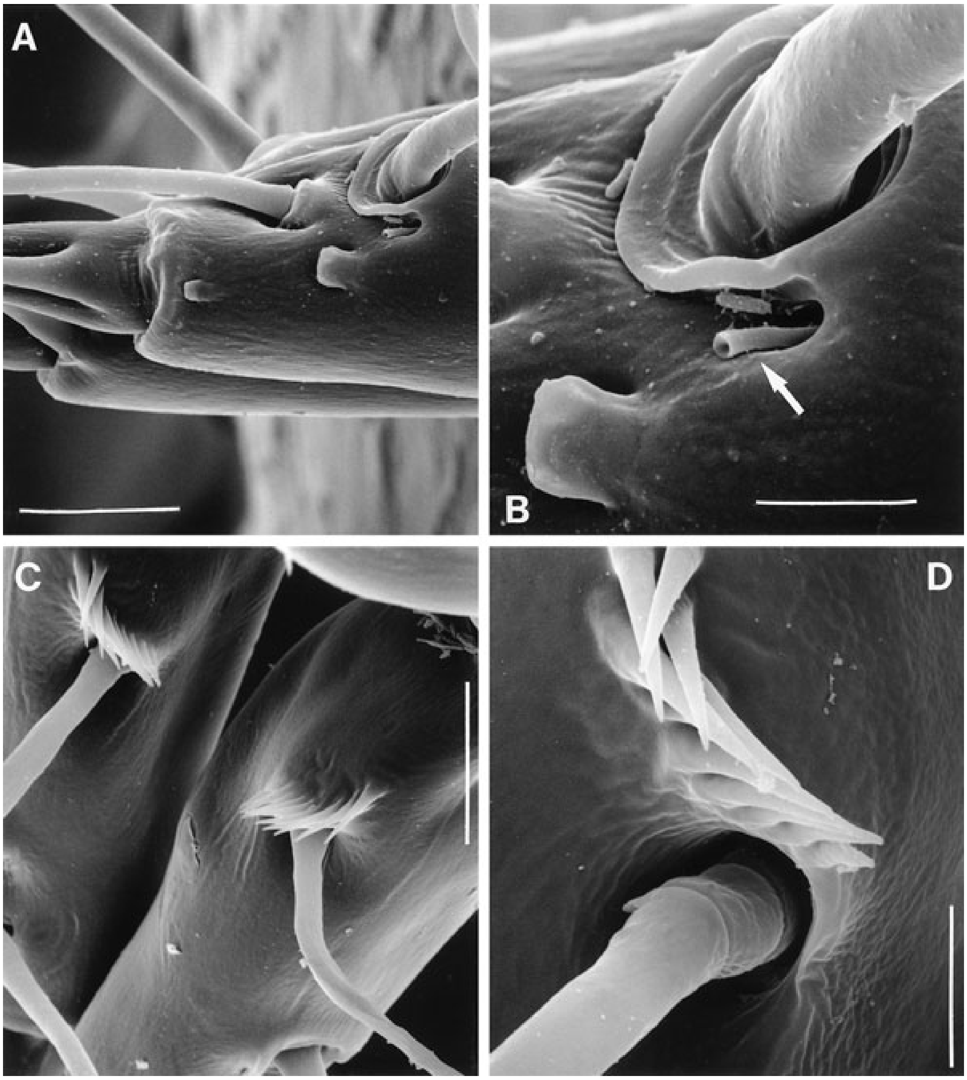

Figure 27. ***Evansula cumbraensis* sp. nov.** Scanning electron micrographs (female). A, caudal ramus, lateral; B, caudal ramus, area around seta I (arrowed); C, caudal rami, dorsal, showing raised spinular row anterior to seta VII; D, close-up of seta VII, showing tri-articulate base. Scale bars: 6 µm (A), 2 µm (B, D), 6 µm (C).

Etymology: The species name is derived from the Latin *spina*, meaning spine, and refers to the dorsal spinous process on the caudal ramus.

Description

Female: Total body length: 700 µm. Body slender, cylindrical (Fig. 28A, B), semitransparent, light brown; no distinct separation between prosome and urosome. Genital double-somite completely fused (Figs 28A, B, 29D); original segmentation marked dorsally by paired anterior and posterior sensillae (Fig. 28A). Anal somite only slightly longer than wide (72 × 66 µm), with three pairs of secretory pores laterally (Fig. 32D); anterior margin with ventral transverse row of tiny spinules (Fig. 29D); posterior margin with two short spinular rows on either side of ventral midline (Figs 29D, 32E). Anal operculum weakly developed, unarmed (Fig. 32C).

Caudal ramus cylindrical (Figs 29D, 32C–E) with slightly concave inner margin, length (measured along the outer margin) approximately 3.5 times the proximal width; dorsal surface with chitinous spur (Fig. 32C, D); with seven setae, setae I–VI in distal and seta VII in proximal half (Fig. 32C); seta I small, larger than in other species; setae II–III long and bare; seta IV bare, longer than styliform part of V; seta V long, with distinct flexure zone between styliform part and long distal flagellate part, fused at base with seta IV; seta VI vestigial; seta VII tri-articulate at base

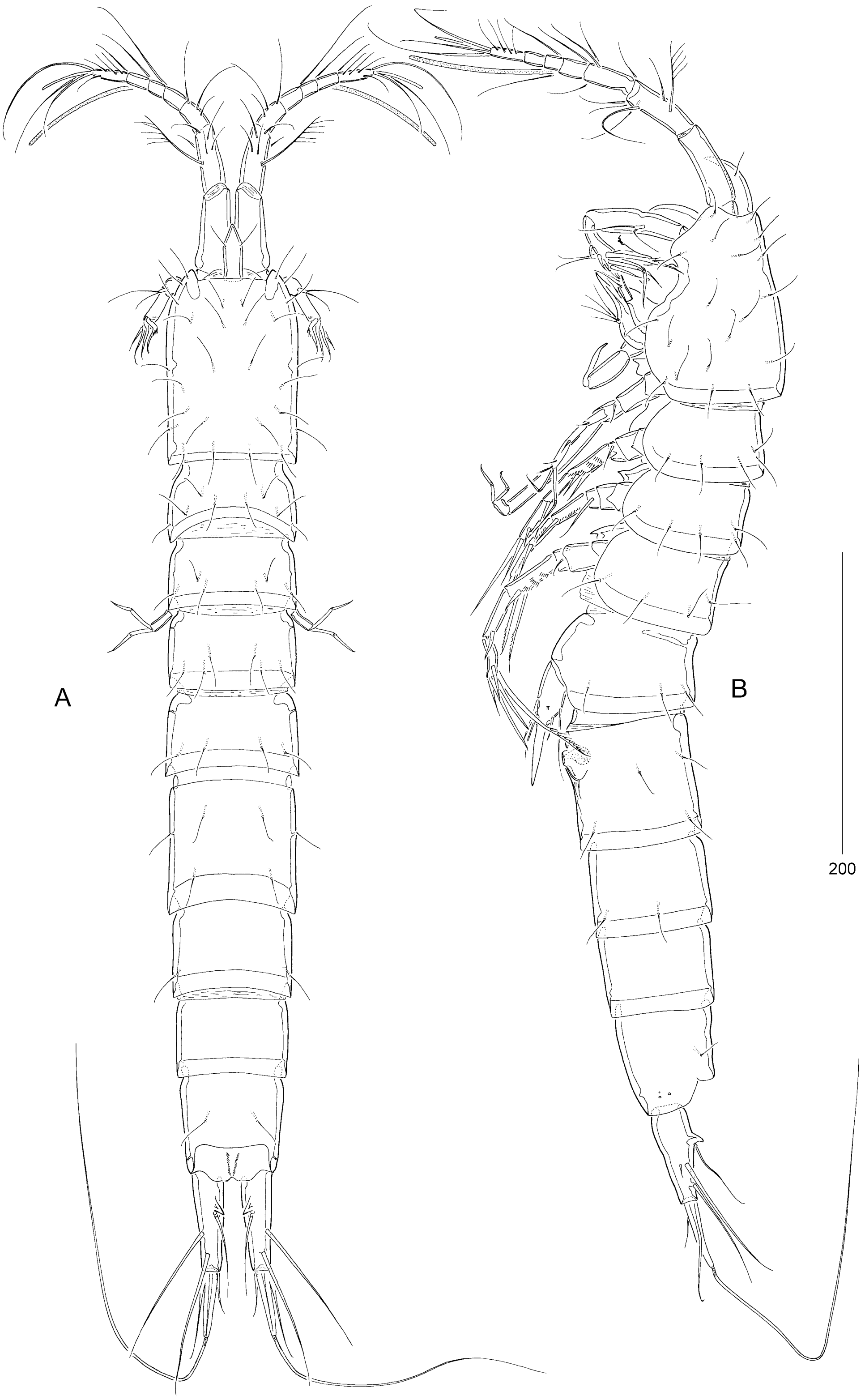

Figure 28. ***Evansula spinosa* sp. nov.** (female). A, habitus, dorsal; B, habitus, lateral.

