

## A revision of *Leptopontia* T. Scott (Copepoda: Harpacticoida) with description of six new species

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The presumed amphiatlantic distribution of *Leptopontia curvicauda* T. Scott, 1902 (Copepoda: Harpacticoida) is reviewed and the species being redescribed on the basis of a single male from the Isle of Sylt. Examination of other material previously attributed to *L. curvicauda*, collected in South Carolina and a wide range of localities in northwestern Europe, resulted in the discovery of four new, morphologically similar species: *L. dovpori* sp. nov., *L. flandrica* sp. nov., *L. punctata* sp. nov. and *L. americana* sp. nov. In addition, two new species, *L. mediterranea* sp. nov. and *L. breviarticulata* sp. nov. are described from the Mediterranean and the Galápagos archipelago, respectively. *L. curvicauda* sensu Marinov (1971) and sensu Apostolov (1973) from the Black Sea and sensu Klie (1950) from Helgoland are regarded as *species inquirendae*. A revised diagnosis of the genus *Leptopontia* T. Scott is presented.

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ADDITIONAL KEY WORDS: — revision – copepod – taxonomy – interstitial.

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### INTRODUCTION

T. Scott (1902) claimed that *Leptopontia* T. Scott resembled *Mesochra* Boeck (now Canthocamptidae) and *Tetragoniceps* Brady (now Tetragonicipitidae) in certain

aspects, a view also held by Monard (1927) who formally allocated it to the Canthocamptidae. The genus was not considered by Sars (1903–1911) but Gurney (1932) placed it, along with *Evansula* T. Scott and *Leptastacus* T. Scott, in the *Evansula* series, one of six generic groupings defined in Gurney's classification of the Canthocamptidae. The two monotypic genera *Leptopontia* and *Arenopontia* Kunz were moved by Lang (1944) to the Cylindropsyllidae, i.e. in the *Leptopontia*-Reihe which subsequently acquired subfamilial status (Lang, 1948). This classification gained wide usage although some authors continued to include *Leptopontia* in the Canthocamptidae (Apostolov, 1971). Recently, Martinez Arbizu & Moura (1994) dramatically altered the concept of the Leptopontiinae and raised it to family rank. For reasons outlined elsewhere (Huys, in prep.) these changes are not adopted here.

*Arenopontia* currently represents one of the most speciose interstitial genera, encompassing 29 species (and subspecies) contained in two subgenera *Arenopontia* Kunz, 1937 and *Neoleptastacus* Nicholls, 1945. The genus *Leptopontia*, however, has remained monotypic since its establishment at the turn of the century (T. Scott, 1902). *Leptopontia curvicauda* T. Scott was one of the very few interstitial copepods discovered during the era marked by the numerous surveys of Thomas and Andrew Scott, long before Wilson (1935) and Nicholls (1935) drew attention on the existence of meiofaunal harpacticoids in sandy beaches on both sides of the Atlantic. Originally described from St. Monans in the Firth of Forth, Scotland, *L. curvicauda* has now been reported from numerous localities in the British Isles, N.W. European coast, the Mediterranean and the Atlantic seaboard of North America. In addition, Mielke (1982) recorded a single specimen of an undescribed *Leptopontia* species from the Galápagos.

In view of the limited distribution and dispersal of interstitial copepods in general, and Leptastacidae and Paramesochridae in particular (Huys, 1992), a survey of existing records was undertaken in order to test the presumed amphi-Atlantic and boreo-Mediterranean distribution patterns of *L. curvicauda*. The present revision, which was based on material from a wide range of localities, resulted in the discovery of six new species, some of which have been confused previously with the type species *L. curvicauda*.

#### MATERIAL AND METHODS

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, UK). All drawings have been prepared using a camera lucida on a Leitz Diaplan microscope equipped with differential interference contrast. The descriptive terminology applied to segmentation and setation of body appendages is adopted from Huys & Boxshall (1991). Abbreviations used in the text and figures are: P1–P6, first to sixth thoracopods; exp., exopod; enp., endopod; exp(enp)–1(–2, –3), to denote the proximal (middle, distal) segment of a ramus. Except for *L. breviarticulata* sp. nov., the type series of all new species are deposited in the collections of the Zoology Department, The Natural History Museum, London.

## SYSTEMATICS

The systematics of the Cylindropsyllidae is currently in a state of flux. Huys & Ohtsuka (1993) suggested that the Leptopontiinae is not a natural unit and should encompass only *Leptopontia*, *Notopontia* Bodiou and *Syrcticola* Willems & Claeys. In a controversial paper, Martinez Arbizu & Moura (1994) instead considerably widened the boundaries of the Leptopontiidae (now upgraded to family rank) by maintaining *Arenopontia* and further incorporating the Psammopsyllinae in this family. A discussion of the generic composition and relationships of the Leptopontiinae is beyond the scope of this paper and will be published separately (Huys, in prep.). For the sake of this paper the Leptopontiinae is regarded as a subfamily of the Cylindropsyllidae in the sense of Huys & Ohtsuka (1993).

*Leptopontia* T. Scott, 1902*Diagnosis*

Leptopontiinae. Hyaline frill of cephalothorax and free body somites plain, sometimes striated. Rostrum elongate. Anal operculum with 1 or several small spinous processes, exceptionally without.

Antennule 7-segmented in ♀; 9-segmented in ♂ with segment 5 moderately swollen; terminal acrothek in both sexes consisting of 2 setae basally fused to aesthetasc. Maxillary coxal endite with 1 seta. Maxilla with 3 setae on allobasis; syncoxal endite cylindrical, with 2 unmodified setae.

P1 exopod 3-segmented; suture line between exp-2 and exp-3 sometimes incomplete; exp-2 without outer seta; exp-3 with 1 subapical and 2 apical geniculate setae, outer spine absent. P1 enp-2 with 2 geniculate setae or claws apically and 1 minute accessory seta subapically.

P2-P4 endopods 2-segmented; inner element enp-1 pinnate and spiniform. Armature formula of female swimming legs:

	Exopod	Endopod
P1	0.0.021 [or 0.021]	1.120
P2	0.0.021	1.120
P3	0.0.112	[0-1].010
P4	0.0.112	1.020

P5 biramous in both sexes; usually incompletely fused medially in ♂; exopod small, with 3 naked setae in both sexes; baseoendopod with outer plumose seta and weakly pronounced, rounded endopodal lobe, bearing 1 or 2 short setae in ♀, unarmed in ♂.

Sixth pair of legs slightly asymmetrical in ♂, with outer setule and inner seta, distal margin rounded; represented by small operculum with 2 setules in ♀.

Sexual dimorphism in antennule, P3 endopod (2-segmented, minute; spine derived from enp-1 in ♀ lost; enp-2 represented by bifid spine), P4 endopod (2-segmented; spine derived from enp-1 in ♀ lost, except for *L. americana* sp. nov.; distal armature consisting of short outer spine and backwardly recurved, denticulate, inner spine), P5, P6, and in genital segmentation.

Caudal ramus produced distally into dorsally recurved spinous process; seta I well developed, fused to and closely adpressed to caudal ramus.

*Type species*

*Leptopontia curvicauda* T. Scott, 1902 [by monotypy]

*Other species*

***L. dovpori* sp. nov.**

***L. punctata* sp. nov.**

***L. flandrica* sp. nov.**

***L. mediterranea* sp. nov.**

***L. breviarticulata* sp. nov.**

***L. americana* sp. nov.**

*Species inquirendae*

*Leptopontia curvicauda* T. Scott, 1902 *sensu* Klie (1950)

*Leptopontia curvicauda* T. Scott, 1902 *sensu* Marinov (1971)

*Leptopontia curvicauda* T. Scott, 1902 *sensu* Apostolov (1973)

*Descriptions*

Since females of the type species *L. curvicauda* were not available for study, the new species *L. dovpori* is selected instead for the model description.

***Leptopontia dovpori* sp. nov.**

*Type locality.* Coal Pit, off Norfolk coast (England); 53°33.40'N, 01°34.70'E; 40 m depth, coarse gritty sand; leg. Dr R. Hamond, 15 June 1989.

*Material examined.* Holotype ♀ (dissected on 8 slides) and paratype ♂ (dissected on 7 slides) deposited in The Natural History Museum, London under reg. nos 1994.5825 and 1994.5826, respectively; additional paratypes (1 ♀, 1 ♂) in alcohol (reg. no. 1995.385-386).

Other material: 16 ♀♀ and 4 ♂♂ (in alcohol; reg. no. 1995.387-396) from off Dutch Delta, S.W. Netherlands (51°45'00"N, 3°30'00"E; depth 14 m); leg. R. Huys, 17 April 1986.

*Description of female.* Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 595 µm (Fig. 1A). Maximum width 65 µm measured at cephalothorax. Integument of thoracic and abdominal somites with distinct pattern of subsurface integumental pits. Pleural areas of cephalothorax not well developed so that cephalic appendages are clearly exposed in lateral aspect (Fig. 2A). Posterior margin of body somites with plain hyaline frill which is striated in the genital double-somite and free abdominal somites (Figs 1A, 6A,B). Individual somites connected by well developed intersomitic membranes (e.g. Fig. 6A,B). Sternal plates with midventral, backwardly directed spinous process (often bifid at tip) located anterior to each pair of swimming legs (Fig. 7C).

*Rostrum* (Figs 1A, 2A,B, 3A) triangular, elongate, with slightly convex lateral margins; about 0.8 times the length of first antennular segment; with 2 delicate sensillae; base surrounded by membranous area (Fig. 7A).

*Genital double-somite* (Figs 1A, 6A,B) slightly longer than wide; original segmentation

not marked by any external or internal cuticular structure. Genital apertures paired (Fig. 6B), located in anterior half of genital double-somite; each closed off by small operculum derived from sixth leg bearing 2 tiny setae of equal length (Fig. 11B). Median copulatory pore located far anteriorly between genital apertures (Fig. 11A). Seminal receptacles not confirmed. Paired secretory pores present on ventral surface of genital double-somite.

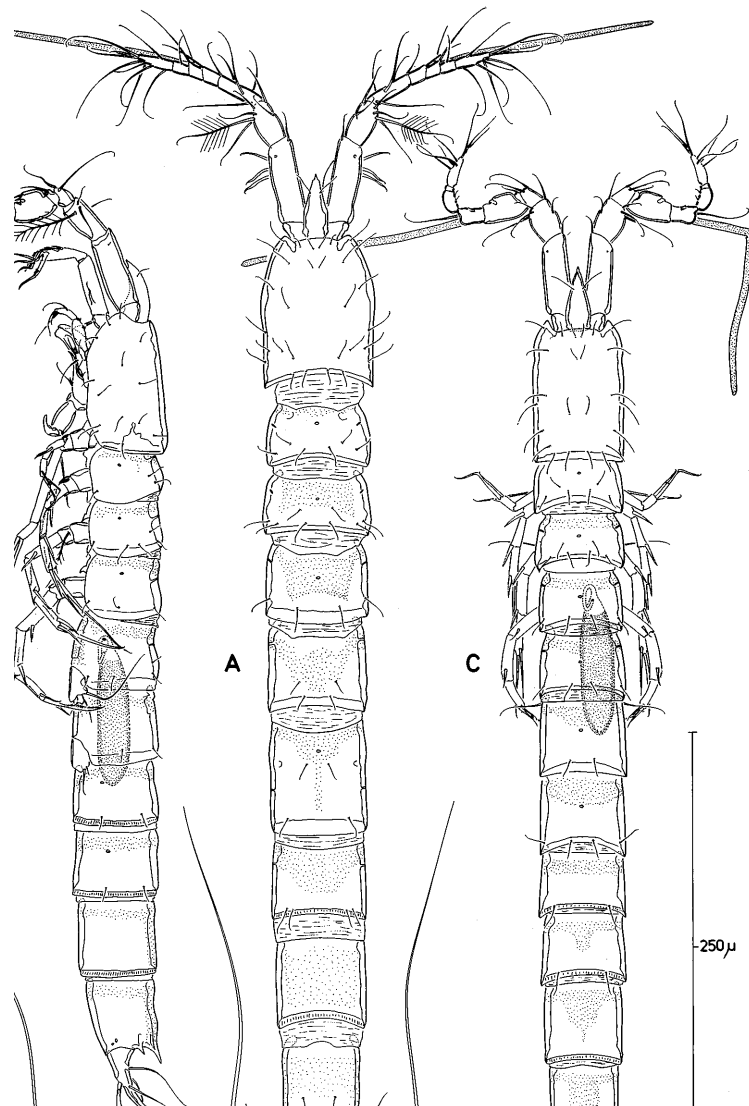


Figure 1. *Leptopontia dovpori* sp. nov. A, habitus (♀), dorsal; B, habitus (♂), lateral; C, habitus (♂), dorsal.

*Anal somite* (Figs 4D, 6F, 9A–C) with dorsal operculum drawn out into median, posteriorly directed, slender spinous process, flanked by two smaller processes which can vary slightly in size and shape (see also Figs 4E, 9A,B). Anus large, terminal, located in between caudal rami (Fig. 9B).

*Caudal rami* (Figs 6E,F, 9A–D) slightly divergent; outer distal corner drawn out into posteriorly directed, dorsally recurved spinous process; with 7 setae; setae I–III well

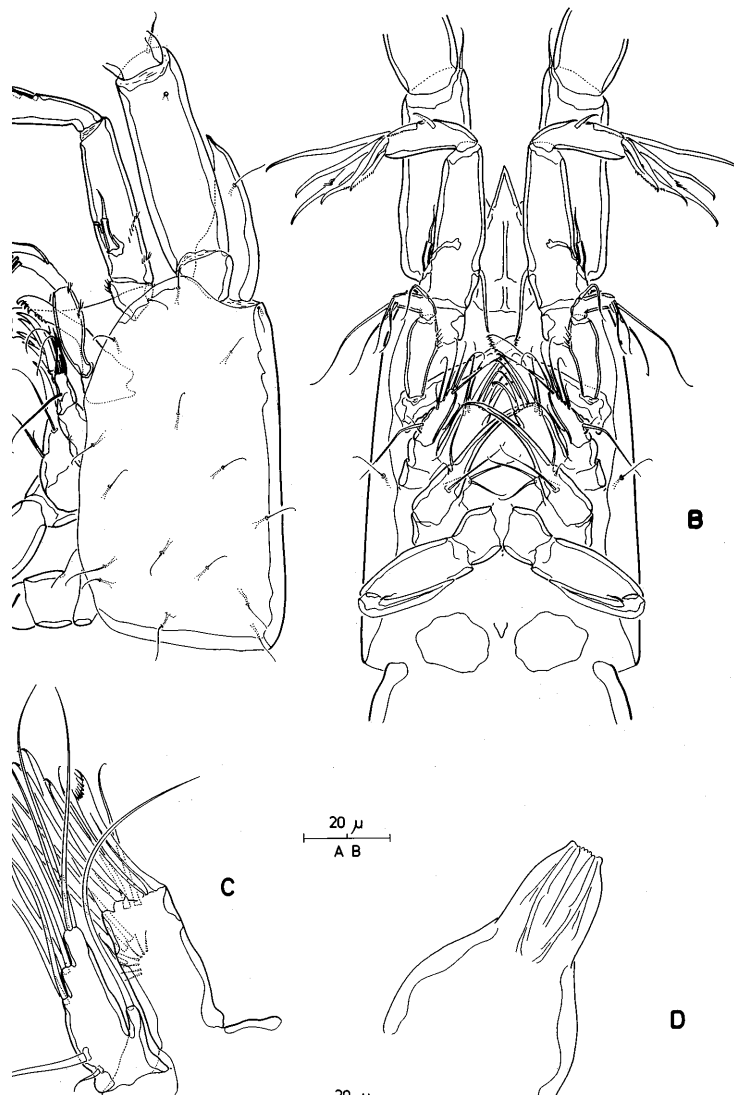


Figure 2. *Leptopontia dovpori* sp. nov. (♀). A, cephalothorax, lateral; B, same, ventral [P1 omitted]; C, maxillule; D, labrum, anterior.

developed, precise identification impossible due to secondary migration, posterodorsal one (probably seta I) fused basally and closely adpressed to ramus, possibly tubular (Fig. 9A, C,D); seta V very long and with fracture plane, seta VI minute, seta VII tri-articulate at base. Ramus about 3.3 times as long as basal width (measured in lateral aspect along ventral margin).

