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A new species of *Cletocamptus* (Copepoda: Harpacticoida) from Chile and some notes on *Cletocamptus axi* Mielke, 2000

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Abstract
Some specimens of *Cletocamptus* were found in Salar de Surire (Chilean Andean plateau) during two sampling trips in October 2004 and October 2005. Although the Chilean material was preliminarily identified as *C. axi*, after careful inspection, it was clearly a new Chilean *Cletocamptus* species, *C. cecsurirensis*. The new species was found to be similar to *C. levis*, *C. sinaloensis*, *C. fourchensis*, *C. deborahdexterae*, and *C. axi* in the combination of the armature formula of the mandibular palp, shape of the lateral spinulose element of the maxillulary arthrite, and armature formula of P1–P4. *Cletocamptus cecsurirensis* and *C. levis* can be distinguished from *C. sinaloensis*, *C. fourchensis*, and *C. deborahdexterae* by the P1 EXP:ENP length ratio. *Cletocamptus cecsurirensis* and *C. levis* can be separated by the P5 baseoendopod:EXP length ratio. *Cletocamptus cecsurirensis* shows the sexual dimorphism typical for the genus. The new species also shows sexual dimorphism in the rostrum, similar to that found for *C. retrogressus*, *C. albuquerquensis*, and *C. levis*.

A complete description of the new Chilean species and some amendments to the original description of *C. axi* are given.

Keywords: *Chile,* Cletocamptus*, Copepoda, Harpacticoida, new species, taxonomy*

Introduction

Freshwater microcrustaceans have been poorly studied in northern Chile mainly because freshwater systems (pools, streams, marshes, and lakes) are located in isolated zones at high altitudes (Zuñiga et al. 1991, 1994; Gajardo et al. 1992). Previous studies have reported the occurrence of copepods, ostracods, and cladocerans (Dole-Olivier et al. 2000; Robertson 2000). Among copepods, the centropagid calanoid genus *Boeckella* Guerne and Richard, 1889 is the most abundant taxon (Hurlbert et al. 1986; Bayly 1993; Williams et al. 1995). Other cyclopoid genera (*Eucyclops* Claus, 1893, *Diacyclops* Kiefer, 1927, and *Paracyclops* Claus, 1893) and one harpacticoid family (Canthocamptidae Sars, 1906) have

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also been previously reported (Reid 1985; Berrios and Siefeld 2000). Specimens of *Cletocamptus* Schmankewitsch, 1875 were found by two of us (R.S. and P.L.) in a freshwater stream and in two shallow ponds in Salar de Surire (Chilean Andean plateau) during two sampling trips in October 2004 and October 2005. Upon preliminary inspection, Dr Gladys Asencio (Institute of Marine Biology, Universidad Austral de Chile) and Dr W. Mielke (Institut für Zoologie und Anthropologie Georg-August-Universität Göttingen) identified the Chilean material as *C. axi* Mielke, 2000, although some minor differences were observed (Mielke in litt.). Subsequent careful inspection of the Chilean material and comparison with female and male specimens of *C. axi* kindly sent by Dr Mielke to one of us (S.G.) revealed the presence of a new species of *Cletocamptus*. In the original description of *C. axi*, Mielke (2000) noted some variability in several characters which were also observed in the material examined herein.

A complete description of the new Chilean species and some amendments to Mielke's (2000) description of *C. axi* are given.

Materials and methods

Sediment samples were taken at three sites in Salar de Surire (Chile) (a freshwater stream with sandy sediments and two shallow ponds with muddy sediments) during two sampling trips carried out on 19 October 2004 and 19 October 2005. Samples were taken using a hand-held plastic corer (3.5 cm in diameter; sampling area 9.6 cm^2). Samples were preserved with 70% ethanol and copepods were sorted using a Zeiss Axioskop stereomicroscope. Three females and three males of *C. axi* collected from the type locality were kindly provided by Dr W. Mielke for comparison. Morphological observations and drawings were made from whole and dissected specimens. Intraspecific variability in armature formulae of P1–P6 was assessed only from dissected specimens. Aberrations, deformed setae/spines and/or segments were not considered as intraspecific variability. Only the presence or lack of well-developed and/or reduced setae/spines, and different patterns of spinular ornamentation of the anal somite were considered as intraspecific variability. Observations and drawings were made using a Leica compound microscope equipped with drawing tube at magnifications of 1000×. The type material of *C. cecsurirensis* sp. nov. and the material of *C. axi* have been deposited in the Copepoda collection of the Institute of Marine Sciences and Limnology, Mazatlan Marine Station.