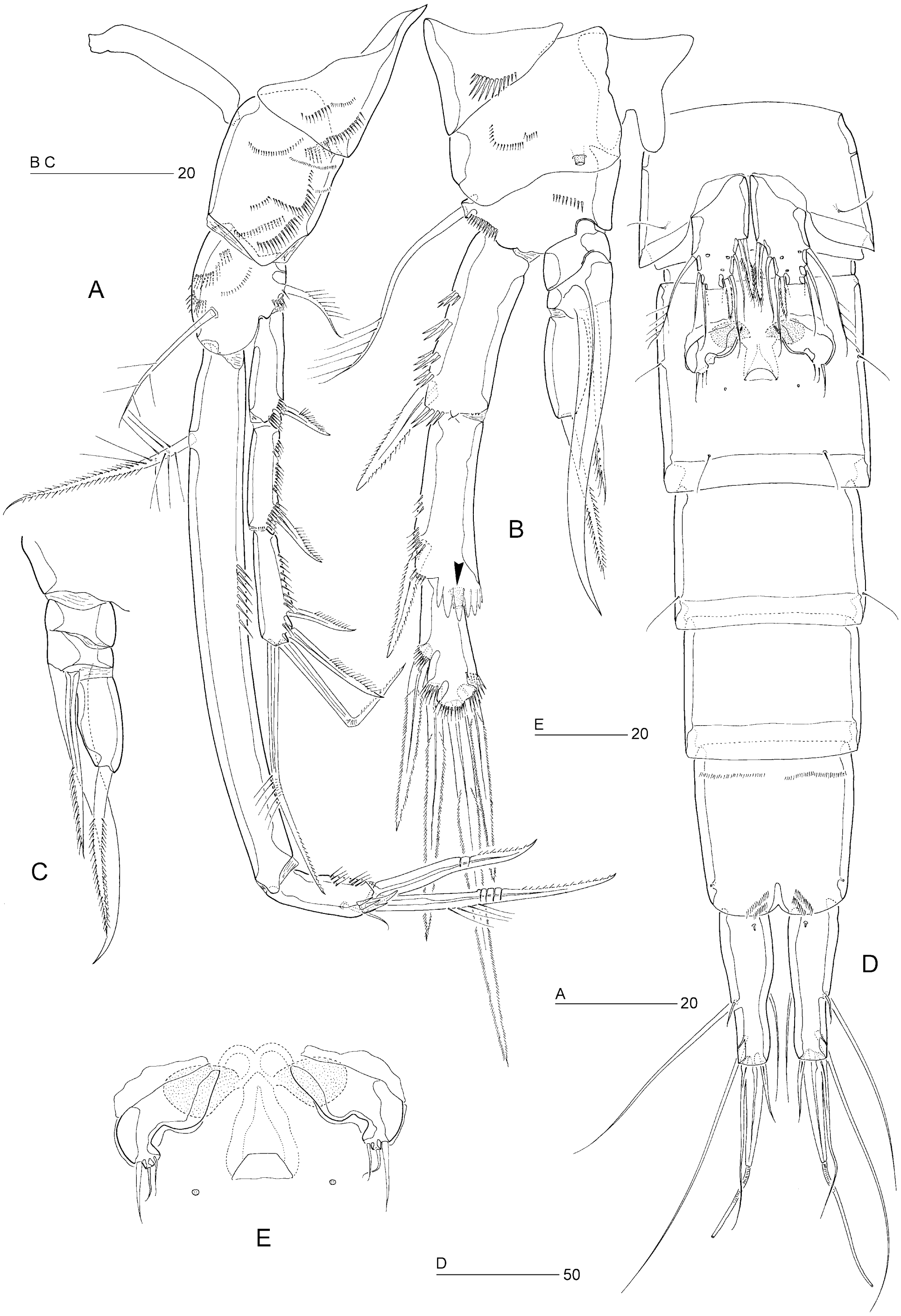

Figure 29. ***Evansula spinosa*** **sp. nov.** A, female P1, anterior; B, male P3, anterior [tube-pore on exp-3 (hidden by hyaline frill of exp-2) arrowed]; C, male P3 endopod, posterior; D, female urosome, ventral; E, female genital field, ventral.

and located near proximal inner margin; ventral surface with one tube-pore (Fig. 32E), lateral surface with one tubular and one simple pore (Fig. 32D).

Rostrum elongate (Fig. 28A), with parallel margins in proximal half, tapering distally; distinctly shorter than first antennulary segment; with two long sensillae.

Antennule seven-segmented (Fig. 28A, B); armature formula as in *E. incerta*; segment 1 slightly longer than segment 2.

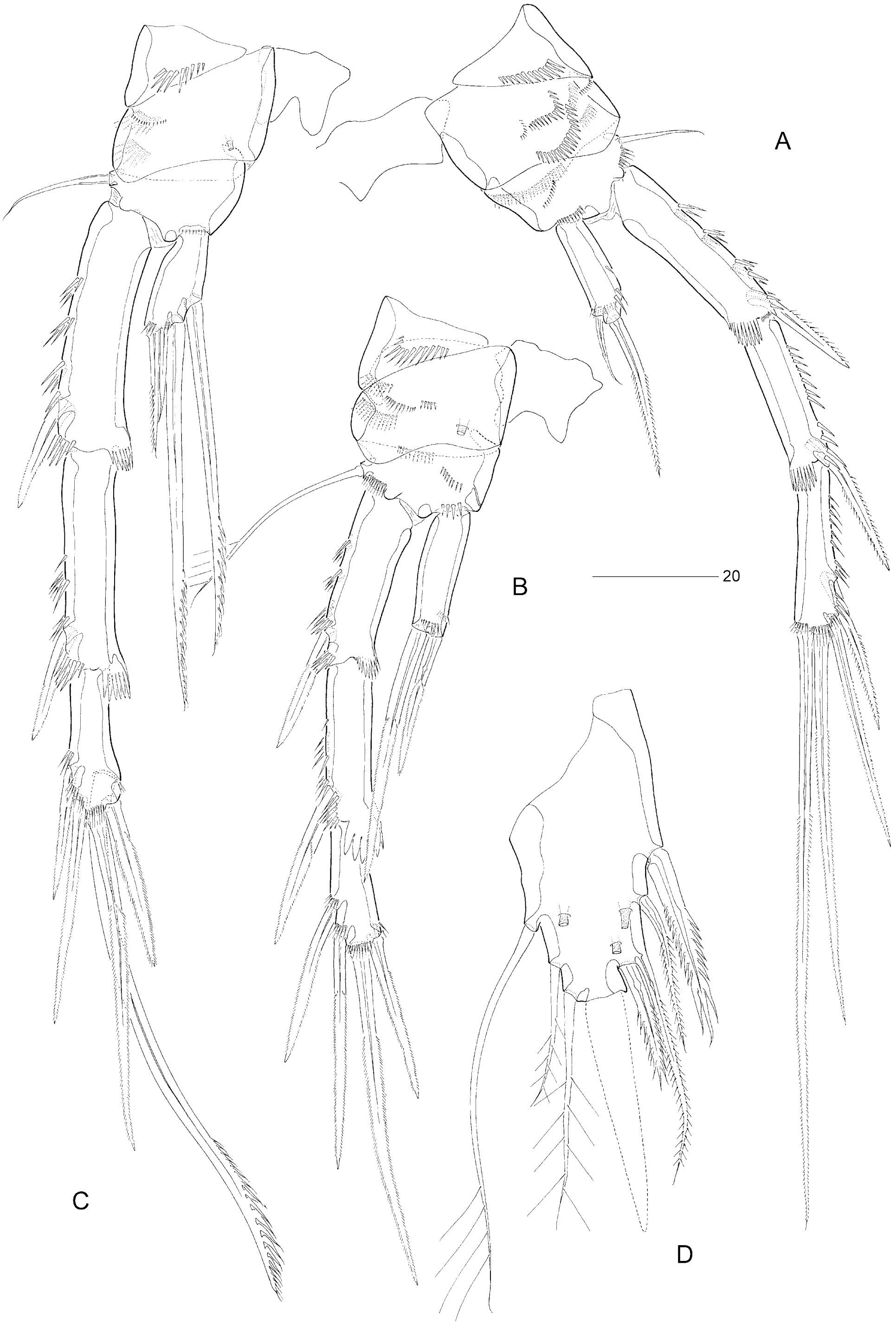

Figure 30. ***Evansula spinosa* sp. nov.** (female). A, P2, anterior; B, P3, anterior; C, P4, anterior; D, P5, anterior.