*Antennule* (Fig. 3A) slender, 7-segmented; segment 1 longest, about 3.3 times as long as wide, surrounded by distinct sclerite around proximal posterior margin (Figs 2A,

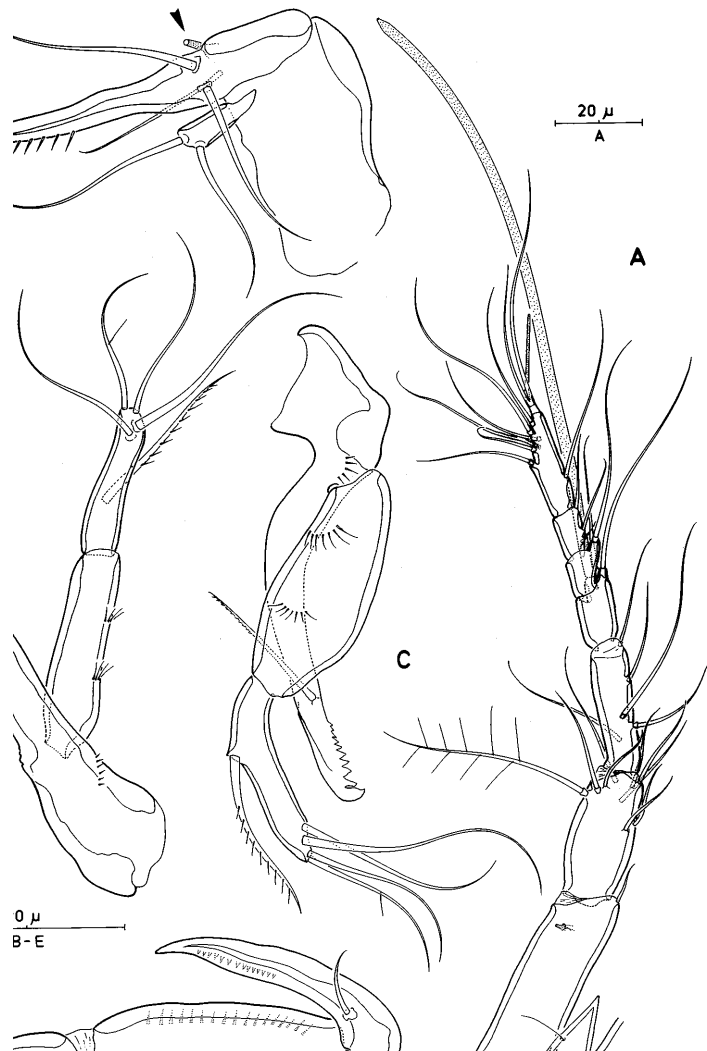


Figure 3. *Leptopontia dovpori* sp. nov. (♀). A, rostrum and antennule, dorsal; B, mandible; C, same, other view; D, maxilla [secretory pore arrowed]; E, maxilliped.

3A, 7A), with 1 short seta at distal anterior corner and dorsal tube pore near distal margin; segment 4 with very long aesthetasc (140  $\mu\text{m}$ ) fused basally to seta and set on distinct pedestal; segment 7 with apical acrothek consisting of short aesthetasc (20  $\mu\text{m}$ ) fused basally to 2 setae. All setae bare except for 1 plumose seta on segment 2. Armature formula: 1-[1], 2-[8 + 1 plumose], 3-[5], 4-[2 + ae], 5-[1], 6-[3], 7-[7 + acrothek].

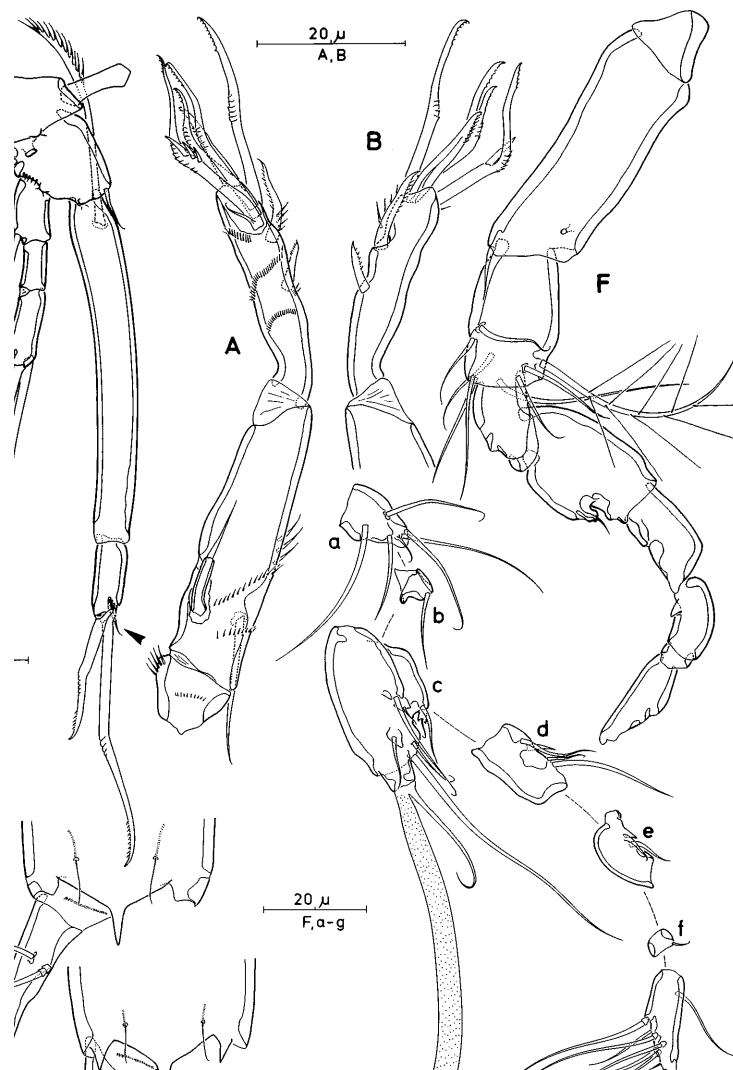


Figure 4. *Leptopontia dovpori* sp. nov. (♀). A, antenna; B, antennary endopod; C, P1, anterior [vestigial seta on enp-2 arrowed]; D, anal operculum and left caudal ramus, dorsal; E, anal operculum of ♂ specimen; F, antennule (♂) [armature posterior to segment 2 omitted], segments 3-9 disarticulated (a-g).



*Antenna* (Fig. 4A,B). Coxa with 2 spinular rows. Allobasis elongate, about 3.8 times as long as maximum width; with 3 spinular rows and backwardly directed seta. Exopod a small segment (Fig. 10D) located in transverse membranous area marking fusion plane of basis and proximal endopod segment; exopodal seta short, about as long as segment. Free endopod with 3 spinular rows along outer margin, 2 pinnate

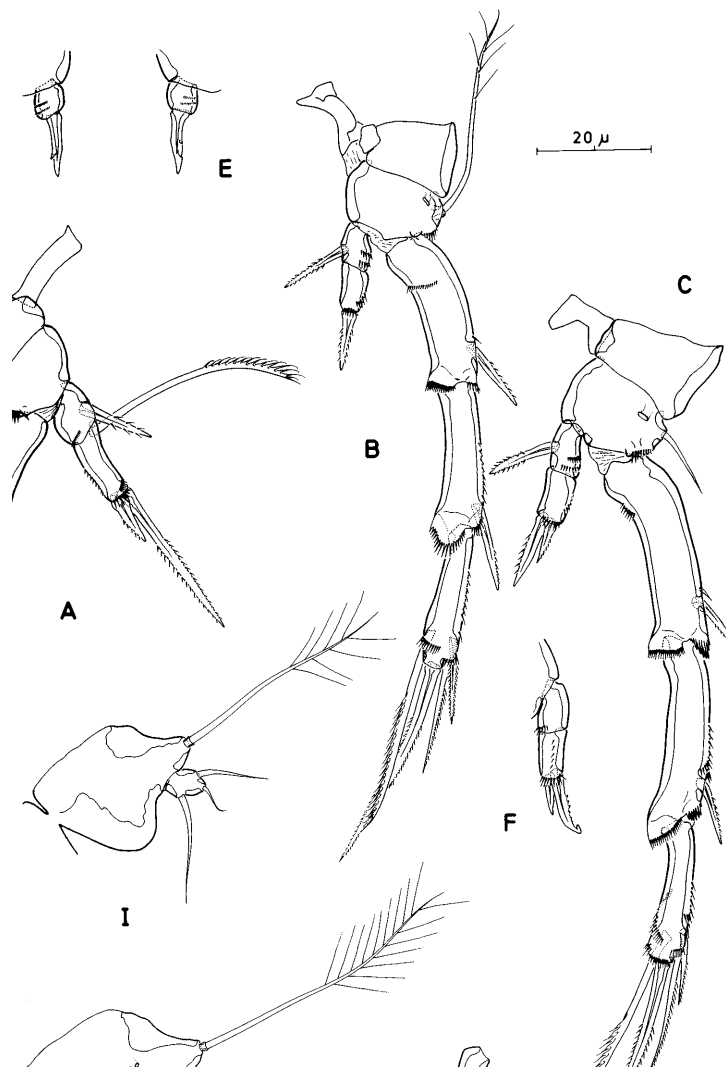


Figure 5. *Leptopontia dovpori* sp. nov. (♀). A, P2 (♀), anterior; B, P3 (♀), anterior; C, P4 (♀), anterior; D, P3 endopod (♂), anterior; E, P3 endopod (♂), lateral; F, P4 endopod (♂), anterior; G, P4 endopod (♂), lateral; H, P5 (♀), anterior; I, P5 (♂), anterior.

spines along inner margin; distal margin with 1 pinnate spine, 3 geniculate setae and 1 spinulose geniculate seta fused basally to small seta.

*Mouthparts* and *labrum* fragile and flimsy (Fig. 10A–C), arranged in distinct cone around oral opening (Fig. 10C).

*Labrum* (Figs 2A, D, 10C) protruding ventrally; distinctly tapering distally; apical part membranous; without any ornamentation.

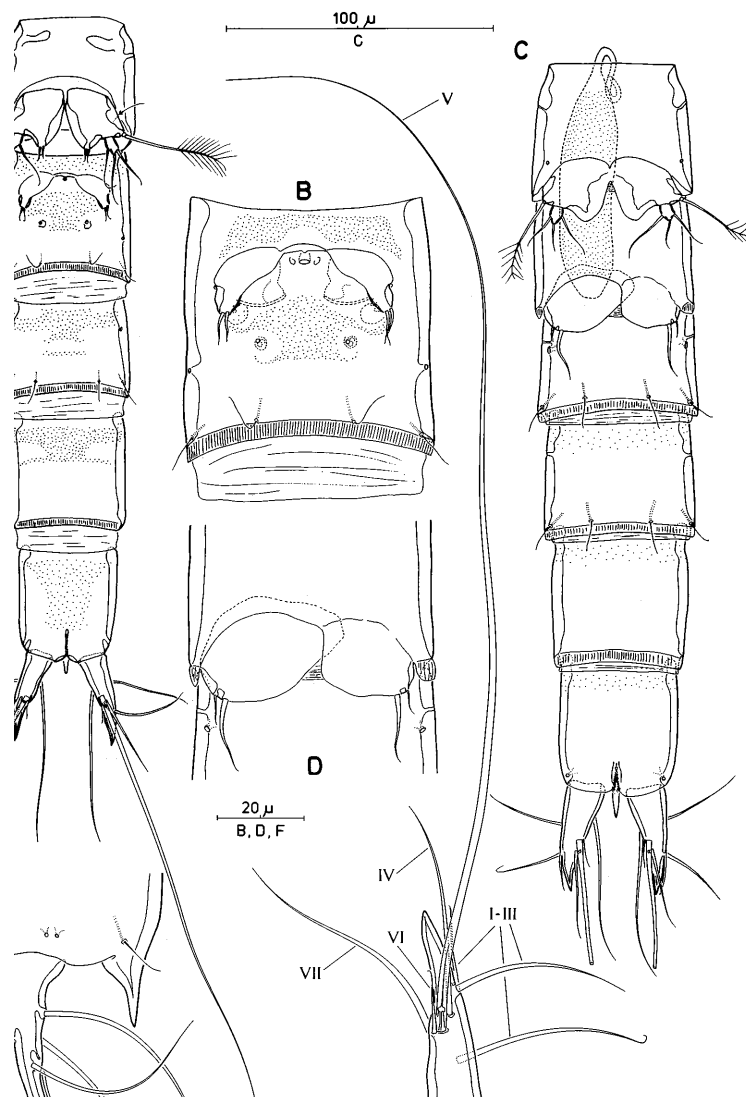


Figure 6. *Leptopontia dovpori* sp. nov. (♀). A, urosome (♀), ventral; B, genital double-somite (♀), ventral; C, urosome (♂), ventral; D, sixth pair of legs (♂); E, posterior margin of anal somite and right caudal ramus, ventral; F, anal somite and left caudal ramus, lateral.

*Mandible* (Fig. 3B,C, 10B,D). Coxa elongate and curved, expanding distally into gnathobase provided with series of small, curved teeth and recurved pinnate seta at dorsal corner; with spinular row near implantation site of palp. Palp 2-segmented (Fig. 10B); basis a swollen elongate segment, unarmed, with 2 spinular rows; endopod elongate, with 1 pinnate seta laterally and 4 bare setae (one with long setule) apically.

*Maxillule* (Fig. 2C). Praecoxa with rectangular, elongate arthrite; arthrite with 1 small seta on the outer margin, 2 long setae and a spinular row at the anterior surface, and 5 setae plus a distally serrate spine around the distal margin. Coxa partly fused to basis; with small endite bearing 1 long seta. Basis with rami entirely incorporated; exopod represented by 1 small and 1 long seta; endopod represented by 2 setae; proximal and distal endites of basis with 2 and 4 setae, respectively.

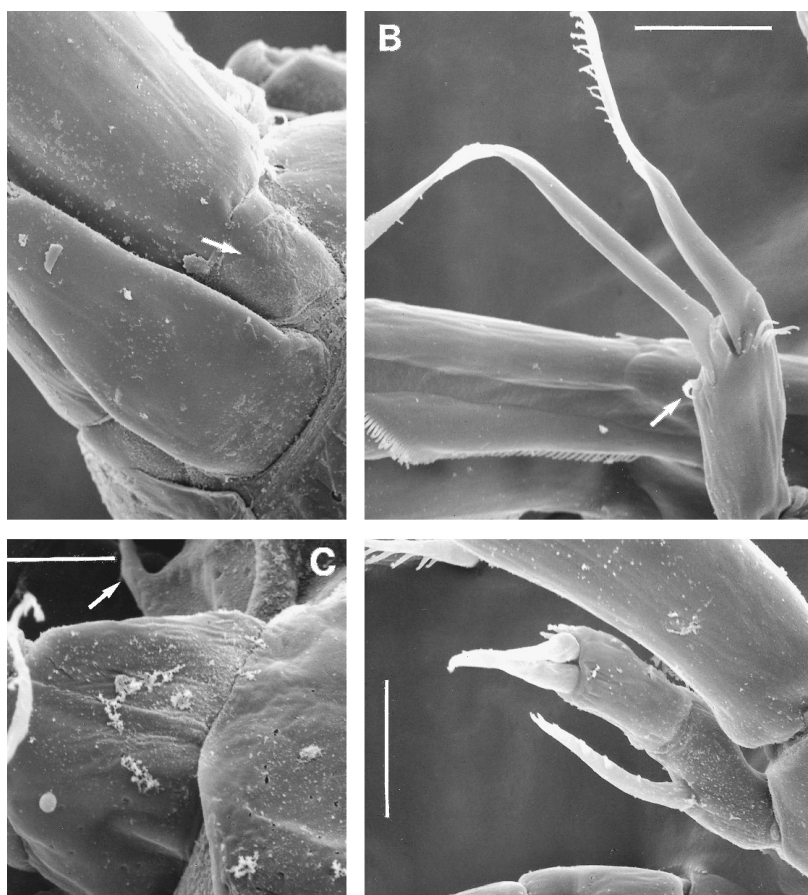


Figure 7. *Leptopontia dovpori* sp. nov. (♀). SEM micrographs. A, rostrum and first antennular segment [small sclerite arrowed]; B, P1 enp-1 [setule arrowed]; C, protopod of P3 (lateral) and spinous processes on sternites [arrowed]; D, P4 endopod. Scale bars: 10  $\mu$ m (A), 7.5  $\mu$ m (B–D).