The terminology proposed by Huys and Boxshall (1991) for morphological descriptions is adopted. The following abbreviations are used in the text and tables: P1–P6, first to sixth swimming legs; EXP, exopod; ENP, endopod; P1(P2–P4) EXP(ENP) 1(2, 3) denotes the proximal (middle, distal) exopodal (endopodal) segment of P1, P2, P3, or P4.

Taxonomic account

Family CANTHOCAMPTIDAE Sars, 1906 (*incertae sedis*) *sensu* Por, 1986
Genus *Cletocamptus* Schmankewitsch, 1875
Cletocamptus cecsurirensis sp. nov.
(Figures 1–11)

Type material

One female holotype (EMUCOP-1004-01) and one male allotype (EMUCOP-1004-02) preserved in alcohol. Thirteen female (EMUCOP-1004-14 to EMUCOP-1004-26) and 10

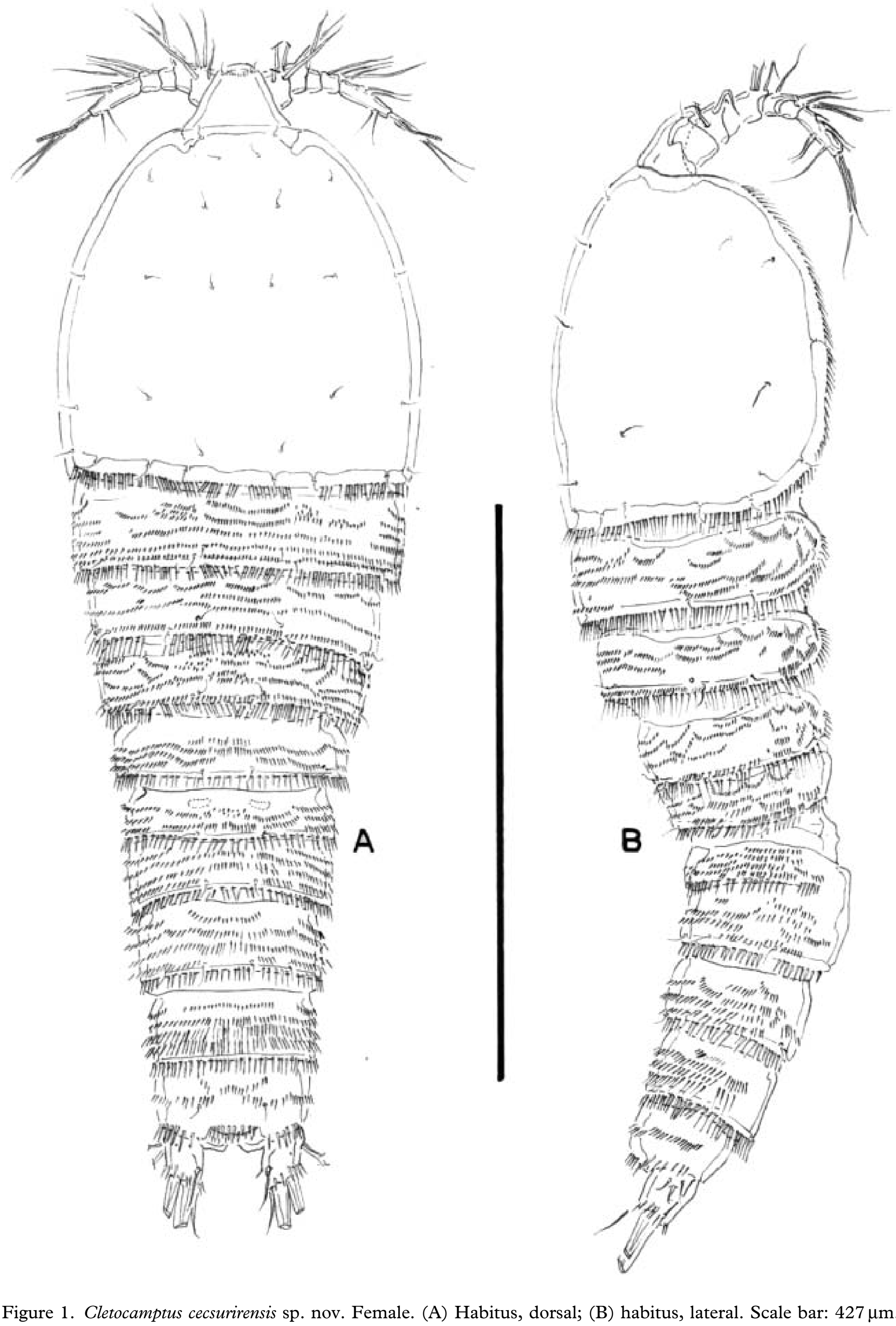

Figure 1. *Cletocamptus cecsurirensis* sp. nov. Female. (A) Habitus, dorsal; (B) habitus, lateral. Scale bar: 427 µm.