Antenna with spinular row on coxa (Fig. 31B); basis and first endopod segment incompletely fused to form allobasis, abexopodal margin without ornamentation; exopod small, with one long, pinnate and one shorter, naked seta.

Antennary endopod, mandible, maxillule, and maxilla as in *E. incerta*.

Maxilliped as in *E. pygmaea*. Syncoxa without seta.

P1 (Fig. 29A). Praecoxa strongly developed, with three spinular rows. Coxa with six spinular rows on

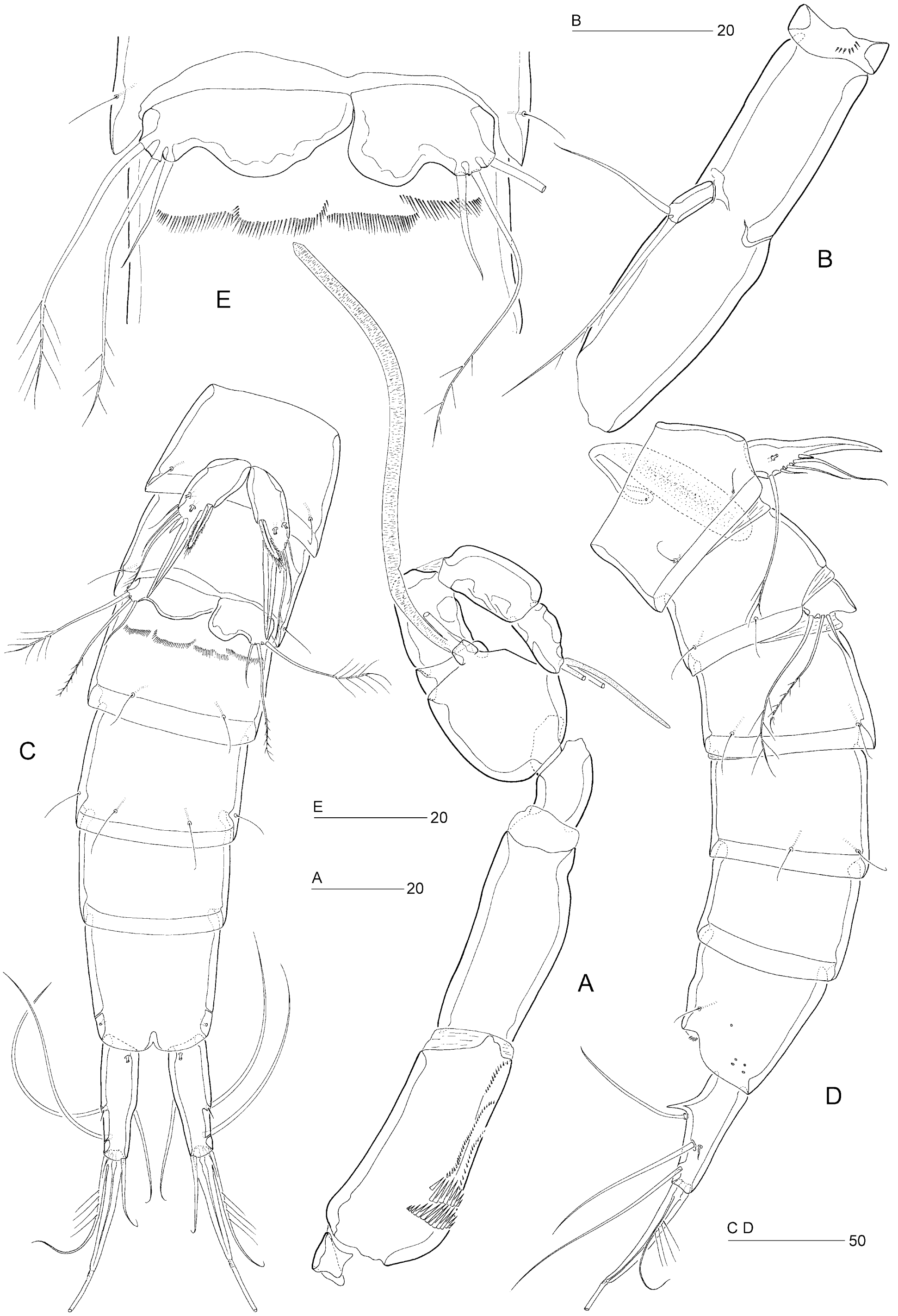

Figure 31. ***Evansula spinosa* sp. nov.** (male). A, antennule (armature omitted); B, antennary coxa and allobasis; C, urosome, ventral; D, urosome, lateral; E, sixth pair of legs and ventral spinule row on first abdominal somite.

anterior and two on posterior surface. Basis with long, sparsely plumose inner seta and shorter, pinnate outer seta. Exopod three-segmented; with two spines and two geniculate setae on exp-3. P1 endopod prehensile, distinctly longer than exopod; proximal segment approximately ten times as long as average width, with pinnate inner seta being plumose in proximal third; distal segment short, with three spinular rows, a subdistal setule, and two geniculate spines distally.

Swimming legs P2–P4 (Fig. 30A–C). P4 distinctly longer than P2–P3. Width of intercoxal sclerites decreasing in antero-posterior direction. Praecoxae well developed, with spinular row on anterior surface in P2–P4. Coxae with pattern of spinules as in Figure 30A,B,C, with large tube-pore on anterior surface of P3 and P4. Bases with outer seta (short and naked in P2 and P4, long and plumose in P3); with spinular rows on anterior surface only. Exopods three-segmented, endopods one-segmented. Exopodal spines of P3–P4 minutely serrate. Inner distal spine of P3–P4 exp-3 shorter than outer distal one. Inner setae of P4 endopod and exp-3 serrate. Inner element of P2 endopod setiform, pinnate, approximately half length of distal spine. Armature elements of P3 endopod spiniform; inner spine longer than half length of outer spine. Seta and spine formulae as for genus.

Fifth pair of legs (Figs 29D, 30D) with baseoendopod and exopod fused into a common elongate plate, tapering distally; apex with strong, articulating spine (lost on both sides during dissection), approximately as long as the plate and with a flagellate tip; outer margin with three sparsely plumose setae (including seta derived from baseoendopod); inner margin with two serrate spines, one pinnate seta and one long pinnate seta fused to plate; anterior surface with three large tube-pores.

Sixth legs (Fig. 29D, E) each represented by small operculum closing off gonopore; armature consisting of spiniform outer element and two accessory setules. Genital apertures not fused medially; copulatory pore large, located slightly posterior to gonopores; leading via short chitinized copulatory duct to paired anterior extensions positioned anterior to genital apertures; copulatory pore flanked by two small secretory pores.

Egg-sac not confirmed.

Male: Body length: 670 μm. Spermatophore 75 μm. Anal somite without spinules near ventral anterior and hind margins (Fig. 31C).

Antennule (Fig. 31A) distinctly nine-segmented; geniculation between segments 7 and 8; segment 1 with one minute seta and spinular pattern as in female; slightly longer than segment 2; segment 5 distinctly swollen, with distal cylindrical process bearing basally fused seta and large aesthetasc (100 μm); acrothek on segment 9 with slender aesthetasc (27 μm).

P2 (Fig. 32A) with inner distal corner of basis not modified into spinous process but lateral margin slightly more chitinized. Exp-3 modified; inner distal element transformed into strong claw, directed medially and posteriorly, and with distal half pinnate. Endopod slightly shorter than in female; outer margin with two spinular rows; apical seta distinctly longer, clearly extending beyond distal margin of exp-2, with sparser ornamentation than in female; inner seta slightly larger than in female, bare.