*Maxilla* (Fig. 3D). Syncoxa with 1 cylindrical endite bearing 1 apical seta and 1 backwardly directed, subapical seta. Allobasis with 3 setae and tube-pore (arrowed in Fig. 3D), drawn out into claw-like, pinnate endite.

*Maxilliped* (Fig. 3E). Syncoxa squarish; unarmed; with 3 spinular rows. Basis unarmed, with spinular row on palmar margin. Endopod represented by stout, distally pinnate claw bearing small seta proximally.

*P1* (Fig. 4C). Praecoxa a well developed sclerite. Coxa without ornamentation. Intercoxal sclerite small, transversely elongate. Basis with slender inner seta and curved outer seta; large anterior surface pore, and spinular row near insertion site of exopod. Exopod distinctly 3-segmented; exp-1 with long pinnate seta; exp-2 bare; exp-3 with 3 geniculate setae, increasing in length adaxially. Endopod with enp-1 8.3

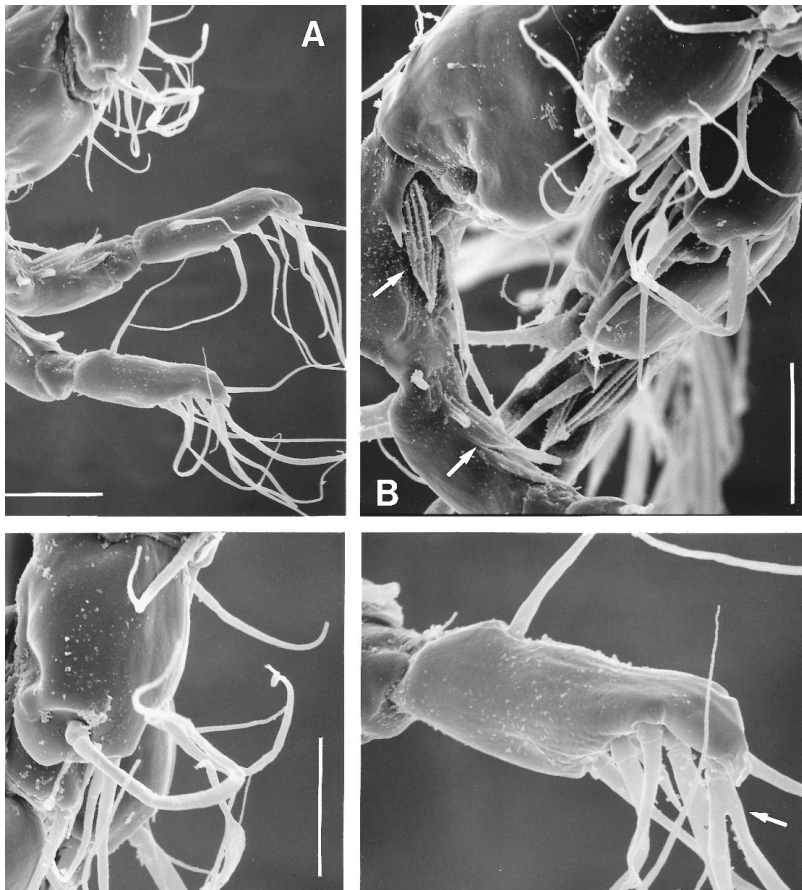


Figure 8. *Leptopontia dovpori* sp. nov. (♂). SEM micrographs. A, antennules, distal part (lateral); B, antennule, segments around geniculation [modified spines arrowed]; C, antennule, middle part [vestigial segment 4 arrowed]; D, antennule, apical segment [acrothek arrowed]. Scale bars: 15  $\mu$ m (A), 10  $\mu$ m (B), 7.5  $\mu$ m (C), 6  $\mu$ m (D).

times as long as wide, and about 1.9 times as long as exopod; with recurved serrate seta near proximal margin; enp-2 with 2 pinnate geniculate setae (longest clearly shorter than enp-1) and 1 tiny seta (arrowed in Figs 4C, 7B); ratio of enp-1:enp-2 about 4.8.

*P2–P4* (Fig. 5A–C). Intercoxal sclerites rectangular, distinctly concave in P3 and P4. Coxae bare. Bases with short naked seta (P2, P4) or long plumose seta (P3). Exopodal segments with well developed hyaline frills. Inner setae of P3–P4 exp-3 serrate. Inner elements of P2–P4 enp-1 spiniform and bipinnate (Fig. 7D). Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.021	1.120
P2	0.0.021	1.120
P3	0.0.112	1.010
P4	0.0.112	1.020

*Fifth legs* (Figs 5H, 6A) closely set together, no intercoxal sclerite. Baseoendopods not fused medially. Baseoendopod with moderately developed endopodal lobe, not extending to distal margin of exopod, with 2 short setae. Exopod a small segment with 1 outer, 1 inner and 1 apical seta. Outer basal seta long and plumose.

*Description of male.* Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 550  $\mu\text{m}$  (Fig. 1B,C). Body slightly more slender than in female. Ornamentation of body generally as in the female except for some small differences in the integumental pit pattern. Lateral processes on anal operculum more spinous than in female (Fig. 4E). Sexual dimorphism in antennule, P3 endopod, P4 endopod, P5, P6 and in genital segmentation. Spermatophore about 90  $\mu\text{m}$  in length.

*Antennule* (Figs 1B,C, 4F:a–g, 8A–D) indistinctly 9-segmented; base surrounded by small sclerite. Relative lengths of first two segments as in female. Fourth segment a small U-shaped sclerite with 1 seta (Figs 4F:a, 8C). Major geniculation between segments 6 and 7 (Fig. 8A); these segments with modified setae (Fig. 8B). Segmental fusion pattern: I, II–VIII, IX–XII, XIII, XIV–XVIII, XIX–XX, XXI–XXII, XXIII, XXIV–XXVIII. Large aesthetasc on segment 5 (Fig. 4F:c) 120  $\mu\text{m}$  long, fused basally with seta. Except for single anterior seta all other armature of segment 9 located in posterior concavity so that setae are directed perpendicular to segment axis (Figs 4F:g, 8A, D). Apical acrothek of segment 9 consisting of small aesthetasc (arrowed in Fig. 4F:g; 17  $\mu\text{m}$  long), fused basally with 2 setae. Armature formula: 1–[1], 2–[8 + 1 plumose], 3–[6], 4–[1], 5–[6 + 2 modified + ae], 6–[4], 7–[3], 8–[1], 9–[7 + acrothek].

*P3 endopod* (Fig. 5D,E) 2-segmented, minute; enp-1 with 2 rows of diminutive spinules; enp-2 represented by 1 barbed spine.

*P4 endopod* (Fig. 5F–G) 2-segmented; enp-1 unarmed but with 1 spinular row; enp-2 with 1 bare spine and a larger, posteriorly recurved, pectinate spine (Fig. 11C).

*P5* (Figs 5I, 6C). Baseoendopods partly fused medially. Endopodal lobe moderately developed, inner margin clearly convex; without armature. Outer basal spine long and plumose. Exopod small, with 1 seta on both outer and inner margins and a smaller one apically.

*Sixth pair of legs* (Fig. 6D) asymmetrical with one member fused to genital somite;

functional member slightly larger and articulating; armature consisting of inner slender seta and outer vestigial setule.

*Variability.* One paratype ♀ had 4 exopodal setae on the right P5; another one had a bifid middorsal process on the anal operculum (Fig. 9C). The accessory smaller processes on the anal operculum are sometimes absent (Fig. 6F).

*Etymology.* The species is named in honour of Prof. Francis Dov Por, The Hebrew University of Jerusalem.

*Remarks.* As a result of their close morphological resemblance and almost similar body size *L. dovpori* and *L. curvicauda* are easily confounded. *L. dovpori* differs from the type species in the relative proportions of the endopodal segments of the P1 and in the

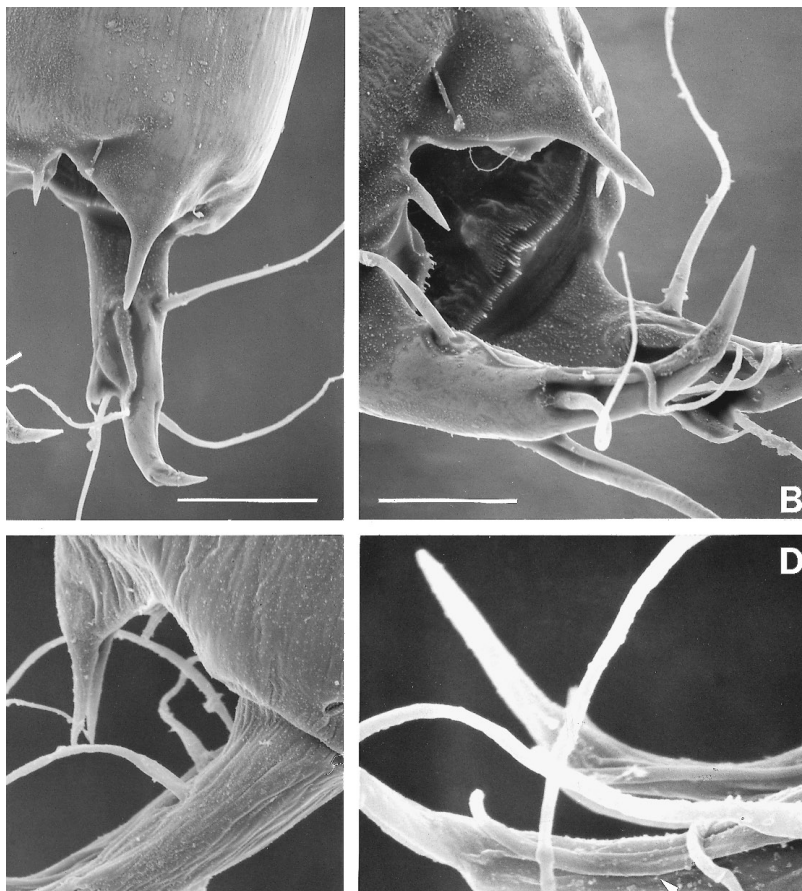


Figure 9. *Leptopontia dovpori* sp. nov. (♀). SEM micrographs. A, anal somite and caudal rami, dorsolateral [seta I arrowed]; B, same, posterolateral; C, same, lateral; D, detail of posterior part of caudal ramus, lateral [seta I arrowed]. Scale bars: 15  $\mu$ m (A), 10  $\mu$ m (B, D), 4.3  $\mu$ m (C).

detailed morphology of the anal operculum (diamond-shaped accessory processes absent). Females can be differentiated by the relative lengths of the endopodal setae on the fifth legs. A character that surprisingly has proven extremely constant within and between populations of *L. doypori* is the punctate integumental pattern on the ventral surface of the genital double-somite (Fig. 6B). Males of *L. doypori* have a first antennular segment that is relatively more slender and longer than in the type species. An additional character that serves to distinguish the males of *L. curvicauda* from all other known species is the elaborate sexual dimorphism on the P3 endopod.

*L. doypori* is thus far known only from a few localities in the southern North Sea.

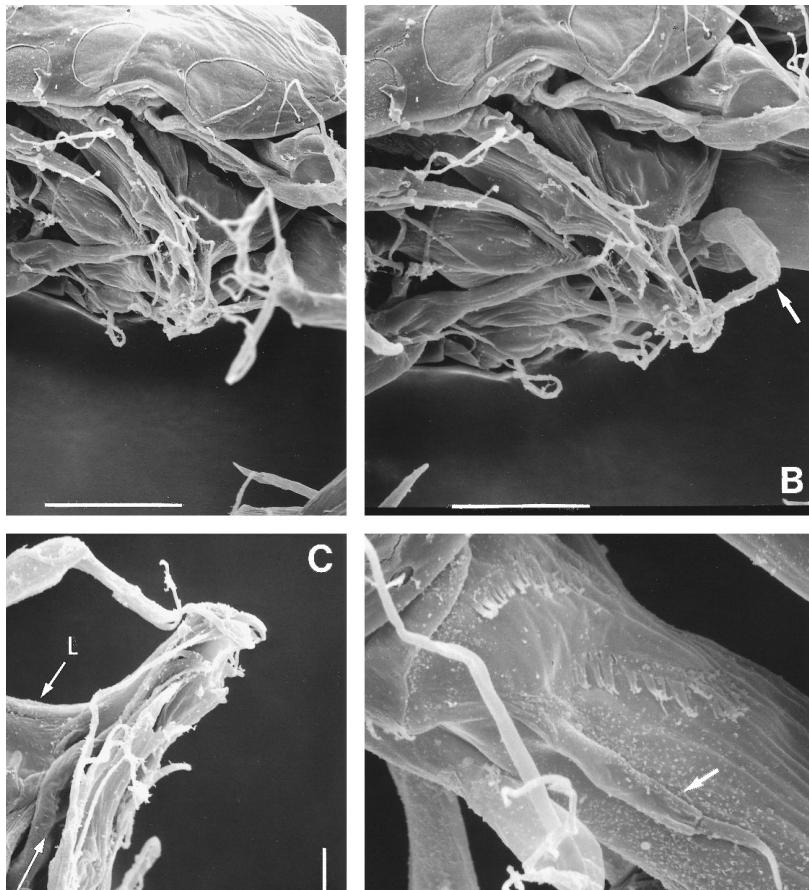


Figure 10. *Leptopontia doypori* sp. nov. (♀). SEM micrographs. A, cephalothorax, ventrolateral; B, same, close-up [Mandibular palp arrowed]; C, oral area and mouthparts, lateral [L = labrum; M1 = maxillule; M2 = maxilla; Mg = mandibular gnathobase; Mp = mandibular palp]; D, Antennary allobasis [exopod arrowed]. Scale bars: 20  $\mu$ m (A), 15  $\mu$ m (B), 10  $\mu$ m (C), 6  $\mu$ m (D).

*Leptopontia curvicauda* T. Scott, 1902

*Original description.* — T. Scott (1902): 463-464; Plate XXII, Figs 26-35.

*Additional description.* — Mielke (1975).

*Type locality.* In dredgings off St. Monans in the Firth of Forth, Scotland.

*Material examined.* The type material no longer exists. The only specimen that could be positively identified as *L. curvicauda* is a male (dissected on 6 slides) collected by Dr Mielke from a sandy beach on the Isle of Sylt, Germany; deposited in The Natural History Museum.