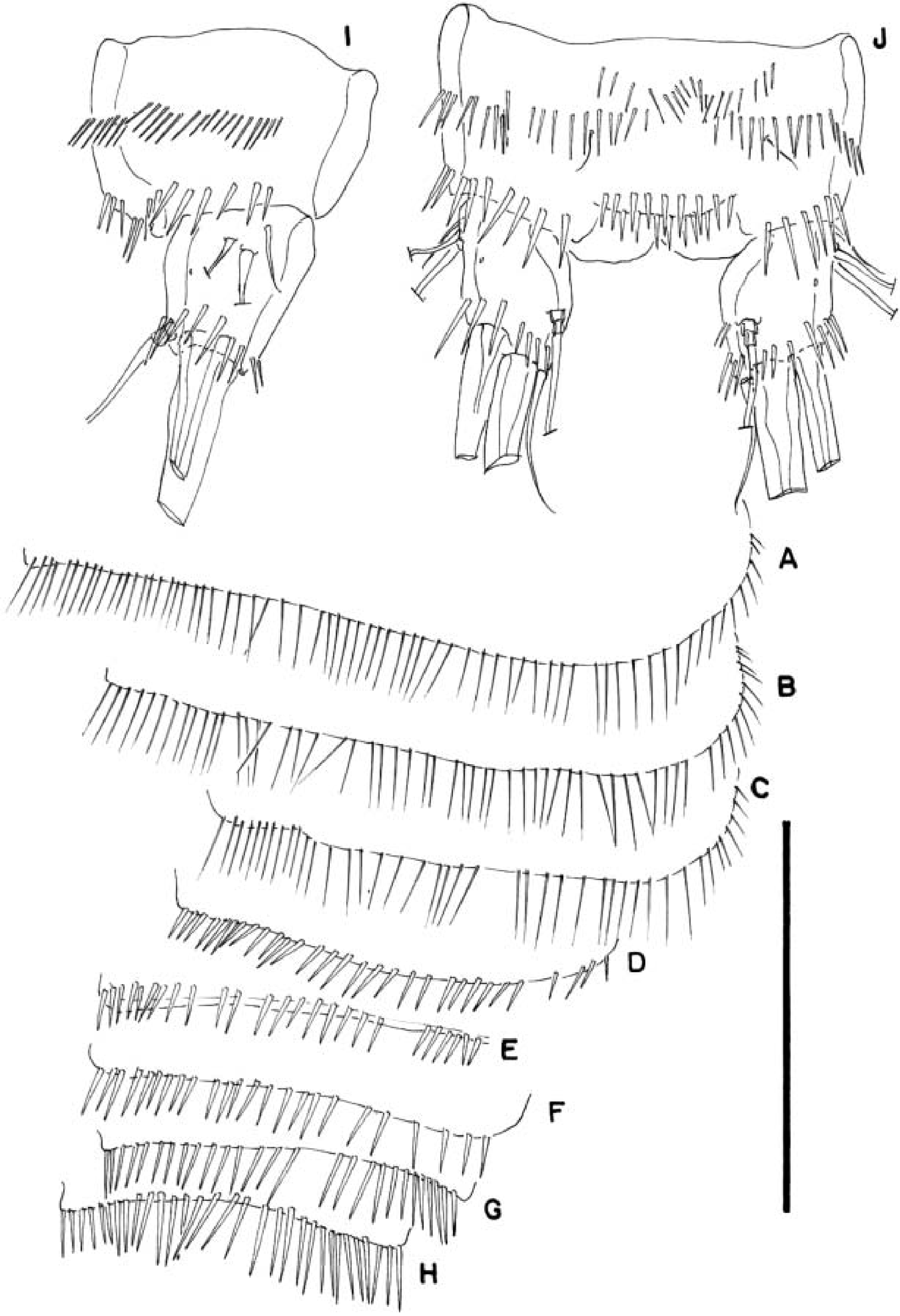

Figure 2. *Cletocamptus cecsurirensis* sp. nov. Female. (A–H) Spinular ornamentation along posterior margin of P2–P5-bearing somites (A–D), genital double-somite (E, F), and fourth and fifth urosomites (G, H); (I) anal somite and right caudal ramus, lateral; (J) anal somite and caudal rami, dorsal. Scale bar: 100 µm.