Spines of P3 exopodal segments with pinnate ornamentation (Fig. 29B); exp-1 with reduced hyaline frill; exp-3 with secretory pore on anterior surface near joint with exp-2. P3 endopod (Fig. 29B, C) distinctly three-segmented; enp-1 small, without armature or ornamentation; enp-2 with serrate, posterior seta and long, rigid sigmoid apophysis arising from anterior surface; enp-3 with weakly chitinized inner margin and one pinnate seta apically.

Fifth legs (Figs 31C, D, 32B) with baseoendopod and exopod fused into a common elongate plate, tapering distally towards long, smooth, spinous process, which is longer than the plate; inner margin with serrate spine; outer margin with small, bare spine completely fused to plate, three naked setae and a sparsely plumose seta derived from baseoendopod; anterior surface with three large tube-pores.

Sixth pair of legs (Figs 31C, E) asymmetrical, with one short, naked and two long, sparsely pinnate setae each. First postgenital somite with transverse spinular row near ventral anterior margin (Fig. 31E).

Caudal ramus cylindrical (Fig. 32F), shorter than in female; seta IV long and uniplumose; styliform part of seta V comparatively longer than in female.

Remarks: Although there are several discrepancies between Scott's (1892) and Sars' (1911) descriptions of *E. incerta*, only the dorsal spinous process has attracted subsequent workers' attention. The presence or absence of this structure was regarded as part of the intraspecific variability and consequently both the Norwegian and Scottish populations were believed to represent two forms of the same species. Kunz (1938) and Scheibel (1972) claimed that they had found both 'forms' in their samples from Helgoland and the Kieler Bucht, respectively. However, at least in Scheibel's case, there is evidence that *E. spinosa* occurred in his material (cf. his illustration of the caudal ramus; Scheibel, 1972: tafel XVII, Fig. 10). It should be noted that Sars (1911) inadvertently reversed the female P2 and P3 in his illustrations.

Differential diagnosis: Evansula spinosa can be readily distinguished by the presence of a dorsal spur on the caudal ramus in both sexes, and by the fused outer spine on the male P5.

Distribution: Norway: Korshavn, near Lindesnes (Sars, 1911; present account), Troldfjord in Lofoten Islands.

Germany: Kieler Bucht (Scheibel, 1972), probably also Helgoland (Kunz, 1938).

Scotland: Firth of Forth (present account).

England: off Suffolk (present account).

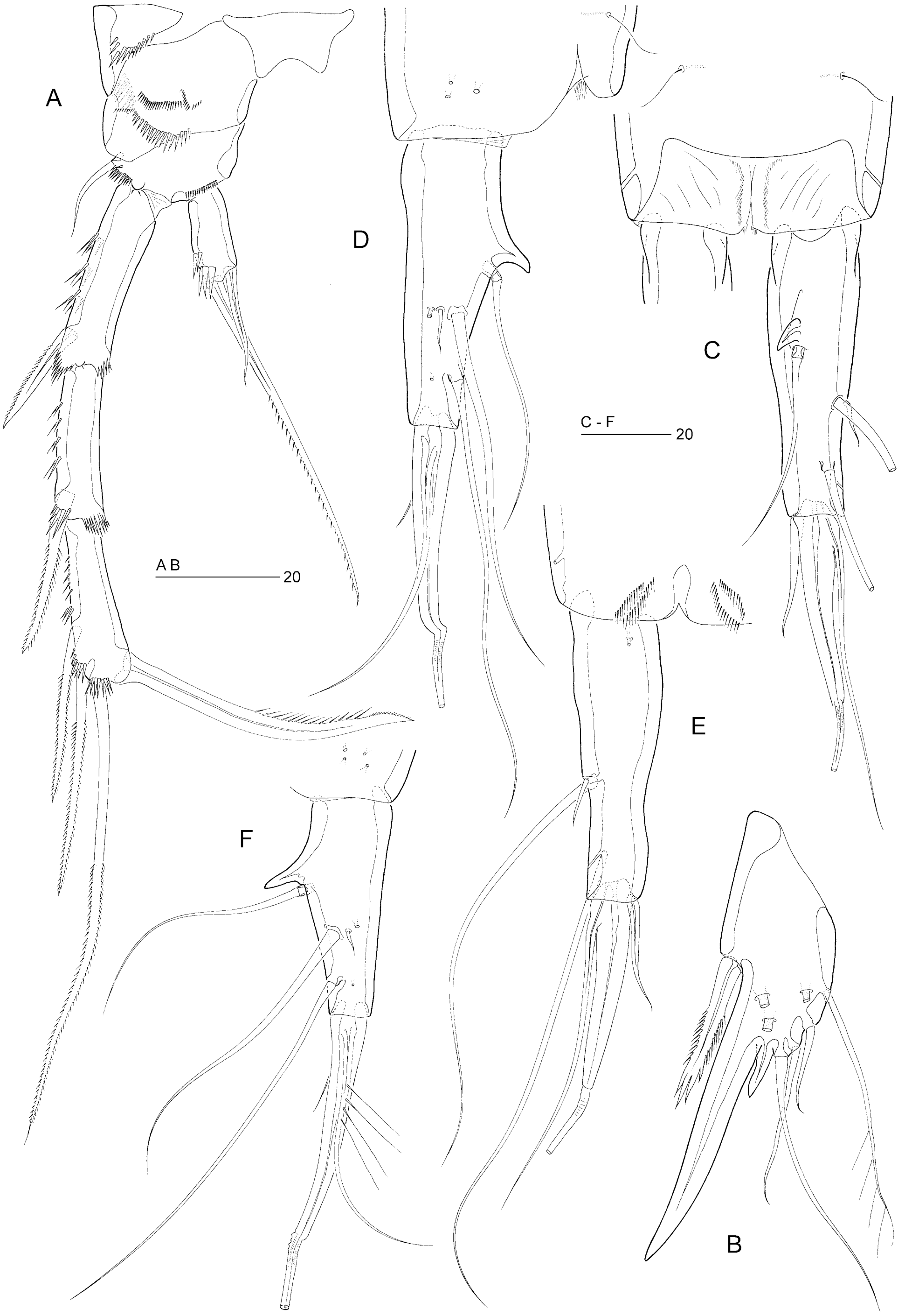

Figure 32. ***Evansula spinosa* sp. nov.** A, male P2, anterior; B, male P5, anterior; C, female anal somite and right caudal ramus, dorsal; D, female anal somite and left caudal ramus, lateral; E, female anal somite and right caudal ramus, ventral; F, male right caudal ramus, lateral.

***EVANSULA POLARIS* SP. NOV.**

Synonym: Evansula incerta (T. Scott, 1892) *sensu* Scott (1903b).

Original description: Scott (1903b) did not provide any descriptive information.

Type locality: Norway, East Finmark, Laksefjord.

Material examined: From type locality: holotype ♂ found among spirit-preserved 'cotypes' of *E. incerta* (reg. nos 44508–509) as part of the Cannon A. M. Norman collection (1911.11.8); coll. A. M. Norman, 30 June 1890; det. T. Scott and labelled *Tetragoniceps incertus*; deposited in NHM (reg. no. 1995.427); dissected on eight slides.

Etymology: The species name is derived from the Latin *polaris*, meaning polar, and refers to the Arctic distribution of this species.

Description

Female: Unknown.

Male: Total body length: 435 µm. Body slender, cylindrical (Fig. 33A), semitransparent, yellowish; no distinct separation between prosome and urosome. Anal somite only slightly longer than wide (46 × 41 µm), with two pairs of secretory pores laterally (Fig. 33B); posterior margin with one short spinular row on either side of ventral midline (Fig. 34D). Anal operculum weakly developed, unarmed (Fig. 34B).

Caudal ramus short and conical (Fig. 34B–D), proximal inner margin slightly convex, length (measured along outer margin) approximately 2.5 times the proximal width; dorsal surface without chitinous spur but with raised spinular row; with seven setae, setae I–VI in distal and seta VII in proximal half (Fig. 34B); seta I diminutive; setae II–III long and bare; seta IV uniplumose, slightly longer than styliform part of V; seta V long, with distinct flexure zone between styliform part and long distal flagellate part, fused at base with seta IV; seta VI vestigial; seta VII tri-articulate at base and located along proximal inner margin, with conspicuous swelling in proximal quarter; ventral surface with one tube-pore near anterior margin (Fig. 34D), lateral surface with two tube-pores (Fig. 34C).