*Characters of female.* By far the best illustrations of the female are those by Mielke (1975) of the P1, P5, anal operculum and caudal rami. Total body length from the

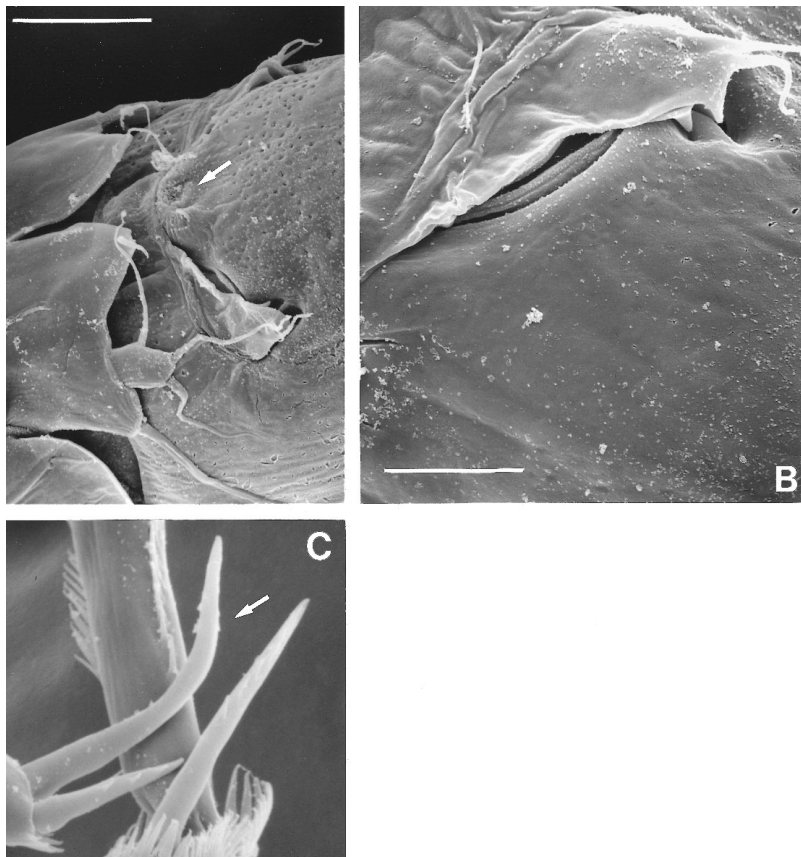


Figure 11. *Leptopontia dovpori* sp. nov. SEM micrographs. A, fifth pair of legs and genital field (♀), lateroventral [copulatory pore arrowed]; B, right genital aperture (♀); C, P4 endopod (♂) [modified spine arrowed]. Scale bars: 15 μm (A), 6 μm (B, C).



tip of the rostrum to the posterior margin of the caudal rami: 510–580  $\mu\text{m}$  (after Mielke, 1975), 600  $\mu\text{m}$  (after T. Scott, 1902). Body less slender than in *L. doypori*.

*Armature formula* of swimming legs:

	Exopod	Endopod
P1	0.0.021	1.120
P2	0.0.021	1.120
P3	0.0.112	1.010
P4	0.0.112	1.020

*Fifth legs.* Baseoendopod with moderately developed endopodal lobe extending to distal margin of exopod, with 2 very long setae (much longer than baseoendopod). Exopod a small segment with 1 outer, 1 inner and 1 apical seta. Outer basal seta long and plumose.

*Redescription of male.* Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 465  $\mu\text{m}$  (Fig. 12A), 550–600  $\mu\text{m}$  (Mielke, 1975). Integument of urosomites with distinct pattern of subsurface integumental pits. Posterior margin of body somites with plain hyaline frill which is striated in the urosomites (Figs 12A, 14A).

*Rostrum* (Fig. 12A,B) triangular, elongate, with straight lateral margins; about 0.85 times the length of first antennular segment; with 2 delicate sensillae.

*Anal somite* (Figs 12D, 14A) with dorsal operculum drawn out into median, posteriorly directed spinous process, flanked by two small processes with diamond-shaped tip.

*Caudal rami* (Figs 12D, 14A) slightly divergent; outer distal corner drawn out into posteriorly directed, dorsally recurved spinous process; with 7 setae; setae I–III well developed, posterodorsal one (probably seta I) fused basally and closely adpressed to ramus; seta V very long and with fracture plane, seta VI minute, seta VII tri-articulate at base. Ramus 6.2 times as long as basal width (measured in lateral aspect along ventral margin).

Sexual dimorphism in antennule, P3 endopod, P4 endopod, P5, P6 and in genital segmentation. Spermatophore about 90  $\mu\text{m}$  in length.

*Antennule* (Fig. 12A,B) indistinctly 9-segmented; base surrounded by small sclerite. Segment 1 longest, about 2.7 times as long as wide, surrounded by distinct sclerite around proximal posterior margin, with 1 short seta at distal anterior corner and dorsal tube pore near distal margin; segment 4 small U-shaped sclerite with 2 setae. Major geniculation between segments 6 and 7. Segmental fusion pattern as in previous species. Large aesthetasc on segment 5 85  $\mu\text{m}$  long, fused basally with seta. Apical acrothek of segment 9 consisting of small aesthetasc (20  $\mu\text{m}$  long), fused basally with 2 setae. Armature formula: 1–[1], 2–[8 + 1 plumose], 3–[7], 4–[2], 5–[6 + 2 modified + ae], 6–[4], 7–[3], 8–[1], 9–[7 + acrothek].

*P1* (Fig. 13A). Praecoxa a well developed sclerite. Coxa without ornamentation. Basis with short inner seta and curved outer seta; large anterior surface pore, and spinular row near insertion site of exopod. Exopod distinctly 3-segmented; exp-1 with long pinnate seta; exp-2 bare; exp-3 with 3 geniculate setae, increasing in length adaxially. Endopod with enp-1 approximately 7.5 times as long as average width (segment distinctly wider in proximal half), and about 1.6 times as long as exopod; with recurved serrate seta near proximal margin; enp-2 elongate, with 2 geniculate

setae (longest about as long as enp-1) and 1 tiny seta; ratio of enp-1:enp-2 about 2.75.

*P2-P4* (Fig. 13B-E). Intercoxal sclerites rectangular, distinctly concave. Coxae bare. Bases with short naked seta (*P2*, *P4*) or long plumose seta (*P3*). Inner setae of *P3-P4* exp-3 serrate. Inner element of *P2* enp-1 spiniform and bipinnate.

*P3* endopod (Fig. 13C) 2-segmented, larger than in other species of the genus; enp-1

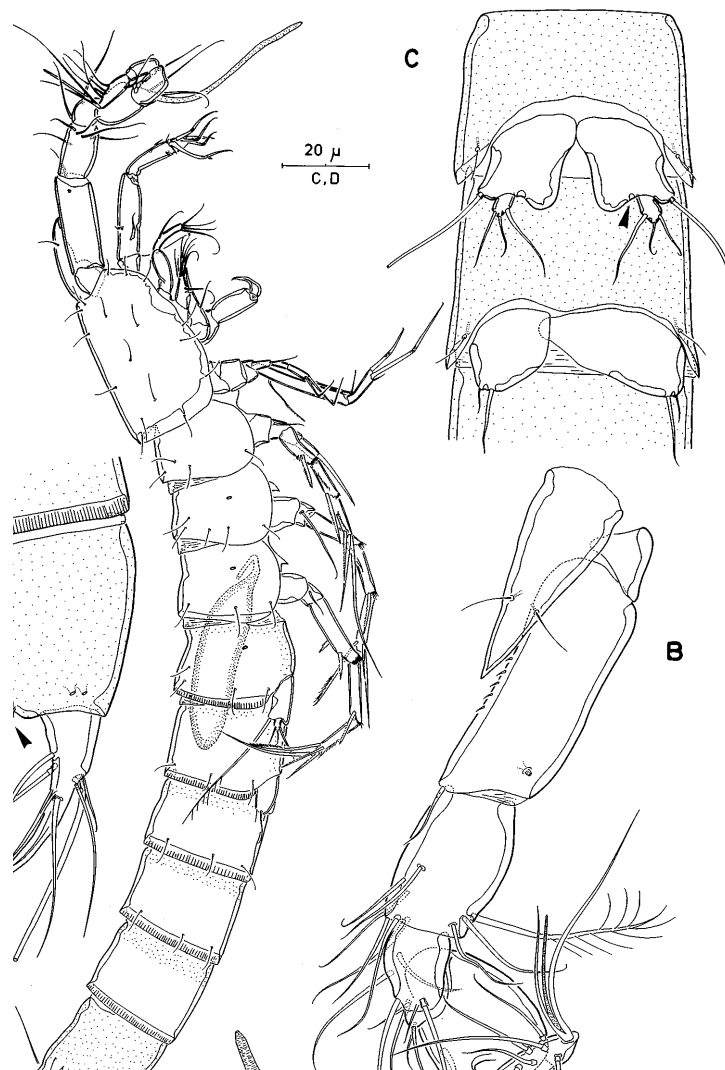


Figure 12. *Leptopontia curvicauda* T. Scott, 1902 ( $\delta$ ). A, habitus, lateral; B, rostrum and antennule, dorsal; C, fifth and sixth pair of legs [marginal pore arrowed]; D, Anal somite and right caudal ramus, lateral [secondary process arrowed].

with 3 rows of diminutive spinules on bulged outer margin; enp-2 elongate, strongly chitinized, with bifid apex.

*P4* endopod (Fig. 13D,E) 2-segmented; enp-1 unarmed but with 1 tiny spinular row; enp-2 with 1 short, unipinnate spine and a larger, posteriorly recurved, pectinate spine.

*P5* (Fig. 12C). Baseoendopods not partly fused medially. Endopodal lobe moderately developed, inner margin slightly concave; without armature but with

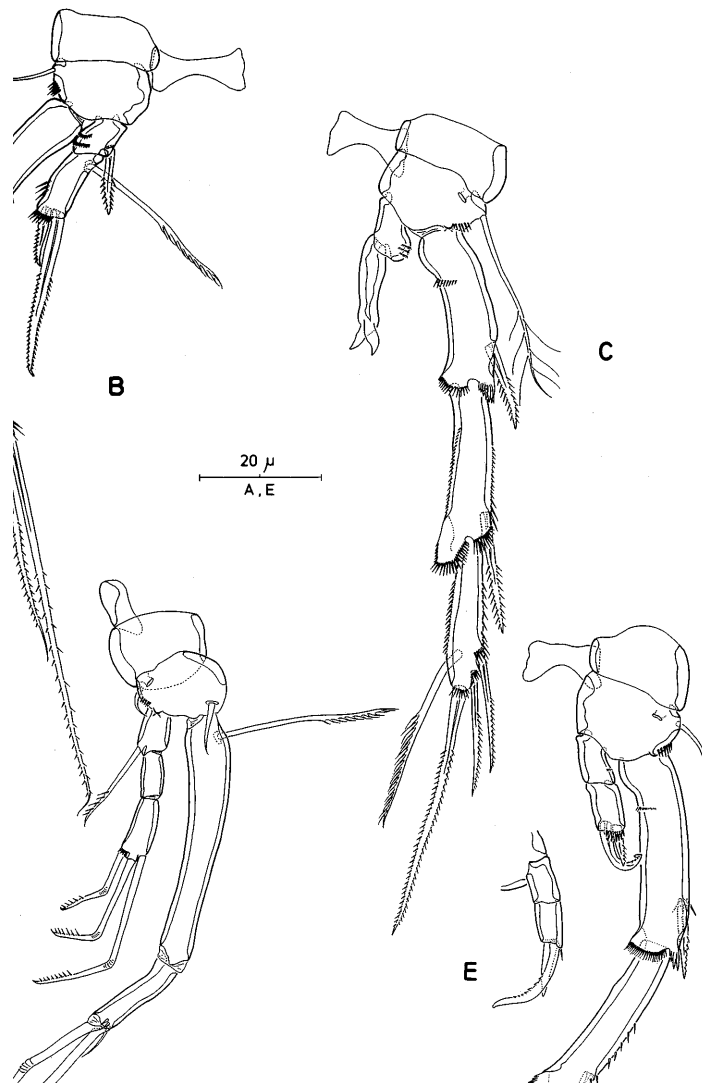


Figure 13. *Leptopontia curvicauda* T. Scott, 1902 (♂). A, P1, anterior; B, P2, anterior; C, P3, anterior; D, P4, anterior; E, P4 endopod, lateral.

pore (arrowed in Fig. 12C). Outer basal spine long and plumose. Exopod small, with 1 seta on both outer and inner margins and a smaller one apically.

*Sixth pair of legs* (Fig. 12C) asymmetrical; armature consisting of inner slender seta and outer vestigial setule.

*Variability.* Mielke (1975) illustrates a specimen with bifid spinous process on the anal operculum.

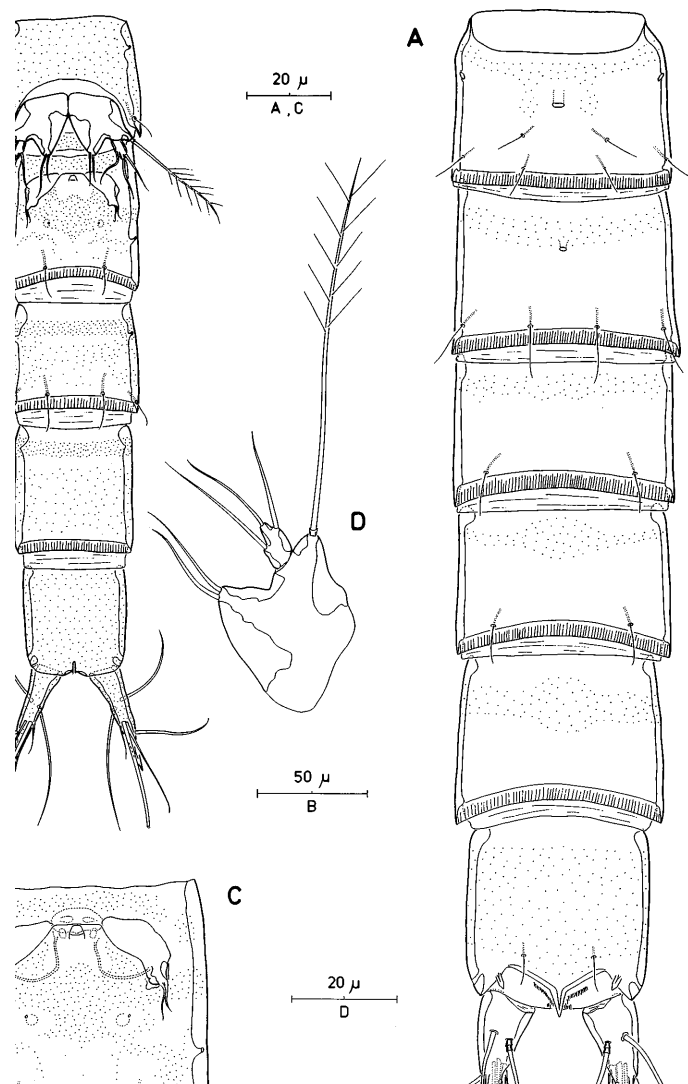


Figure 14. *Leptopontia curvicauda* T. Scott, 1902. A, urosome (♂), dorsal. ***Leptopontia punctata* sp. nov.** B, urosome (♀), ventral; C, Genital double-somite (♀), ventral; D, P5 (♀), anterior.

*Remarks.* It is unlikely that T. Scott's (1902) illustration of the female P5, showing 3 long setae on the endopodal lobe, is correct. All Leptopontiinae have a maximum of 2 setae in this position, and it therefore is conceivable that T. Scott had either drawn an aberrant specimen or that he had mounted his specimen in a ventrolateral posture thereby superimposing the innermost endopodal seta of the right P5 on the left endopodal lobe. This would also explain the unusually wide baseoendopod in T.