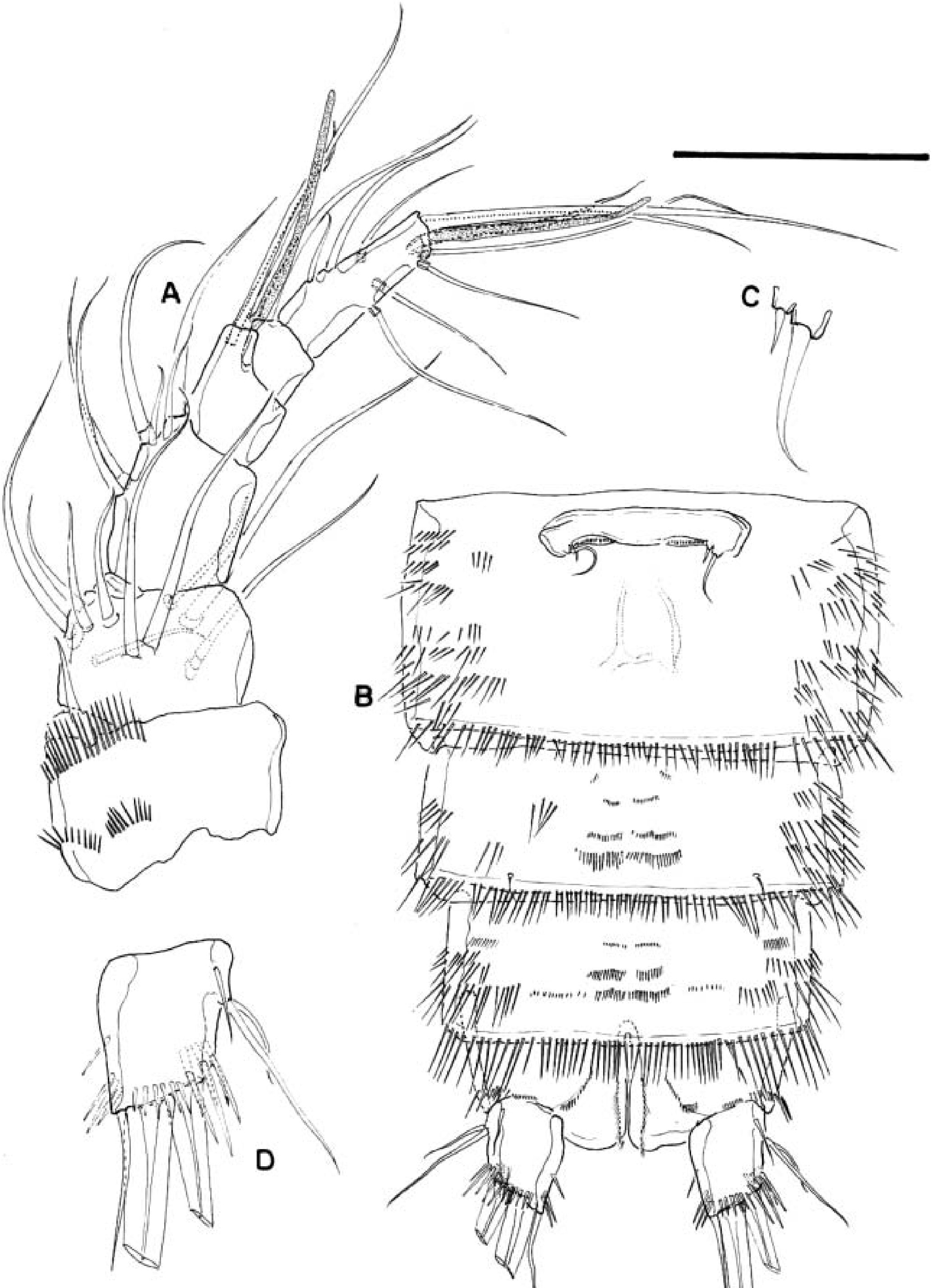

Figure 3. *Cletocamptus cecsurirensis* sp. nov. Female. (A) Antennule; (B) urosome, ventral (P5-bearing somite omitted); (C) P6; (D) left caudal ramus, ventral. Scale bar: 46 µm (A); 107 µm (B); 32 µm (C); 64 µm (D).