Rostrum elongate (Fig. 33C), with slightly convex margins in proximal half, tapering distally; slightly shorter than first antennulary segment; with two long sensillae; median pore positioned dorsally near apex of rostrum.

Antennule distinctly nine-segmented (Fig. 33C), geniculation between segments 7 and 8; segment 1 only slightly shorter than segment 2, with small sclerite around proximal posterior margin, with anterior pattern of spinular rows as illustrated for other species; segment 5 distinctly swollen, with a distal cylindrical process bearing a basally fused seta and large aesthetasc (52 µm); acrothek on segment 9 with slender aesthetasc (17 µm).

Antenna, mandible, maxillule, and maxilla as in *E. incerta*.

Maxilliped well developed, subchelate, directed inwards. Syncoxa well developed, without pinnate seta, with two spinular rows. Basis elongate, with two to three long spinules anteriorly and a posterior spinular row along inner margin. Endopod represented by strong, curved, bare claw.

P1 (Fig. 34A). Praecoxa strongly developed. Coxa with four spinular rows. Basis with sparsely plumose inner seta and pinnate outer seta. Exopod three-segmented; with two spines and two geniculate setae on exp-3. P1 endopod prehensile, distinctly longer than exopod; proximal segment approximately ten times as long as average width, with pinnate inner seta being plumose in proximal third; distal segment short, with three spinular rows, a subdistal setule, and two geniculate spines distally.

Swimming legs P2–P4 (Fig. 35A–D). Praecoxae well developed, with spinular row on anterior surface in P2–P4. Coxae with pattern of spinules as in Figure 35A, B, D, with large tube-pore on anterior surface of P3. Bases with outer seta (short and pinnate in P2, long and plumose in P3, short and naked in P4); with spinular rows on anterior surface only. Exopods three-segmented, endopods one-segmented (P2, P4) or incompletely three-segmented (P3). Inner distal spine of P3–P4 shorter than outer distal one. Inner setae of P4 endopod and exp-3 serrate. Seta and spine formulae as for genus.

P2 (Fig. 35A) with inner distal corner of basis not modified into spinous process but with well-chitinized lateral margin. Endopod with three spinular rows; apical seta pinnate and clearly extending beyond distal margin of exp-2; inner element setiform and naked. Exp-3 modified; outer distal seta very long; inner distal element transformed into slender claw, directed medially and posteriorly, and with middle third pinnate and distal third denticulate.

Spines of P3 exopodal segments with pinnate ornamentation (Fig. 35B); exp-1 with reduced hyaline frill; exp-3 with secretory pore on anterior surface near joint with exp-2. P3 endopod (Fig. 35B, C) indistinctly three-segmented with middle and distal segments partly fused along posterior surface; enp-1 small, without armature or ornamentation; enp-2 with serrate, posterior seta and rigid, slightly sigmoid apophysis arising from anterior surface; enp-3 with weakly chitinized inner margin and with one short pinnate seta apically.

Fifth legs (Fig. 33B, D) with baseoendopod and exopod fused into a common elongate plate, tapering distally towards long, pinnate, spinous process, which is longer than the plate; inner margin with serrate spine; outer margin with small, pinnate spine, three naked setae and sparsely plumose seta derived from baseoendopod; anterior surface with three large tube-pores.

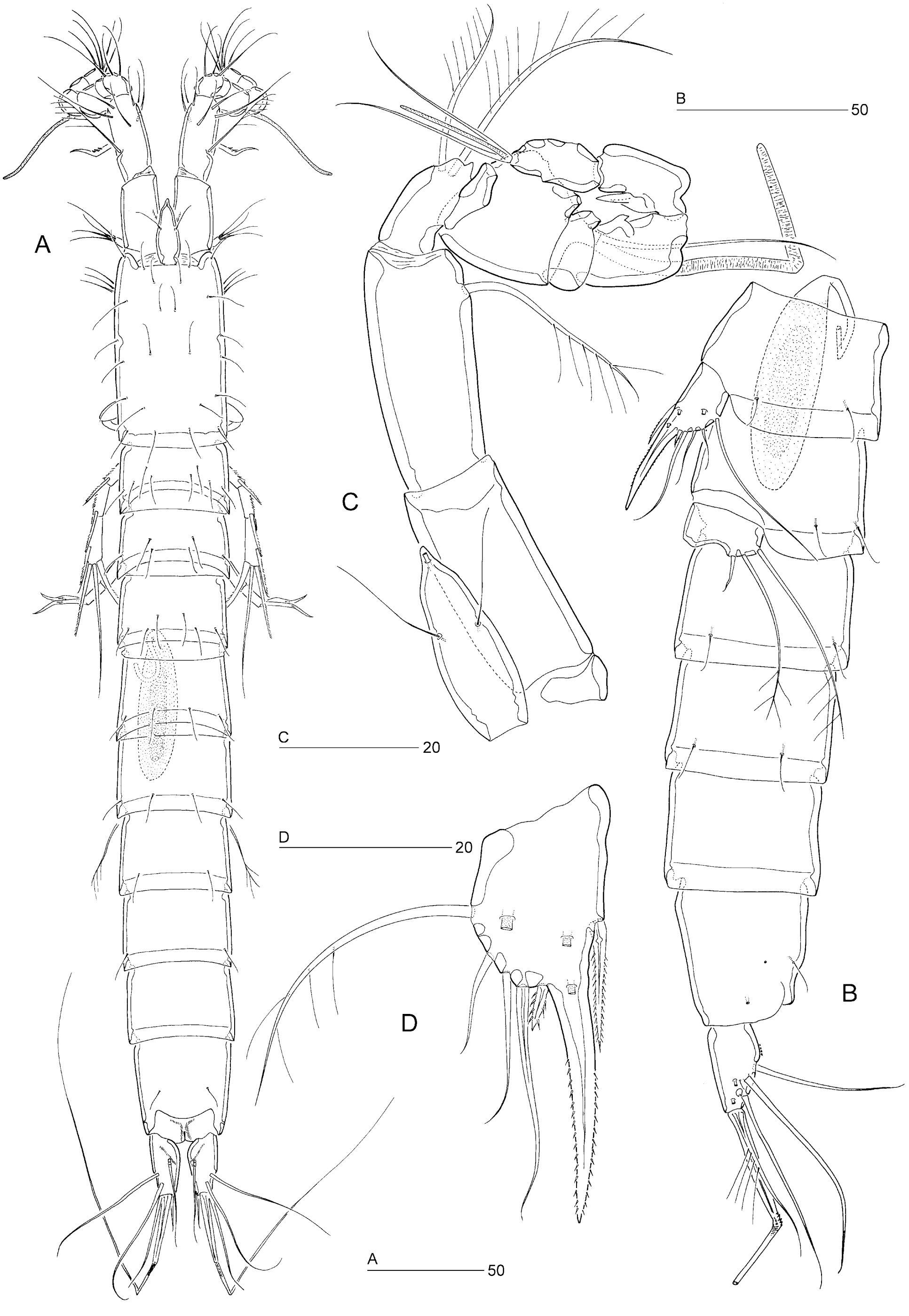

Figure 33. ***Evansula polaris* sp. nov.** (male). A, habitus, dorsal; B, urosome, lateral; C, antennule and rostrum, dorsal (armature largely omitted); D, P5, anterior.

Sixth pair of legs (Figs 33B, 35E) asymmetrical, with one short, naked and two long, sparsely pinnate setae each. First postgenital somite with transverse spinular row near ventral anterior margin (Fig. 35E).