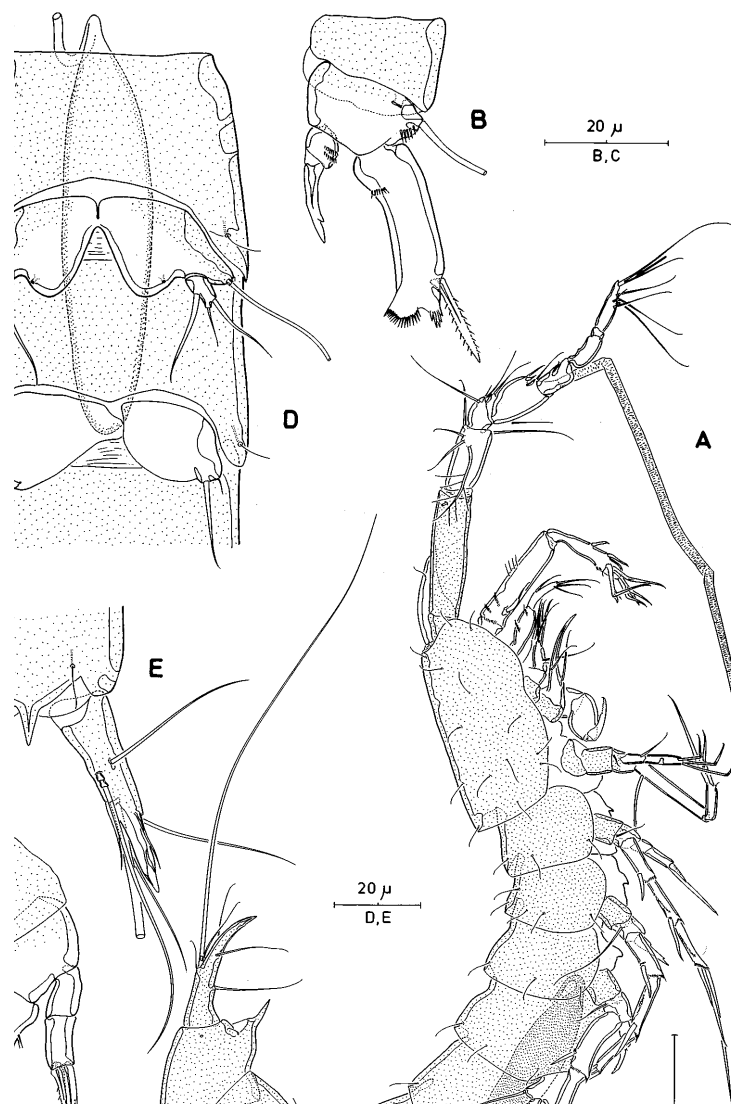


Figure 15. *Leptopontia punctata* sp. nov. A, habitus ( $\delta$ ), lateral; B, P2 protopod, endopod and exp-1 ( $\delta$ ), anterior; C, P4 protopod, endopod and exp-1 ( $\delta$ ), anterior; D, fifth and sixth legs ( $\delta$ ), anterior; E, anal operculum and right caudal ramus, dorsal.

Scott's illustration. There is little doubt that Mielke's (1975) material is *L. curvicauda* since his drawings and the present redescription agree with the original description in virtually every important aspect, such as the general body facies, the relative lengths of P1 enp-1 and enp-2, the length of the endopodal setae on the female P5,

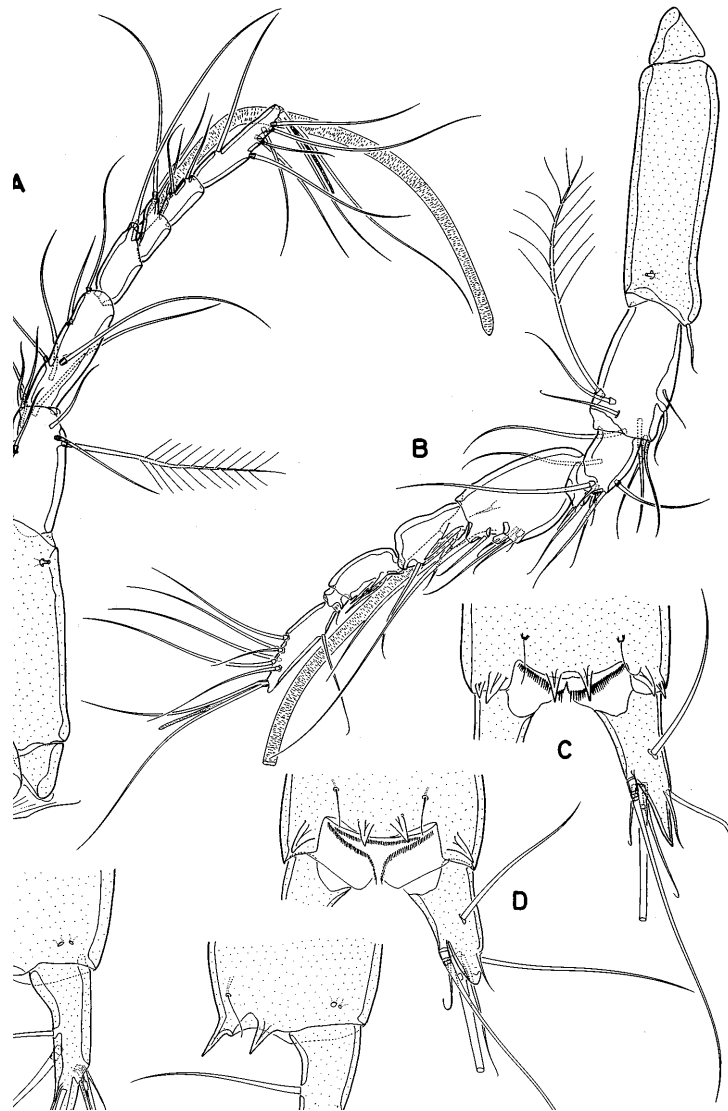


Figure 16. *Leptopontia punctata* sp. nov. A, rostrum and antennule (♀), dorsal; B, antennule (♂), ventral; C, anal operculum and right caudal ramus (Copepodid IV), dorsal; D, same (Copepodid V), dorsal; E, same (Copepodid V), lateral; F, same (adult ♀), lateral.

and the anal operculum. The different setal formula of P4 exp-3 is not considered relevant here since it is almost certainly the result of an erroneous observation.

In the absence of female specimens it is difficult to define diagnostic characters permitting the separation of species, however, it seems that the very long setae on the P5 baseoendopod serve as a reliable character. Males can easily be differentiated on the basis of the modification on the P3 endopod.

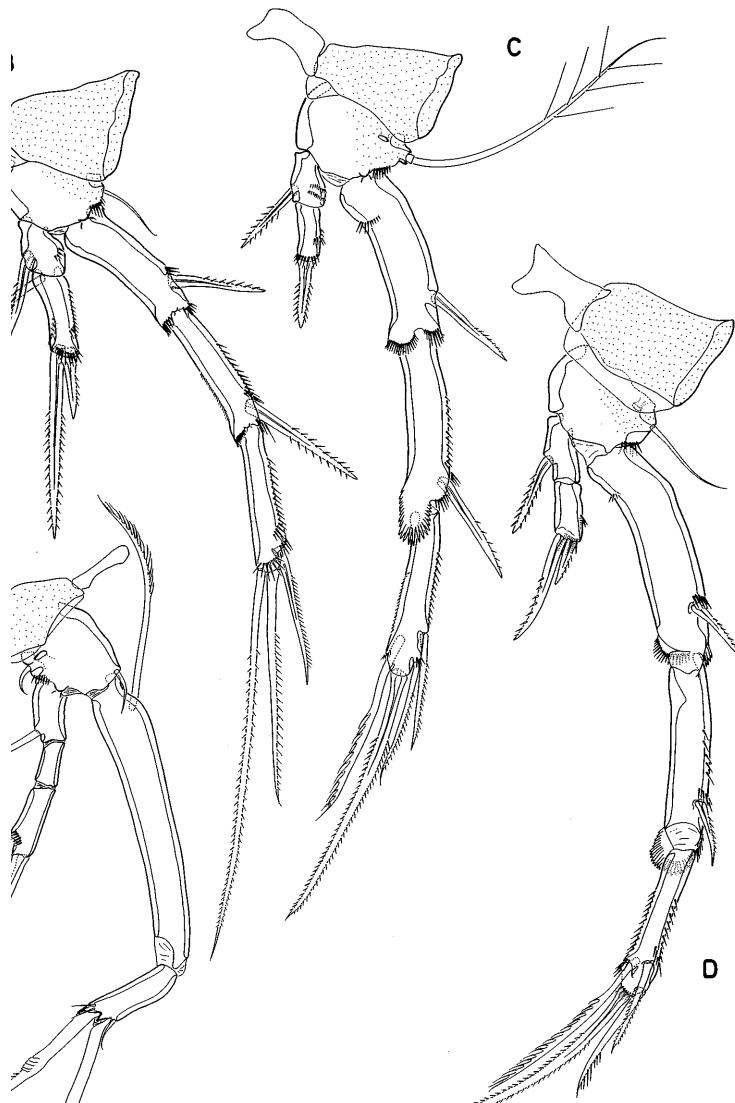


Figure 17. *Leptopontia punctata* sp. nov. A, P1, anterior; B, P2, anterior; C, P3, anterior; D, P4, posterior.

Many of the records of *L. curvicauda* are suspect as most workers failed to distinguish between the type species and closely related species such as *L. doypori*, ***L. flandrica* sp. nov.** and ***L. punctata* sp. nov.** In reviewing the situation it seems that the majority of the published European records are false, mainly because they contain insufficient information to distinguish between these four species. Apart from the original description (T. Scott, 1902, 1906), the only published record that can be verified absolutely is that of Mielke (1975) of the Isle of Sylt.

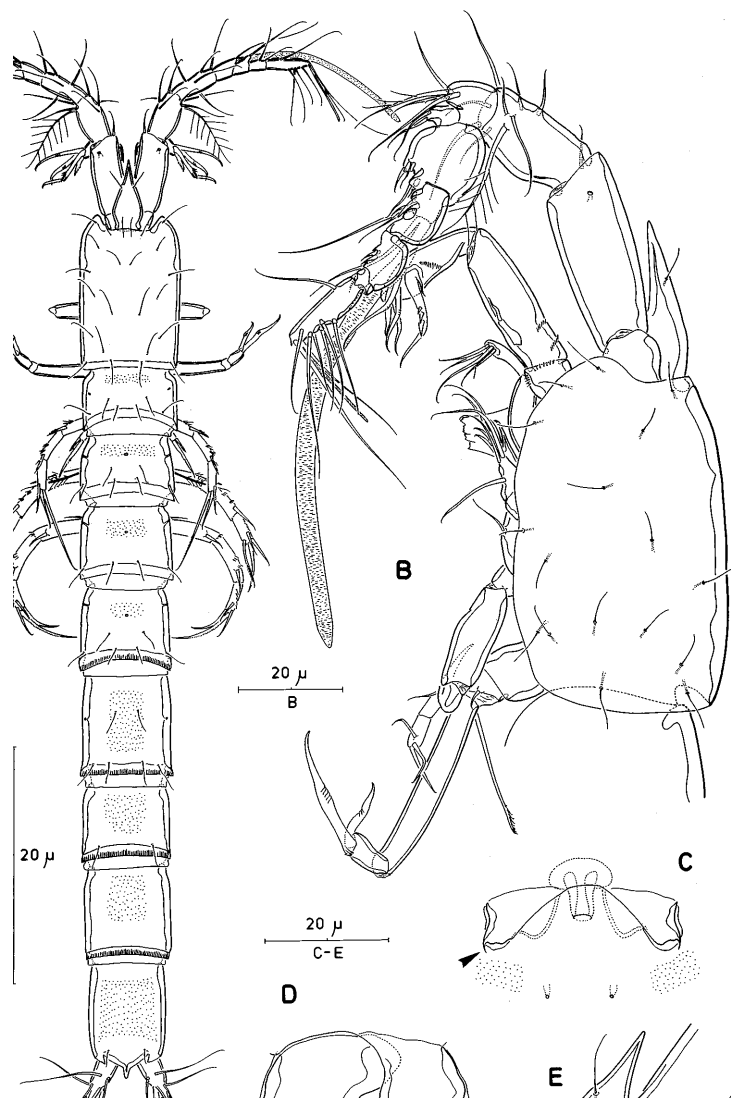


Figure 18. *Leptopontia flandrica* sp. nov. A, habitus (♀), dorsal; B, cephalothorax (♂), lateral; C, genital field (♀) [vestigial setule on genital operculum arrowed]; D, sixth legs (♂); E, rostrum, dorsal.



- (1) *L. curvicauda* of Kunz (1938) and Wells *et al.* (1975) is *L. punctata* sp. nov.  
 (2) *L. curvicauda* of Por (1964) may be *L. punctata* sp. nov.  
 (3) Indeterminable and improbable records: Germany: Vejsnaes-Flach, Gabelsflach and Stoller Grund in Kieler Bucht (Scheibel, 1972), Boknis Eck in Kieler Bucht (Scheibel & Rumohr, 1979); Wales: Porth-y-Post, Anglesey (Geddes, 1972); England: Tresco and St. Martin's, Isles of Scilly (Wells, 1961, 1970); Ireland:

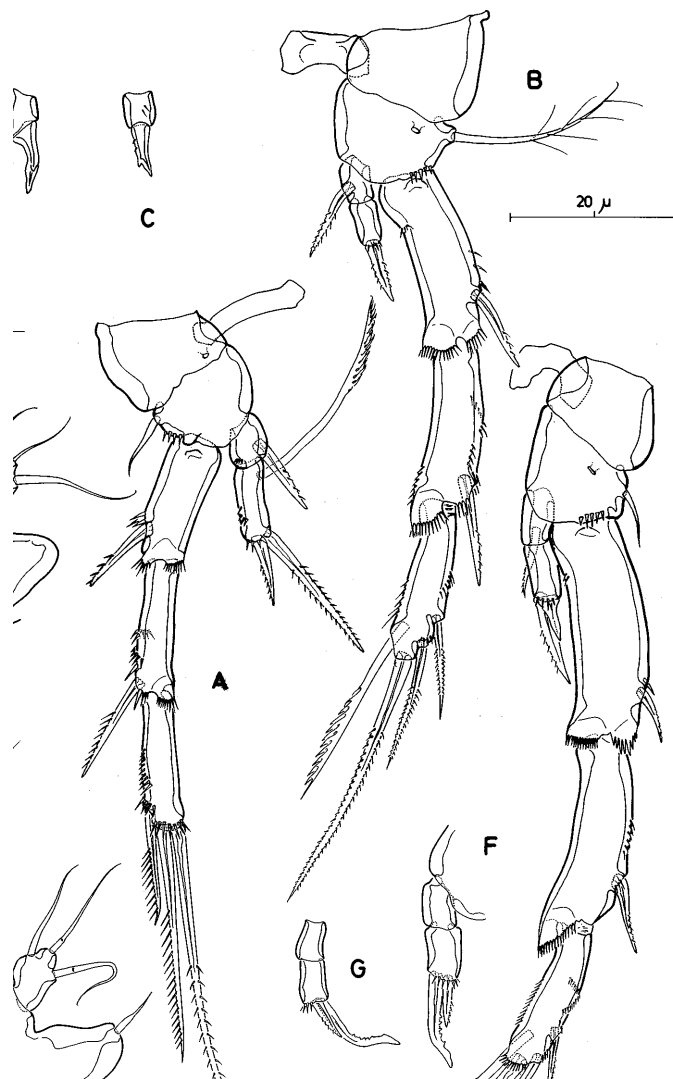


Figure 19. *Leptopontia flandrica* sp. nov. A, P2 (♀), anterior; B, P3 (♀), anterior; C, P3 endopod (♂), anterior; D, P3 endopod (♂), lateral; E, P4 (♀), anterior; F, P4 endopod (♂), anterior; G, P4 endopod (♂), lateral; H, P5 (♀), anterior; I, P5 (♂), anterior.

Silver Strand, Galway Bay (Bodin & Jackson, 1989; Holmes & O'Connor, 1990); France: Kersaint (Bodin, 1988; Bodin & Boucher, 1981; Bodin & Jackson, 1989) and Bay of Douarnenez (Bodin, 1984), Finistère; Banyuls-sur-Mer (Soyer, 1971); U.S.A.: North Carolina, northern part of continental shelf (Coull, 1971).