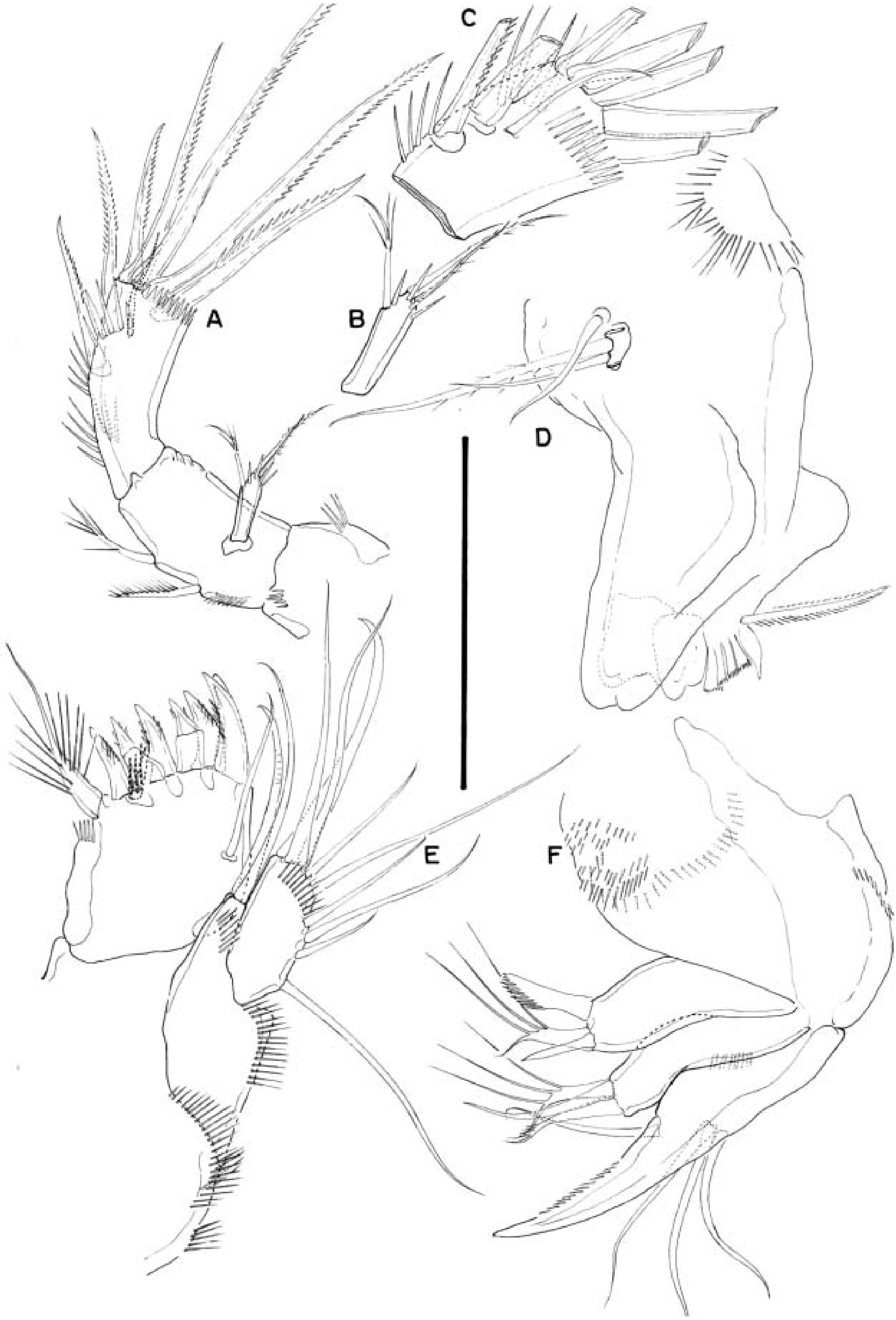

Figure 4. *Cletocamptus cecsurirensis* sp. nov. Female. (A) Antenna; (B) antennal exopod; (C) distal part of antennal endopod; (D) mandible; (E) maxillule; (F) maxilla. Scale bar: 86 μm (A); 51 μm (B–F).