Differential diagnosis: Evansula polaris is thus far the only species that possesses spinule rows on the ventral posterior margin of the anal somite in the male (the condition in *E. pygmaea* is unknown). The characteristic shape of the male P3 endopod is an

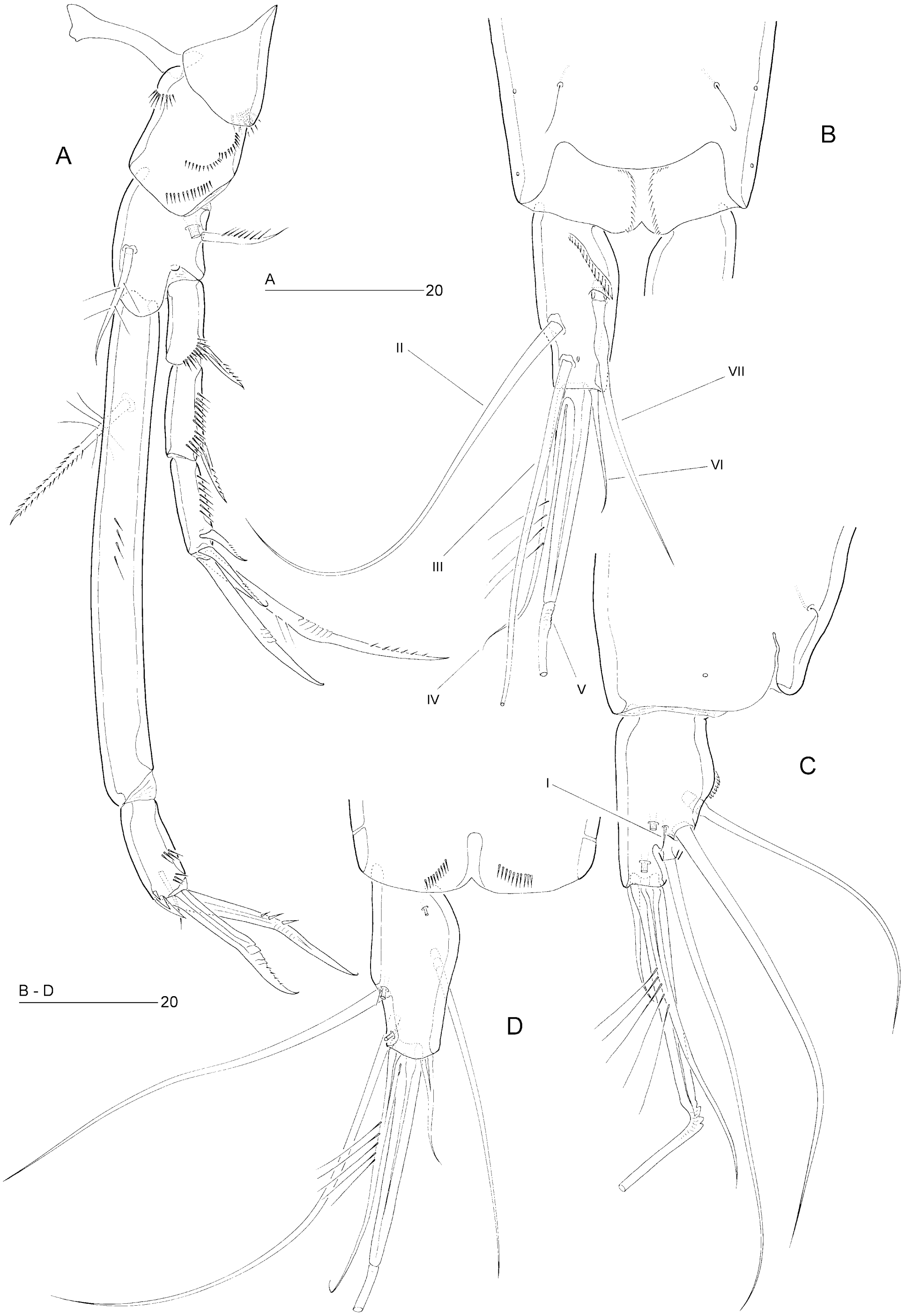

Figure 34. ***Evansula polaris* sp. nov.** (male). A, P1, anterior; B, anal somite and left caudal ramus, dorsal; C, anal somite and left caudal ramus, lateral; D, anal somite and right caudal ramus, ventral.

additional differentiating feature. *E. polaris* is the smallest representative of the genus.

Distribution: Norway: Laksefjord (Scott, 1903b). Perhaps also in Troldfjord inside the Lofoten Islands [one male recorded by Sars (1911) as *E. incerta*].

EVANSULA (?) SPEC. *SENSU* NOODT (1955C)

Noodt (1955c) briefly mentions the presence of a very small male specimen in a sample taken at the volcanic sandy beach near Los Cristianos on Tenerife, Canary Islands. Because of the lack of sufficient material, a

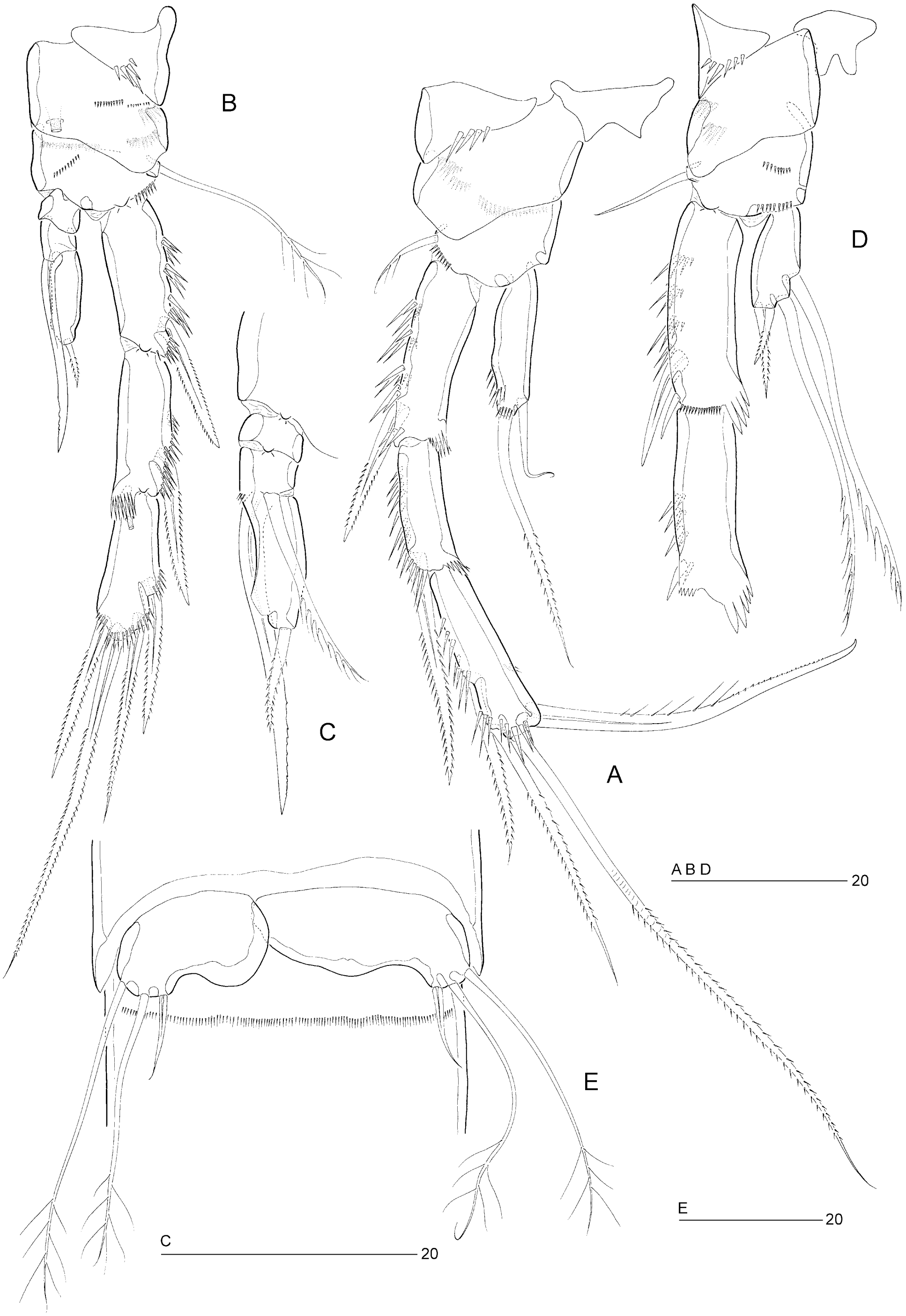

Figure 35. ***Evansula polaris* sp. nov.** (male). A, P2, anterior; B, P3, anterior; C, P3 endopod, posterior; D, P4 (exp-3 omitted), anterior; E, sixth pair of legs and first abdominal somite, ventral.

description was not given, but the author stated that it was most closely allied to *Evansula* but differed from it in '. . . eine Reihe primitiver Merkmale'. It is possible that Noodt was dealing with an undescribed species of *Cylinula*, the only other genus in the family that exhibits a prehensile P1 endopod but has retained two-segmented endopods on all swimming legs.