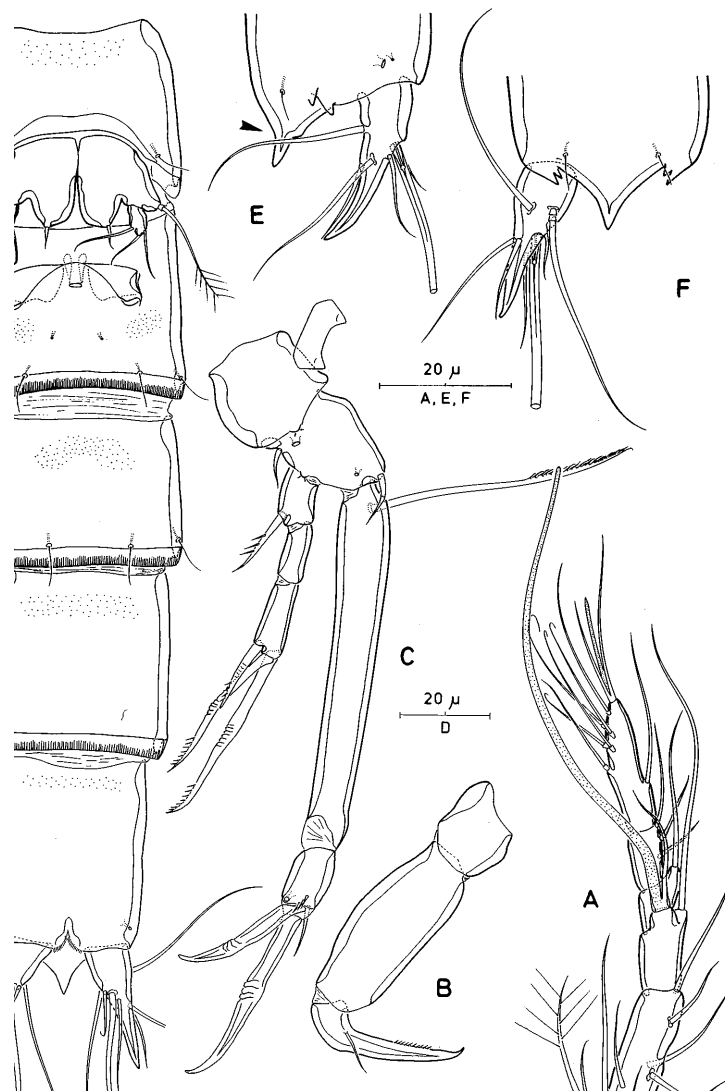


Figure 20. *Leptopontia flandrica* sp. nov. A, antennule (♀), ventral; B, maxilliped; C, P1, anterior; D, urosome (♀), ventral; E, anal somite and right caudal ramus [arrow marking convex dorsal margin of median process]; F, anal somite and left caudal ramus, dorsal.

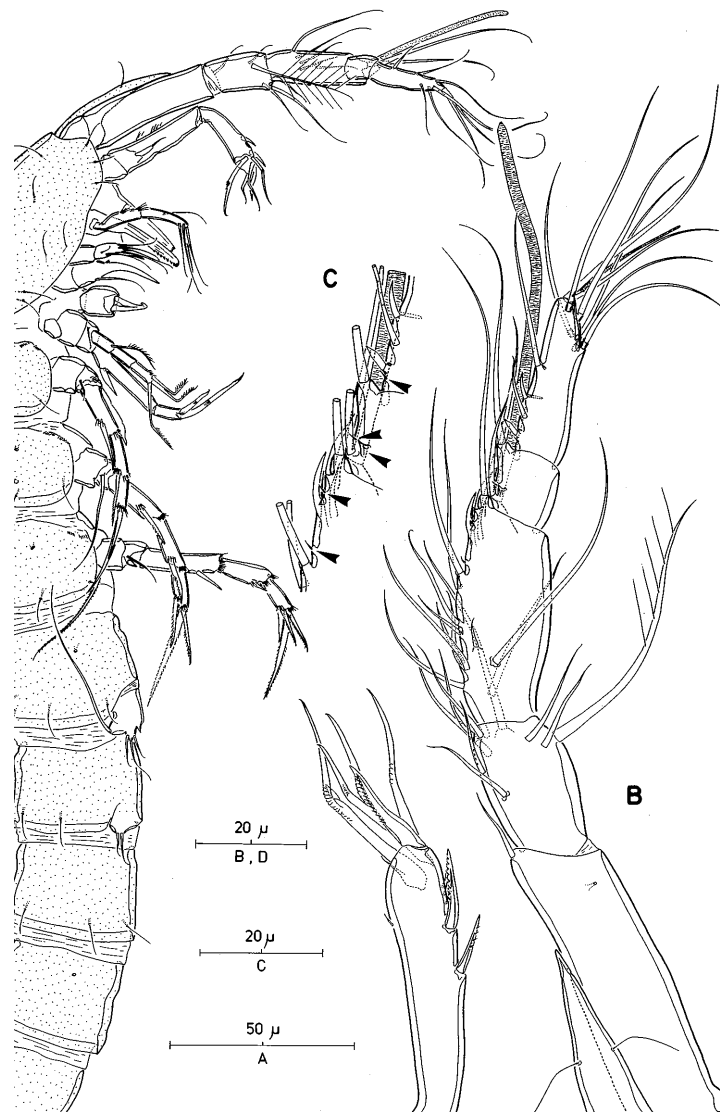
***Leptopontia punctata* sp. nov.***L. curvicauda* T. Scott, 1902 *sensu* Kunz (1938)*Type locality.* Isle of Bonden, Bohuslän, Sweden.

Figure 21. ***Leptopontia mediterranea* sp. nov.** (Copepodid V ♂). A, habitus, lateral; B, rostrum and antennule, dorsal; C, detail of anterior margin of antennular segments 3–5 [vestigial setae arrowed]; D, antenna [seta-like element on allobasis arrowed].

*Material examined.* Holotype ♀ (dissected on 7 slides) and paratype ♂ (dissected on 7 slides) deposited in The Natural History Museum, London; additional paratypes (7 ♀♀, 1 CopIV and 1 CopV) in alcohol; coll. H. Kunz.

*Description of female.* Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 485 µm. Maximum width 60 µm measured at

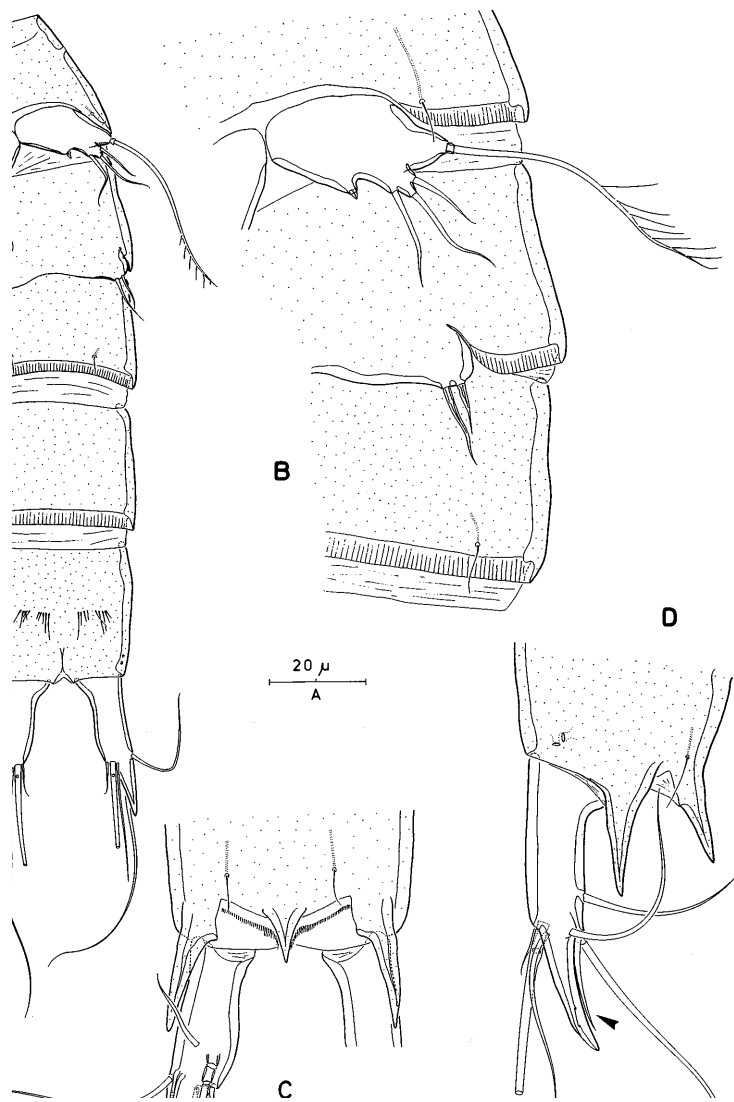


Figure 22. *Leptopontia mediterranea* sp. nov. (Copepodid V ♂). A, urosome, ventral; B, left P5 and P6, ventral; C, posterior half of anal somite and left caudal ramus, dorsal; D, same, lateral [seta I arrowed].

cephalothorax. Integument of thoracic and abdominal somites strongly chitinized, yellow-brownish, completely covered with subsurface integumental pits. These pits also present on segments 1 and 2 of antennule (Fig. 16A), and on the protopodal segments of maxillule, maxilla, and P1 to P4 (Fig. 17A–D). Posterior margin of body somites with plain hyaline frill which is striated in the genital double-somite (Fig.

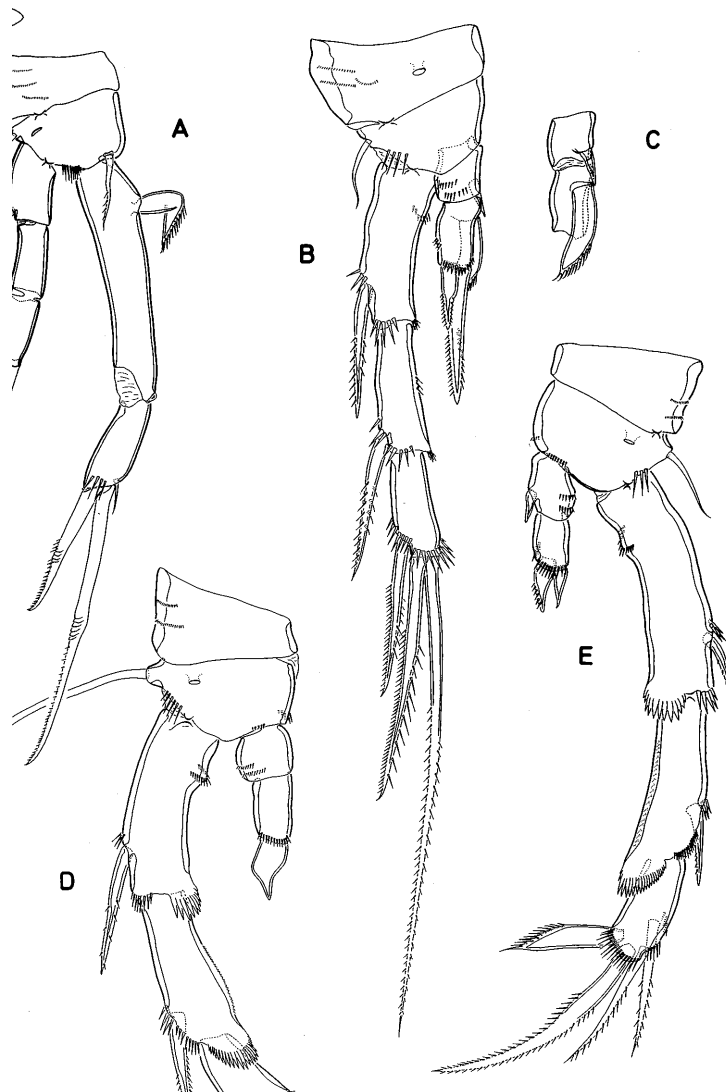


Figure 23. *Leptopontia mediterranea* sp. nov. (Copepodid V ♂). A, P1, anterior; B, P2, anterior; C, P2 endopod, posterior [distal elements omitted]; D, P3, anterior; E, P4, anterior.

14C) and free abdominal somites (Fig. 14B). Individual somites connected by well developed intersomitic membranes (Fig. 14B; see also ♂: Fig. 15A).

*Rostrum* (Fig. 16A) triangular, elongate; about 0.8 times the length of first antennulary segment; with 2 delicate sensillae.

*Genital double-somite* (Fig. 14B,C) slightly longer than wide; original segmentation not marked by any external or internal cuticular structure. Genital apertures paired

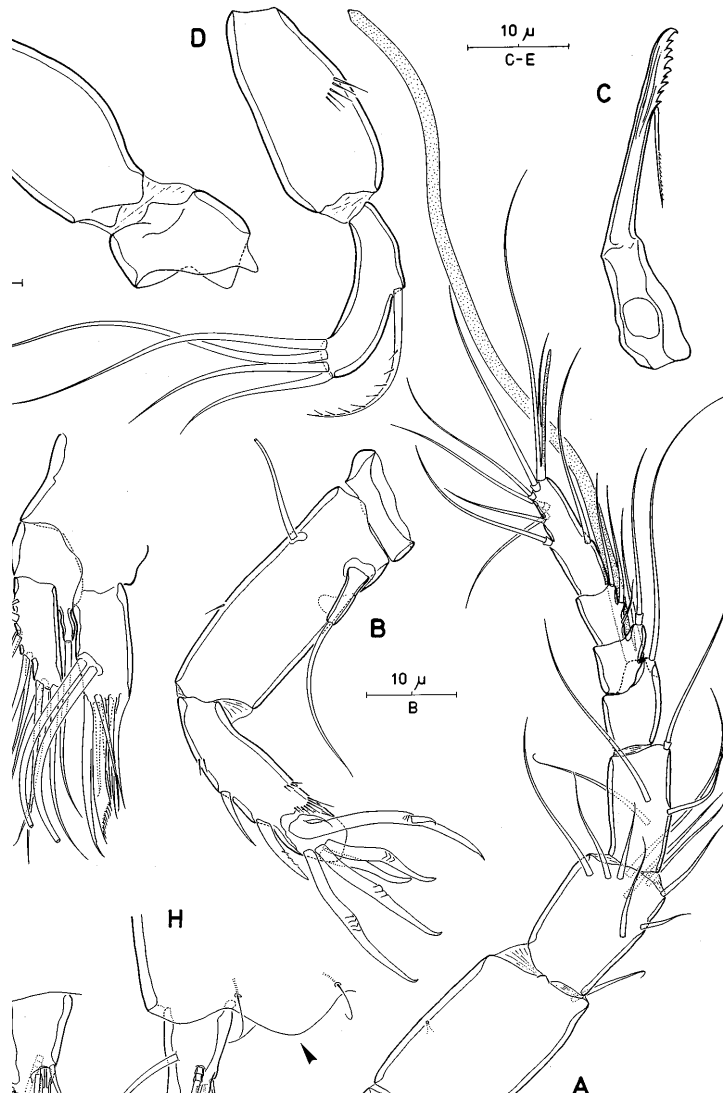


Figure 24. *Leptopontia breviarticulata* sp. nov. (♀). A, rostrum and antennule, dorsal; B, antenna; C, mandibular gnathobase; D, mandibular palp; E, maxillule; F, maxilliped; G, right caudal ramus, ventral; H, anal operculum [arrowed] and left caudal ramus, dorsal.

(Fig. 14C), located in anterior half of genital double-somite; each closed off by small operculum derived from sixth leg bearing 2 tiny setae. Median copulatory pore located far anteriorly between genital apertures. Seminal receptacles not confirmed. Ventral surface of genital double-somite with paired secretory pores and characteristic pattern of integumental pits as in Fig. 14C.