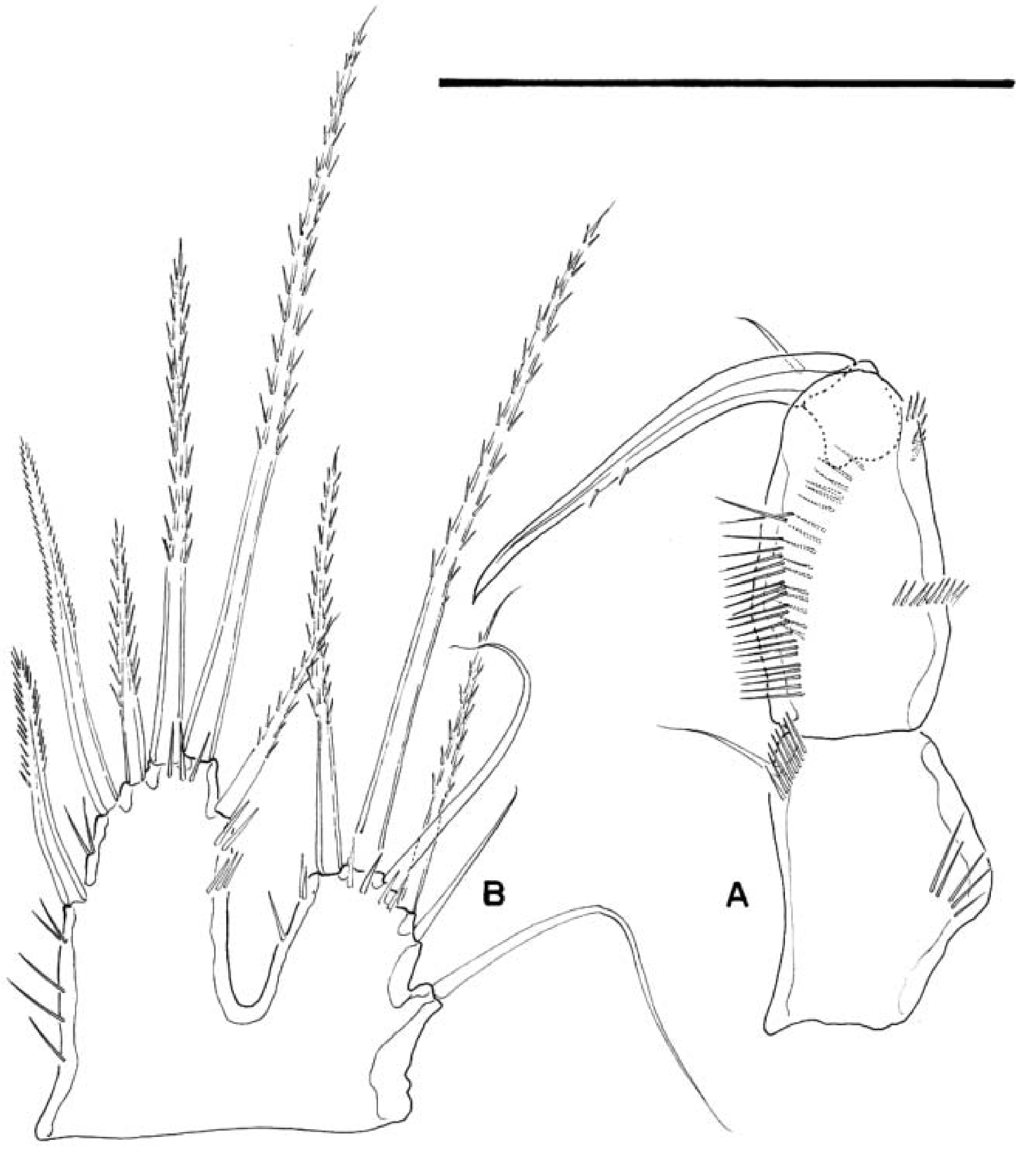

Figure 5. *Cletocamptus cecsurirensis* sp. nov. Female. (A) Maxilliped; (B) P5. Scale bar: 60 µm (A); 100 µm (B).

male (EMUCOP-1004-04 to EMUCOP-1004-13) dissected paratypes, and 10 female and nine male paratypes preserved in alcohol (EMUCOP-1004-03). Collected on 19 October 2004 and 19 October 2005; small freshwater stream with sandy bottom (18°47′24.7″S, 69°05′17.6″W), two shallow ponds (18°51′43″S, 69°07′59.3″W and 18°47′34.6″S, 69°05′27.7″W) with muddy bottom; 4180 m a.s.l.; coll. Rodrigo Scheihing.