DISCUSSION

SPECIES DISCRIMINATION

As a result of the present revision, it is clear that the traditional criteria of species differentiation within the genus *Evansula* can no longer be applied. Nicholls' (1939) key was based solely on caudal ramus morphology, whereas other authors (e.g. Scheibel, 1972; Mielke, 1975) have used body size, the P1 endopod, the female P5, and the proportional lengths of the proximal and distal parts of the composite caudal seta V. A simple dichotomous key is difficult to construct and would still require confirmation of the identification against the original description. It is also known that several, as yet unnamed, species occur in European waters, not infrequently in sympatry with the species reported in the present paper. The salient features compiled in Table 1 are meant to facilitate identification, but checking against the relevant descriptions remains a necessity.

PHYLOGENETIC RELATIONSHIPS

The isolated position of *Evansula* and its early divergence in the evolution of the Cylindropsyllidae have been repeatedly postulated (Huys, 1988; Huys & Conroy-Dalton, 1993; Huys & Willems, 1993). This assertion was primarily based on the absence of the sexually dimorphic process on the male P2 basis, which is present in a variety of types in all other genera of the family. In *Evansula*, the inner margin of the male basis is at most slightly more chitinized than in the female (e.g. *E. incerta*, Fig. 8A). However, in most species, such a difference was not found (e.g. *E. arenicola*, Fig. 16B; *E. cumbraensis*, Fig. 19D). In addition, it is unlikely that the marginal reinforcement represents the positional homologue of the anterior process in other Cylindropsyllidae. Martínez Arbizu & Moura (1994) listed the basal process as one of the diagnostic synapomorphies of the Cylindropsyllinae. However, their claim that the process in *Evansula* is represented by a short spine is based on an observational error. In their attempt to homologize sexually dimorphic structures on the P2 of *E. cumbraensis* (their Fig. 4c), the authors misinterpreted the chitinous rim between the exopod and the endopod as the spinous process.

The presence of a sexually dimorphic secretory pore on the anterior surface of the male P3 exp-2 is another synapomorphy that separates the remaining cylindropsyllid genera from *Evansula*. This pore is presumably secondarily lost in the highly derived genus *Willemsia* (Huys & Conroy-Dalton, 1993) but seems to be primitively absent in *Evansula*. It is remarkable that in the latter genus, a similar kind of pore was found on the distal segment of the male P3 exopod. This pore is frequently concealed by the hyaline frill of the middle segment (e.g. Figs 15C, 25A) and consequently difficult to observe. We tested the alternative hypothesis that the *Evansula* pore position is in fact a synapomorphy for a wider group of families (including the Cylindropsyllidae). This would imply that the character is only a diagnostic plesiomorphy for *Evansula* without any significant phylogenetic importance and that it has been secondarily lost and replaced by a pore on a different segment (i.e. the middle one) in its sister group encompassing all other Cylindropsyllidae. One of the most probable candidates for the cylindropsyllid sister group position is the Canthocamptidae. Examination of a number of genera revealed that the pore is present in *Canthocamptus staphylinus* (Jurine, 1820), but absent in *Mesochra* Boeck, and a wide range of freshwater genera such as *Elaphoidella* Chappuis, *Attheyella* Chappuis, and *Moraria* T. & A. Scott. It is also absent in brackish-water representatives of *Cletocamptus* Shmankevich (Gee, 1999) and a number of marine genera excluded from the Cletodidae and attributed to the Canthocamptidae by Por (1986): *Parepactophanes* Kunz, *Taurocletodes* Kunz, *Heteropsyllus* T. Scott, and *Hemimesochra* Sars (Karaytuğ & Huys, 2004; R. Huys, pers. observ.). Within the Cletodidae, a sexually dimorphic tube-pore has been reported in species belonging to *Schizacron* Gee & Huys and *Strongylacron* Gee & Huys, but appears to be absent in all other genera of that family (Gee, 1994; Gee & Huys, 1996). From these observations it seems that the pore on the male P3 exp-3 might be an autapomorphy for *Evansula* that convergently also became expressed in *Canthocamptus* Westwood and in two of the 22 genera currently recognized as valid within the Cletodidae. It does not, however, provide any indication for the inclusion of the Cylindropsyllidae in the Canthocamptidae, as suggested by Martínez Arbizu & Moura (1994). Moreover, the presence of this pore on the male P3 exp-3 seems to be widely distributed among other harpacticoids, as it has now been found in at least five families. Gee & Fleeger (1990) reported it from a range of miraciid genera and we have found it to be expressed in the leptastacid genus *Paraleptastacus* Wilson.

In addition to the maximum segmentation and setation expressed in the antennules and mouthparts among the Cylindropsyllidae, a number of other unique characters reinforce the primitive status of *Evansula*. Perhaps the most important one is the presence of two well-developed serrate setae on the inner margin of the P4 endopod (e.g. Fig. 5E). These elements are lost in all other genera. The two-segmented P4 endopod expressed in the male (and partly in the female) of *E. arenicola* indicates that both setae are derived from the distal segment (Fig. 17B, C). *Evansula* is also the only genus that has retained seven ele-

Table 1. Salient features discriminating *Evansula* species

	incerta	*pygmaea*	*arenicola*	***cumbraensis* sp. nov.**	***polaris* sp. nov.**	***spinosa* sp. nov.**
Maxilliped, syncoxal seta	Present	Absent	Present	Absent	Absent	Absent
Female P2 endopod, inner element	Setiform, bare. Less than one-third length of distal element	Setiform, pinnate. Slightly shorter than distal element	Spiniform, pinnate. Slightly less than half length of distal element	Spiniform, pinnate. Slightly less than half length of distal element	?	Setiform, pinnate. Half length of distal element
Male P3 endopod	Distinctly two-segmented	Distinctly three-segmented	Distinctly three-segmented	Distinctly three-segmented	Indistinctly three-segmented	Distinctly three-segmented
Male P4 endopod	One-segmented	One-segmented	Two-segmented	One-segmented	One-segmented	One-segmented
Female P5, seta c	Fused to segment	Defined at base	Fused to segment	Defined at base	?	Fused to segment
Female copulatory pore	Large. Slightly posterior to genital apertures	Large. Slightly posterior to genital apertures	Of moderate size. Slightly anterior to genital apertures	Very large. At level of genital apertures	?	Large. Slightly posterior to genital apertures
Anal somite, ventral spinular rows						
(female)	Posterior only	Anterior + posterior	Anterior + posterior	Posterior only	?	Anterior + posterior
(male)	Absent	?	Absent	Absent	Posterior	Absent
Caudal ramus, dorsal surface	Smooth	Raised spinular row	Smooth	Raised spinular row	Raised spinular row	Spur
Female body length (µm)	695–710	475	710–750	500–560	?	700
Male body length (µm)	705	?	690	480–525	435	670