*Anal somite* (Figs 15E, 16F) with dorsal operculum drawn out into median,

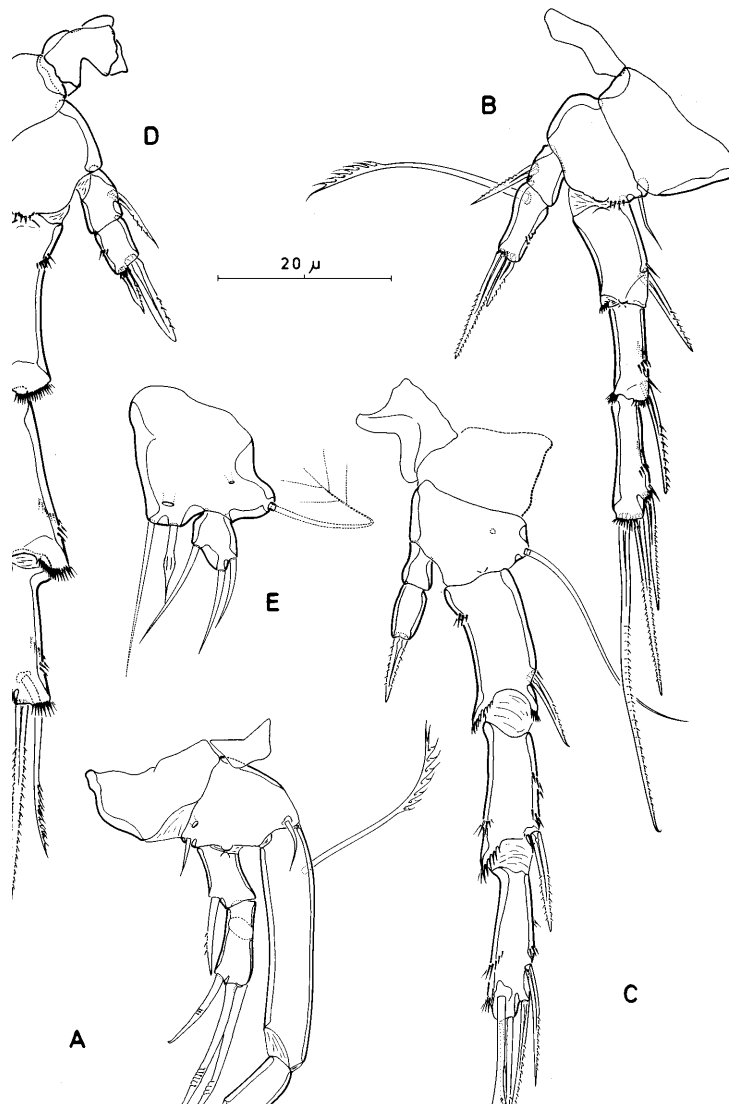


Figure 25. *Leptopontia breviarticulata* sp. nov. (♀). A, P1, anterior; B, P2, anterior; C, P3, anterior; D, P4, anterior; E, P5, anterior.

posteriorly and dorsally directed spinous process, not flanked by accessory processes.

*Caudal rami* (Figs 15E, 16F) divergent; outer distal corner drawn out into posteriorly directed, dorsally recurved spinous process; with setal pattern as in other species. Ramus about 7.1 times as long as basal width (measured in lateral aspect along ventral margin).

*Antennule* (Fig. 16A) slender, 7-segmented; segment 1 longest, about 3.3 times as long as wide, surrounded by distinct sclerite around proximal posterior margin, with 1 short seta at distal anterior corner and dorsal tube pore near distal margin; segment 4 with long aesthetasc (115  $\mu\text{m}$ ) fused basally to seta and set on distinct pedestal; segment 7 with apical acrothek consisting of short aesthetasc (21  $\mu\text{m}$ ) fused basally to 2 setae. All setae bare except for 1 plumose seta on segment 2. Armature formula: 1-[1], 2-[8 + 1 plumose], 3-[5], 4-[2 + ae], 5-[1], 6-[3], 7-[7 + acrothek].

*Antennae to maxillipeds* as in *L. dovpori*.

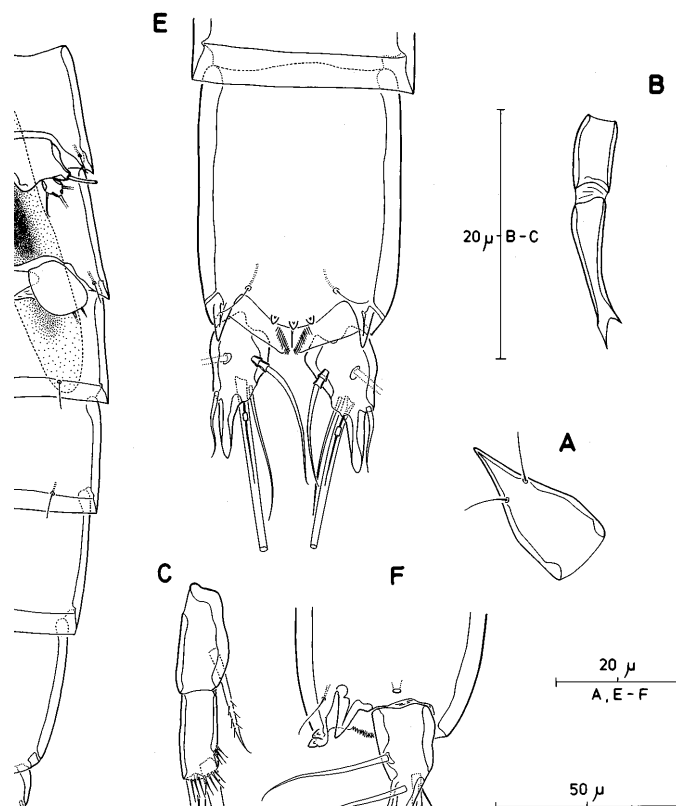


Figure 26. *Leptopontia americana* sp. nov. (♂). A, rostrum; B, P3 endopod; C, P4 endopod; D, urosome, ventral; E, anal somite and caudal rami, dorsal; F, anal somite and right caudal ramus, lateral.



*P1* (Fig. 17A). Praecoxa a well developed sclerite; coxa without ornamentation; both segments with integumental pits. Intercoxal sclerite small, transversely elongate. Basis with slender inner seta and curved outer seta; large anterior surface pore, and spinular row near insertion site of exopod. Exopod distinctly 3-segmented; exp-1 with long pinnate seta; exp-2 bare; exp-3 with 3 geniculate setae, increasing in length adaxially. Endopod with enp-1 7 times as long as wide, and about 1.67 times as long as exopod; with recurved serrate seta near proximal margin; enp-2 with 2 geniculate setae and 1 tiny seta; ratio of enp-1:enp-2 3.1.

*P2-P4* (Fig. 17A-C). Intercoxal sclerites rectangular, distinctly concave in P3 and P4; coxae bare; both with integumental pits. Bases with short naked seta (P2, P4) or long plumose seta (P3). Exopodal segments with well developed hyaline frills. Inner setae of P3-P4 exp-3 serrate. Inner elements of P2-P4 enp-1 spiniform and bipinnate. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.021	1.120
P2	0.0.021	1.120
P3	0.0.112	1.010
P4	0.0.112	1.020

*Fifth legs* (Fig. 14B,D) closely set together, no intercoxal sclerite. Baseoendopods not fused medially. Baseoendopod with well developed endopodal lobe, about extending to distal margin of exopod, with 2 long setae. Exopod a small segment with 1 outer, 1 inner and 1 apical seta. Outer basal seta long and plumose.

*Description of male.* Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 505  $\mu\text{m}$  (Fig. 15A). Ornamentation of body generally as in the female. Sexual dimorphism in antennule, P3 endopod, P4 endopod, P5, P6 and in genital segmentation. Spermatophore about 100  $\mu\text{m}$  in length.

*Antennule* (Figs 15A, 16B) indistinctly 9-segmented; base surrounded by small sclerite. Relative lengths of first two segments as in female. Fourth segment a small U-shaped sclerite with 1 seta. Major geniculation between segments 6 and 7. Segmental fusion pattern: I, II-VIII, IX-XII, XIII, XIV-XVIII, XIX-XX, XXI-XXII, XXIII, XXIV-XXVIII. Large aesthetasc on segment 5 (Fig. 15A) 200  $\mu\text{m}$  long, fused basally with seta. Apical acrothek of segment 9 consisting of small aesthetasc (27  $\mu\text{m}$  long), fused basally with 2 setae. Armature formula: 1-[1], 2-[8 + 1 plumose], 3-[7], 4-[2], 5-[6 + 2 modified + ae], 6-[2 + 3 modified], 7-[3 modified], 8-[1], 9-[7 + acrothek].

*P3 endopod* (Fig. 15B) 2-segmented, minute; enp-1 with 2 rows of diminutive spinules; enp-2 represented by 1 barbed spine.

*P4 endopod* (Fig. 15C) 2-segmented; enp-1 unarmed; enp-2 with 1 small pinnate spine and a larger, posteriorly recurved, pectinate spine.

*P5* (Fig. 15D). Baseoendopods partly fused medially; endopodal lobe moderately developed, without armature; outer basal spine long and plumose. Exopod small, with 1 seta on both outer and inner margins and a smaller one apically.

*Sixth pair of legs* (Fig. 15D) asymmetrical with one member partly fused to genital somite; functional member slightly larger and articulating; armature consisting of inner slender seta and outer vestigial setule.

*Etymology.* The species name is derived from the Latin *punctum*, meaning point and refers to the pitted cuticle.

*Remarks.* Kunz (1938) redescribed and figured *L. curvicauda* from Helgoland and for the first time presented drawings of a male *Leptopontia*. From his illustrations of the P1 (relative proportions of endopodal segments), female P5 (length of endopodal setae) and male anal operculum it appears that he might well have been dealing with *L. punctata*. The female anal operculum showing two median processes was probably taken from a copepodid V or an aberrant specimen (cf. Fig. 16C-E). Klie (1950) also reported *L. curvicauda* from Helgoland and suspected certain inaccuracies in Kunz' (1938) description of the male. Detailed comparison suggests that Klie's material is different from *L. punctata* and *L. curvicauda* and cannot be identified with any of the species recognized herein. Evidence for this is found in his illustration of the male fifth leg which has a distinctive endopodal lobe and is unusual in the outer exopodal seta being distinctly shorter than the distal and inner ones, a feature also explicitly mentioned in the text description. In addition, Klie's male differs in the unusually long endopodal segments of the P4. Although Klie was the first to recognize the sexual dimorphism on the swimming legs in *Leptopontia*, his illustration of the male P3 rules out the possibility that he was dealing with the type species *L. curvicauda*. He also pointed out that females were carrying paired egg-sacs each containing 4 eggs rather than 2 as reported in *L. punctata* (cfr. Kunz, 1938) and ***L. flandrica* sp. nov.** (cfr. Huys & Boxshall, 1991). In the absence of sufficiently detailed information on the female, Klie's material from Helgoland can only be considered *species inquirenda* in the genus.

*L. punctata* can readily be distinguished from its congeners by the strongly chitinized, punctate integument covering the body somites and the bases of most appendages, including the antennules, maxillules and maxillae. The species resembles *L. curvicauda* in P1 endopod structure, however, differs from it in the length:width ratio of the caudal rami, the shape of the anal operculum, and the sexual dimorphism on the P3 endopod.

*L. punctata* is known from the Isle of Bonden (Wells *et al.*, 1975) and Helgoland (Kunz, 1938).

### ***Leptopontia flandrica* sp. nov.**

*Leptopontia* sp. *sensu* Huys & Boxshall (1991: p. 122, fig. 2.4.2A,B).

*Type locality.* Southern Bight of the North Sea; 51°45'00" N, 3°30'00" E; 14 m depth.

*Material examined.*

- (1) Holotype ♀ (dissected on 7 slides) and paratype ♂ (dissected on 5 slides); other paratypes 10 ♀♀ and 7 ♂♂ in alcohol; coll. R. Huys, 17 April 1986; deposited in The Natural History Museum, London;
- (2) National Museum of Ireland: reg. no. 28.990; 1 ♀ *in toto* on slide; Finavarra, Co. Clare, Ireland; coll. J.M.C. Holmes, 13 May 1990, littoral sand.

*Description of female.* Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 405 µm (Fig. 18A). Maximum width 45 µm measured at

cephalothorax. Integument of thoracic and abdominal somites with distinct pattern of subsurface integumental pits (Figs 18A, 20D). Posterior margin of body somites with plain hyaline frill which is striated in the genital double-somite and free abdominal somites (Figs 18A, 20D). Individual somites connected by well developed intersomitic membranes (Fig. 20D).

*Rostrum* (Fig. 18A, E) triangular, elongate; lateral margins concave in distal half; about 0.9 times the length of first antennular segment; with 2 delicate sensillae.

*Genital double-somite* (Figs 18A, 20D) slightly longer than wide; original segmentation not marked by any external or internal cuticular structure. Genital apertures paired (Fig. 18C), located in anterior half of genital double-somite; each closed off by small operculum derived from sixth leg bearing 1 diminutive setule fused to operculum. Median copulatory pore located far anteriorly between genital apertures. Seminal receptacles not confirmed. Ventral surface of genital double-somite with paired secretory pores and patch of cuticular pits on either side of midline.

*Anal somite* (Figs 18A, 20D–F) with dorsal operculum drawn out into short and broad median, posteriorly directed spinous process, typically flanked by one or two small, sharp processes on either side; process in lateral aspect with distinct kink in dorsal curvature (arrowed in Fig. 20E).

*Caudal rami* (Fig. 20D–F) divergent, typically flask-shaped; outer distal corner drawn out into posteriorly directed, dorsally recurved spinous process; with setal arrangement as in the other species; ramus about 3.5 times as long as basal width (measured in lateral aspect along ventral margin).

*Antennule* (Fig. 20A) slender, 7-segmented; segment 1 longest, about 2.5 times as long as wide, surrounded by distinct sclerite around proximal posterior margin (Figs 18A, 20A), with 1 short seta at distal anterior corner and dorsal tube pore near distal margin; segment 4 with very slender aesthetasc (72  $\mu$ m) fused basally to seta and set on distinct pedestal; segment 7 with apical acrothek consisting of short aesthetasc (16  $\mu$ m) fused basally to 2 setae. All setae bare except for 1 plumose seta on segment 2. Armature formula: 1–[1], 2–[8 + 1 plumose], 3–[5], 4–[ + ae], 5–[1], 6–[3], 7–[7 + acrothek].

*Antennae to maxillae* as in *L. dovpori*.

*Maxilliped* (Fig. 20B). Syncoxa squarish; unarmed; without spinular rows. Basis unarmed. Endopod represented by stout, distally pinnate claw bearing small seta proximally.

*P1* (Fig. 20C). Praecoxxa a well developed sclerite. Coxa without ornamentation. Intercoxal sclerite small, transversely elongate. Basis with short inner seta and curved outer seta; with 2 secretory pores on anterior surface. Exopod distinctly 3-segmented; exp-1 with pinnate seta; exp-2 bare; exp-3 with 3 geniculate setae, increasing in length adaxially with outermost one less than half the size of other ones. Endopod with enp-1 8.0 times as long as wide, and about twice as long as exopod; with recurved serrate seta near proximal margin; enp-2 with 2 geniculate claws and 1 tiny seta; ratio of enp-1:enp-2 6.6.

*P2–P4* (Fig. 19A–B, E) shorter and stouter than in preceding species. Intercoxal sclerites decreasing in width in successive legs. Coxae bare, with pore in P2. Bases with short naked seta (P2, P4) or long plumose seta (P3). Exopodal segments with well developed hyaline frills. Inner setae of P3–P4 exp-3 serrate. Inner elements of P2–P4 enp-1 spiniform and bipinnate. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.021	1.120
P2	0.0.021	1.120
P3	0.0.112	1.010
P4	0.0.112	1.020

*Fifth legs* (Fig. 19H) closely set together (Fig. 20D), no intercoxal sclerite. Baseoendopods not fused medially. Baseoendopod with strongly developed sub-cylindrical endopodal lobe, extending to distal margin of exopod, with 1 short seta. Exopod a small segment with 1 outer, 1 inner and 1 apical seta, all of about the same length. Outer basal seta long and sparsely plumose.

*Description of male.* Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 390 µm. Body slightly more slender than in female. Ornamentation of body generally as in the female. Sexual dimorphism in antennule, P3 endopod, P4 endopod, P5, P6 and in genital segmentation.

*Antennule* as in previous species.

*P3 endopod* (Fig. 19C,D) minute, 2-segmented; enp-1 with 2 spinules; enp-2 represented by 1 barbed spine.