Type locality

Salar de Surire, Chilean high Andean Plateau (18°47′24.7″S, 69°05′17.6″W).

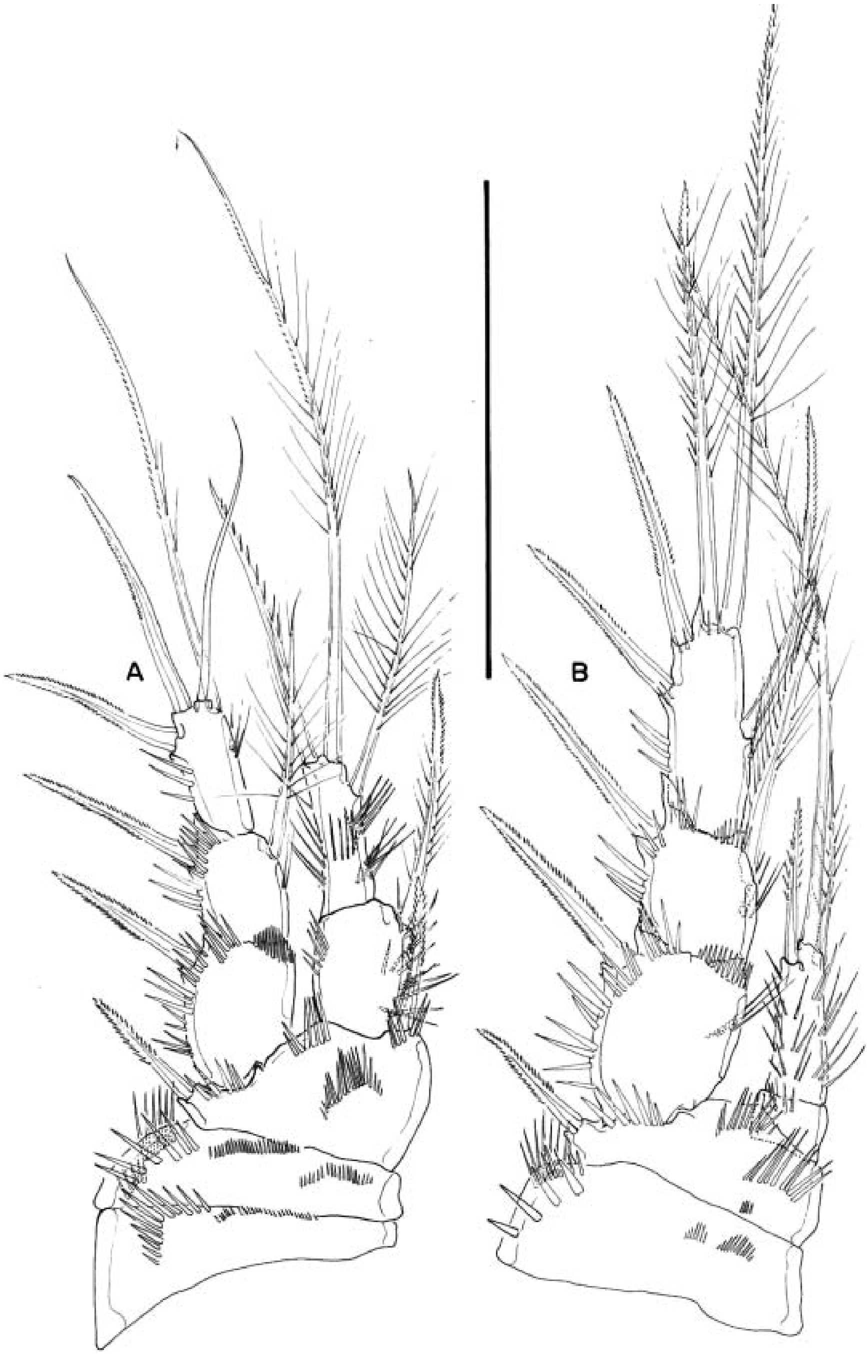

Figure 6. *Cletocamptus cecsurirensis* sp. nov. Female. (A) P1; (B) P2. Scale bar: 117 μm.