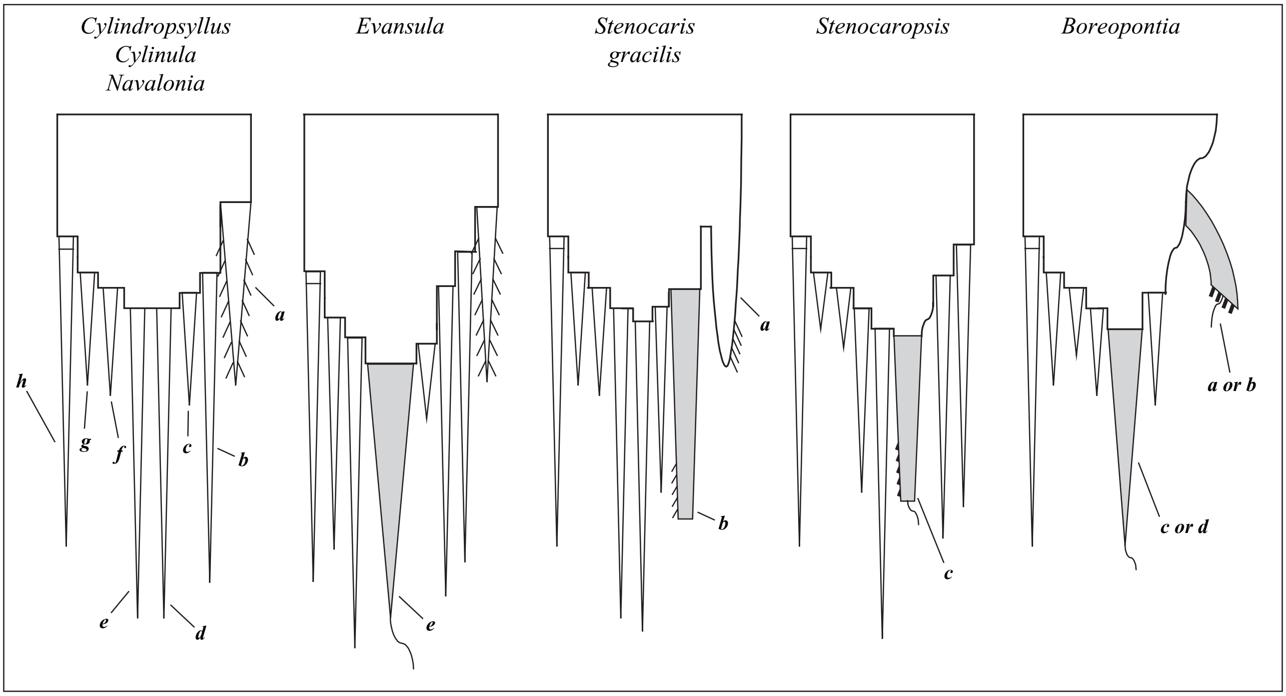

Figure 36. Position and modification of armature elements on female P5 in cylindropsyllid genera that have retained the ancestral complement of setae/spines (except *Boreopontia*). Setation elements are homologized with reference to the ancestral state in *Cylindropsyllus–Cylinula–Navalonia*. h, outer basal seta. Elements modified into spines are shaded.

ments on the male leg 5 (Fig. 37). Six of these elements are defined at the base (being the maximum number in other Cylindropsyllidae) and the seventh, which is clearly pinnate in *E. incerta* (Fig. 8E), is completely incorporated in the segment forming a long spinous process.

The retention of many primitive features makes *Evansula* a useful outgroup for character evolution assessment in the more advanced genera of the family. For example, the composite caudal ramus seta V consisting of a proximal styliform part and a distal flagellate part is found in most of the genera. Its presence in *Evansula* suggests that the absence in the genera *Navalonia* and *Willemsia* is secondary (Huys & Conroy-Dalton, 1993) and that the composite seta constitutes a synapomorphy at the basal node of the Cylindropsyllidae. Similarly, the morphological signature of the female genital field in *Evansula* and its resemblance to that of other more advanced genera also provide evidence for the secondary displacement of the copulatory pore in both *Cylindropsyllus* and *Cylinula*. Martínez Arbizu & Moura (1994) mistakenly considered the latter derived state as a family diagnostic of the Cylindropsyllidae and therefore wrongly employed it as supporting evidence for the inclusion of the Cylindropsyllinae in the Canthocamptidae.

Its primitive position is, however, uninformative with regard to the polarity of the character evolution of the rostrum and maxilliped within the family. *Evansula* is the only genus that exhibits an elongate rostrum (Fig. 2C). In the absence of information on the sister-group relationships of the Cylindropsyllidae, it is not clear whether this is either an autapomorphy for the genus or the plesiomorphic alternative of the triangular rostrum found in all other cylindropsyllids. Similarly, the powerful maxilliped with a distinctly curved endopodal claw (Figs 2A, B, 3F) is fundamentally different from the more slender type having a geniculate, frequently pinnate, claw found in the remaining genera (except *Cylindropsyllus* and *Cylinula* where it is atrophied). It is impossible to decide on the polarity of this character as, again, both alternatives are equally plausible.

Despite its basal position, *Evansula* can be diagnosed by a high number of autapomorphies: (1) prehensile P1 endopod (Fig. 4D, E): the elongation of enp-1 presumably evolved convergently in *Cylinula* where one of the distal claws has lost its geniculate flexure zone; (2) inner seta of P1 enp-1 plumose proximally and pinnate distally (Fig. 4E): in all other genera, this seta is serrate in the distal half; (3) P2–P4 endopods one-segmented in the female (Fig. 5A, C, E): segmental reductions of P2 and P3 endopods also occur convergently in other genera. However, *Evansula* is the only genus with a one-segmented P4 endopod, although an incomplete suture line is expressed in

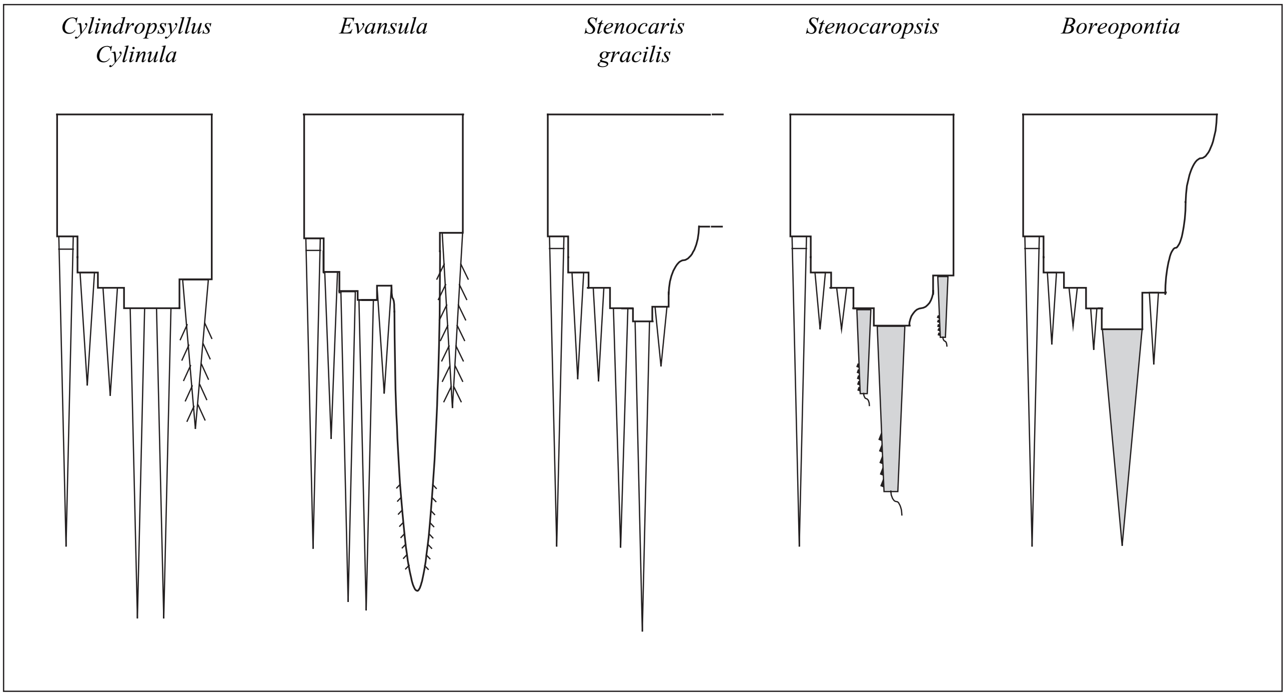

Figure 37. Position and modification of armature elements on male P5 in *Evansula* and cylindropsyllid genera that have retained at least six setae/spines. Left element with basal socle is outer basal seta. Elements modified into spines are shaded.

some specimens of *E. arenicola* (Fig. 17B); (4) inner distal spine on P3–P4 exp-3 is considerably shorter than the outer distal one (Fig. 4C, E): a similar reduction is found in the highly derived genus *Willemsia*, where it occurs on P2–P4 exp-3; (5) loss of inner serrate seta on P2 endopod: this seta (derived from enp-1) is present in all other genera except for the morphologically advanced genera *Navalonia* and *Willemsia*; (6) loss of inner setule on P3 endopod and displacement of outer subdistal spine to distal position (Fig. 5C); (7) first abdominal somite of male with a sexually dimorphic spinular row on the ventral surface (Fig. 8F); (8) female P5, modification of element e into a strong apical spine (Fig. 11G): various other cylindropsyllid genera have similar spiniform elements or structures on the female P5 (Fig. 36), but using the ancestral unmodified state in *Cylindropsyllus* as a reference it is clear that none of them is homologous with the *Evansula* condition; (9) male P5 with a spinous process (Figs 8E, 37).

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