*P4 endopod* (Fig. 19F,G) 2-segmented; enp-1 unarmed; enp-2 with 1 short pinnate spine and a larger, posteriorly recurved, pectinate spine.

*P5* (Fig. 19I). Baseoendopods partly fused medially; endopodal lobe strongly developed, without armature; outer basal spine long and plumose. Exopod small, with 1 seta on both outer and inner margins and a finer one apically.

*Sixth pair of legs* (Fig. 18D) asymmetrical with one member fused to genital somite; functional member slightly larger and articulating; armature consisting of inner slender seta and outer vestigial setule.

*Etymology.* The species name is derived from the Latin *Flandricus*, -a, meaning Flemish, and refers to the fact that this species is often the most abundant *Leptopontia* in Belgian offshore waters.

*Remarks.* *L. flandrica* can be differentiated on the basis of the following combination of characters: (1) P5 ♀ with subcylindrical endopodal lobe extending to the distal margin of the exopod, (2) rostrum with concave lateral margins in the distal half, (3) P1 endopod with 2 claw-like geniculate setae on enp-2, (4) the compact ♀ genital field with 1 rudimentary armature element on the P6, and (5) the contour of the anal operculum in lateral aspect (cf. Fig. 20E).

The species is relatively widely distributed in the Southern Bight of the North Sea, however the Irish record from Finavarra indicates that it occurs further north.

### ***Leptopontia mediterranea* sp. nov.**

*Type locality.* Bay of Calvi, Corsica, France; in washings of *Posidonia oceanica* (L.) Delile taken by SCUBA diving at 4 m depth.

*Material examined.* Holotype copepodid V ♂ (dissected on 7 slides) deposited in The Natural History Museum, London; coll. C. Heip & L. Thielemans, May 1985.

*Description of copepodid V ♂.* Total body length from the tip of the rostrum to the

posterior margin of the caudal rami: 330  $\mu\text{m}$  (Fig. 21A). Maximum width 40  $\mu\text{m}$  measured at cephalothorax. Integument of thoracic and abdominal somites with dense pattern of subsurface integumental pits. Pleural areas of cephalothorax not well developed so that cephalic appendages are clearly exposed in lateral aspect (Fig. 21A). Posterior margin of body somites with plain hyaline frill, finely striated in abdominal somites (Fig. 22A,B). Individual somites connected by well developed intersomitic membranes (Fig. 21A).

*Rostrum* (Fig. 21A,B) large, triangular, elongate; distinctly tapering in second third; only slightly shorter than first antennular segment; with 2 delicate sensillae.

*Anal somite* (Figs 21A; 22A, C,D) with fine spinules ventrally (Fig. 22A); with dorsal operculum drawn out into median, posteriorly directed spinous process, flanked by two large processes which are longer than the median one.

*Caudal rami* (Fig. 22C,D) slightly divergent; outer distal corner drawn out into posteriorly directed, dorsally recurved spinous process; with setal arrangement as in other species. Ramus about 3.4 times as long as basal width (measured in lateral aspect along ventral margin).

*Antennule* (Fig. 21A, B), long, 5-segmented with partial suture line on segment 5. First segment longest, making up about 1/3 of total antennule length, surrounded by distinct sclerite around proximal posterior margin, with 1 short seta at distal anterior corner and dorsal tube pore near distal margin; segments 3 to 5 with several vestigial setae (arrowed in Fig. 21B); segment 3 with large aesthetasc (L: 70  $\mu\text{m}$ ); segment 5 with apical acrothek consisting of short aesthetasc (23  $\mu\text{m}$ ) fused basally to 2 setae. All setae bare except for 1 plumose seta on segment 2. Armature formula: 1-[1], 2-[8 + 1 plumose], 3-[16 + 2 setules + ae], 4-[2 + 1 setule + 1 spinous process], 5-[12 + 1 setule + acrothek].

*Antenna* (Fig. 21D). Coxa with spinular row. Allobasis elongate, with small exopod bearing short seta; with swollen seta-like structure on abexopodal margin at level of exopod (arrowed in Fig. 21D). Free endopod with 2 unipinnate spines laterally, and 1 spine, 3 geniculate setae and 1 geniculate spine fused basally to small seta.

*P1* (Fig. 23A). Praecoxa a well developed sclerite. Coxa with 5 rows of tiny spinules on anterior surface. Basis with slender, pinnate inner seta and short outer seta; large anterior surface pore, and spinular row between insertion sites of rami. Exopod indistinctly 3-segmented; exp-1 with long pinnate seta; exp-2 and exp-3 partly fused along anterior surface; exp-3 with 3 geniculate setae, increasing in length adaxially. Endopod with enp-1 5 times as long as wide, and about 1.12 times as long as exopod; with swollen serrate seta near proximal margin; enp-2 with 2 geniculate setae and 1 tiny seta; ratio of enp-1:enp-2 2.65.

*P2-P4* (Fig. 23B-E). Coxae with tiny spinule rows on anterior surface. Bases with short naked seta (P2, P4) or long plumose seta (P3). Exopodal segments with well developed hyaline frills in P3-P4. Inner setae of P3-P4 exp-3 distinctly swollen and serrate.

*P3 endopod* (Fig. 23D) 2-segmented; enp-1 with 2 spinular rows; enp-2 with articulating swollen spine distally.

*P4 endopod* (Fig. 23E) 2-segmented; enp-1 with short inner spine and 2 spinular rows; enp-2 with 1 short pinnate spine and 1 slightly smaller bare spine. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.021	1.120
P2	0.0.021	1.120
P3	0.0.112	1.010
P4	0.0.112	1.020

*P5* (Fig. 22B). Baseoendopods completely free medially; endopodal lobe minute, with 1 very small spine; outer basal spine long and plumose. Exopodal lobe small, with 1 seta on both outer and inner margins and a longer one apically.

*Sixth pair of legs* (Fig. 22B) largely fused to somite, with 2 short setae on either side.

*Adults*. Unknown.

*Etymology*. The species name alludes to the type locality.

*Remarks*. Despite *L. mediterranea* being based on a late copepodid, the shape and size of the rostrum, in addition to the peculiar structure of the anal operculum bearing paired massive lateral processes leave little doubt that it represents a distinct species. Although it has been shown for *L. punctata* (Fig. 16C–F) that smaller lateral processes on the anal somite can disappear at the final moult, and consequently would weaken their usefulness as a species discriminant for adults, it seems unlikely that the large processes in *L. mediterranea* would get absorbed completely as a result of a single moult. The incomplete separation of the middle and distal endopod segments of the P1 suggests that the 3-segmented condition of the endopod is not fully expressed until the final moult towards the adult. Post-displacement of characters that usually appear late in development provides a relatively simple heterochronic mechanism that can produce instant loss of a character or character state. In this case the 2-segmented condition of the P1 endopod found in the other leptopontiniid genera *Notopontia* and *Syrtilcola* can easily be the result of delaying the developmental pattern of *Leptopontia* with a single moult. The reduced setation elements on the distal antennular segments (arrowed in Fig. 21C) and the armature of the P3 endopod (spine on enp-1 absent) leave no doubt that the holotype is a male copepodid. It is noteworthy that at this stage modifications of the P4 endopod are not yet expressed.

The species is known from the type locality only and represents the second record of the genus in the Mediterranean (Soyer, 1971).

### ***Leptopontia breviarticulata* sp. nov.**

*Leptopontia* sp. *sensu* Mielke (1982).

*Type locality*. Playa Borrero, Santa Cruz, Galápagos.

*Material examined*. Holotype ♀ (dissected on 2 slides); W. Mielke's personal collection.

*Description of female*. Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 300 µm. Integument of thoracic and abdominal somites smooth. Posterior margin of body somites with plain hyaline frill.

*Rostrum* (Fig. 24A) triangular, elongate; only slightly shorter than first antennular segment; with 2 delicate sensillae.

*Anal somite* with dorsal operculum not drawn out into median spinous process but rounded (Fig. 24H).

*Caudal rami* (Fig. 24G,H) divergent; outer distal corner drawn out into posteriorly directed, dorsally recurved spinous process; setal arrangement as in other species. Ramus about 3 times as long as basal width (measured in lateral aspect along the ventral margin).

*Antennule* (Fig. 24A) shorter than in other species of the genus, 7-segmented; segment 1 longest, about 2.6 times as long as wide (but probably slightly squashed in preparation), surrounded by distinct sclerite around proximal posterior margin, with 1 short seta at distal anterior corner and dorsal tube pore near posterior margin; segment 4 with very long aesthetasc (105  $\mu\text{m}$ ) fused basally to seta and set on distinct pedestal; segment 7 with apical acrothek consisting of short aesthetasc (18  $\mu\text{m}$ ) fused basally to 2 setae. All setae bare. Armature formula: 1-[1], 2-[9], 3-[4], 4-[2 + ae], 5-[1], 6-[3], 7-[7 + acrothek].

*Antenna* (Fig. 24B). Coxa small, without spinular rows. Allobasis elongate, about 2.7 times as long as maximum width; with backwardly directed tubular seta. Exopod a small segment located in transverse membranous area marking fusion plane of basis and proximal endopod segment; exopodal seta long, about 2.7 times as long as segment. Free endopod with 2 spinular rows along outer margin, 2 pinnate spines along inner margin; distal margin with 1 pinnate spine, 3 geniculate setae and 1 spinulose geniculate seta fused basally to small seta.

*Mandible* (Fig. 24C,D). Coxa elongate, expanding distally into gnathobase provided with series of small, curved teeth and recurved pinnate seta at dorsal corner. Palp 2-segmented; basis a swollen elongate segment, unarmed, with 1 spinular row; endopod elongate, with 1 pinnate seta laterally and 4 bare setae apically.

*Maxillule* (Fig. 24E). Praecoxa with rectangular, elongate arthrite; arthrite with 6 setae and a distally serrate spine around the distal margin, and 2 tubular setae on the anterior surface. Coxa with small endite bearing 1 long seta. Basis with rami entirely incorporated; exopod represented by 1 small and 1 long seta; endopod represented by 2 setae; proximal and distal endites of basis with 2 and 4 setae, respectively.

*Maxilla* as in *L. doypori*.

*Maxilliped* (Fig. 24F). Syncoxa and basis unarmed; without spinular rows. Endopod represented by stout, distally pinnate claw bearing small seta proximally.

*P1* (Fig. 25A). Praecoxa not observed. Coxa without ornamentation. Basis with short inner and outer seta; with anterior surface pore. Exopod 2-segmented, with posterior membranous insert marking fusion plane of exp-2 and exp-3; exp-1 with pinnate seta; exp-2 with 3 geniculate setae, increasing in length adaxially. Endopod with enp-1 5.2 times as long as wide, and about 1.7 times as long as exopod; with recurved serrate seta near proximal margin; enp-2 with 2 geniculate setae and 1 tiny seta; ratio of enp-1:enp-2 3.25.

*P2-P4* (Fig. 25B-D). Intercoxal sclerites rectangular, distinctly concave in P3 and P4. Coxae bare. Bases with short (P2-P4) or long (P3) naked seta. Exopodal segments with well developed hyaline frills in P3-P4. Inner setae of P3-P4 exp-3 serrate. Inner elements of P2 and P4 enp-1 spiniform and bipinnate. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.021	1.120
P2	0.0.021	1.120
P3	0.0.112	1.010
P4	0.0.112	1.020

*Fifth legs* (Fig. 25E) closely set together, no intercoxal sclerite. Baseoendopods not fused medially. Baseoendopod with slightly developed endopodal lobe, not extending to distal margin of exopod, with long inner and short, swollen outer seta. Exopod a small segment with 1 outer, 1 inner and 1 apical seta. Outer basal seta long and plumose.

*Male*. Unknown.

*Etymology*. The species name is derived from the Latin *brevis*, meaning short, and *articulus*, meaning joint, and refers to the short P1 endopod.

*Remarks*. This species is clearly different from all others in the absence of any processes on the anal operculum, the very long seta on the antennary exopod, the relatively short first antennary segment, the 2-segmented P1 exopod, the short P1 endopod and the absence of the inner seta on P3 enp-1.

*L. breviarticulata* is known from the type locality only.

### ***Leptopontia americana* sp. nov.**

*Leptopontia curvicauda* T. Scott, 1892 *sensu* Coull & Dudley (1985) [partim]

*Type locality*. North Inlet, South Carolina, U.S.A. (35°20'N 79°10'W), subtidal sand, 1 m below MLW.

*Material examined*. Holotype: a damaged ♂ (dissected on 1 slide) deposited in The Natural History Museum, London.

*Description of male*. Only the most important differentiating characters are presented here.

Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 425 µm. Integument of thoracic and abdominal somites smooth. Posterior margin of body somites with plain hyaline frill (Fig. 26D).

*Rostrum* (Fig. 26A) triangular, elongate; with concave lateral margins in distal half.

*Anal somite* (Fig. 26E,F) with operculum not drawn out into median spinous process but provided with 3 little processes medially and flanked by large spinous process laterally.

*Caudal rami* (Fig. 26D–F) divergent; short; outer distal corner drawn out into posteriorly directed, dorsally recurved spinous process; with setal arrangement as in the other species of the genus.

*Sexual dimorphism* in antennule, P3 endopod, P4 endopod, P5, P6 and in genital segmentation. Spermatophore very large, about 1/4 of total body length (100 µm).

*Antennules to maxillipeds* as in *L. dovpori*.



*P3 endopod* (Fig. 26B) 2-segmented, minute; enp-1 unarmed and bare; enp-2 drawn out into a distally bifid spine.

*P4 endopod* (Fig. 26C) 2-segmented; enp-1 with inner pinnate seta; enp-2 with pinnate spine apically and subapical pectinate spine. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.021	1.120
P2	0.0.021	1.120
P3	0.0.112	modified
P4	0.0.112	1.020

*P5* (Fig. 26D). Baseoendopods not fused medially; endopodal lobe moderately developed, without armature; outer basal spine long and plumose. Exopod small, with 1 seta on both outer and inner margins and a smaller one apically.

*Sixth pair of legs* (Fig. 26D) asymmetrical with one member fused to genital somite; functional member slightly larger and articulating; armature consisting of inner slender seta and outer vestigial setule.

*Etymology.* This is the first species to be described from the North American continent.

*Remarks.* The vial with specimens from North Inlet contained at least two species of *Leptopontia*, however since the material was in a very bad condition no detailed descriptions could be provided. The current description of *L. americana* is fragmentary but nevertheless serves to distinguish the species from all its European congeners. *L. americana* is the only species that has retained the inner seta on the proximal endopod segment of the male P4. The very short caudal rami, the morphology of the anal operculum with the three knob-like structures and the shape of the male P3 endopod are additional differentiating characters.

The species is known from the type locality only.

*Leptopontia curvicauda* T. Scott, 1892 *sensu* Marinov (1971)

Marinov's (1971) redescription of *L. curvicauda* on the basis of Bulgarian specimens from Sozopol lacks the necessary detail for reliable species identification. His illustration of the male P3 showing 2 apical setae on the distal endopod segment is almost certainly based on the male P4. Pending the collection of new material from the Bulgarian Black Sea coast this species has to be ranked *species inquirenda* in the genus.

*Leptopontia curvicauda* T. Scott, 1892 *sensu* Apostolov (1973)

Similarly, Apostolov (1973) attributed his material from Nessebar to *L. curvicauda*. The presence of several spinous processes on the anal operculum raises the suspicion that part of his illustrations were based on copepodids. This is corroborated by Fig. 16C–E showing the anal operculum in the copepodid IV and V stages of *L. punctata*.

In the CIV stage three pairs of spinous processes are found and this number is reduced to two at the following moult towards CV. At the final moult to adult the median pair of processes is replaced by a single middorsal one. In view of the limited information contained in his fragmentary description Apostolov's material can at best be considered *species inquirenda* in *Leptopontia*. It is also unclear whether the three specimens of *L. curvicauda* from the Gulf of Varna listed in an earlier report (Apostolov, 1971) belong to the same species.

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