Etymology

The specific epithet refers to the Centro de Estudios Científicos where two of us (R.S. and P.L.) work, and to the type locality where the species was found.

Figure 7. *Cletocamptus cecsurirensis* sp. nov. Female. (A) P3; (B) P4. Scale bar: 100 µm.

Female

Habitus (Figure 1A, B) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 680 to 820 µm (mean 737 mm,

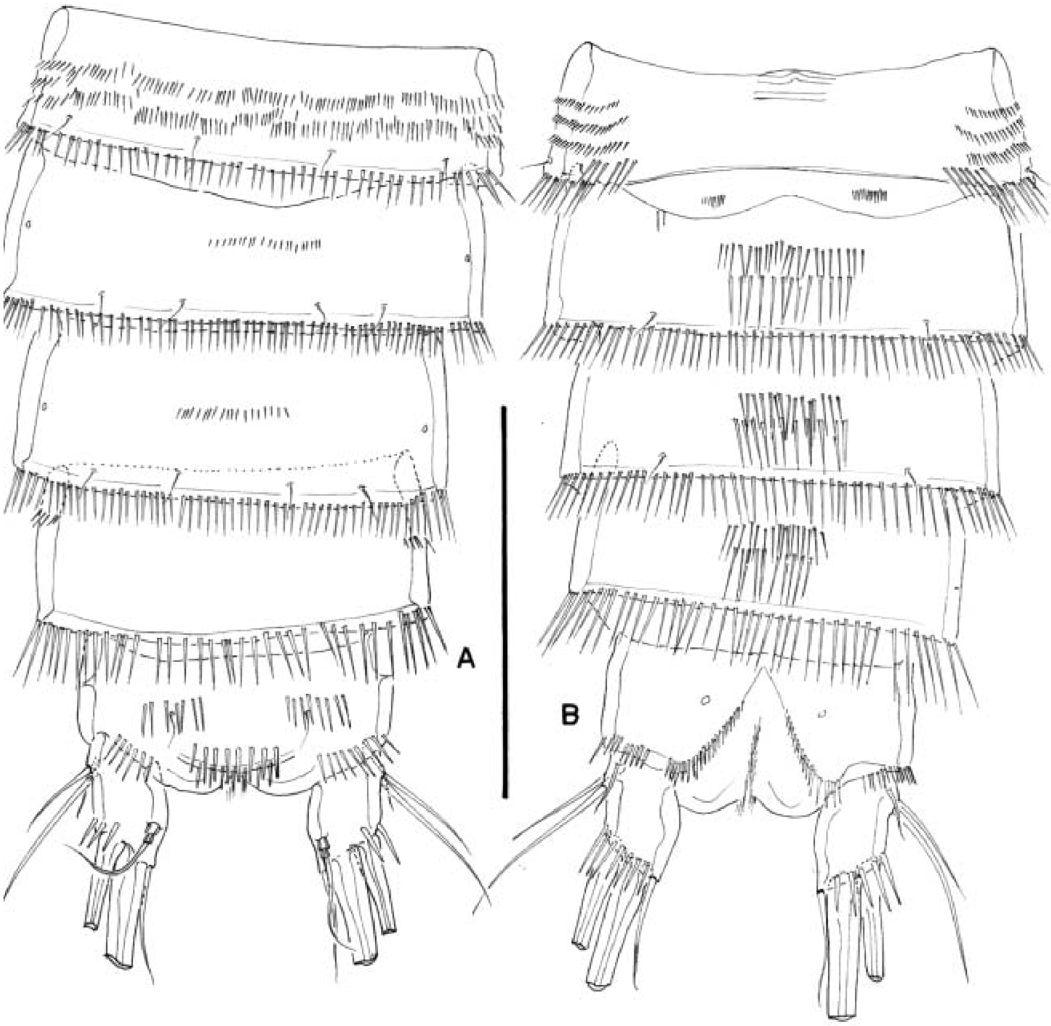

Figure 8. *Cletocamptus cecsurirensis* sp. nov. Male. (A) Urosome, dorsal (P5-bearing somite omitted); (B) urosome, ventral (P5-bearing somite omitted). Scale bar: 100 µm.

$n=18$; holotype 740 mm). Rostrum defined at base, triangular, with pair of setules subapically and ornamented with small spinules distally on ventral surface. Cephalic shield (Figure 1A, B) with small, fine spinules along margin dorsally and laterally. Dorsal and lateral surface of free thoracic somites (P2–P4-bearing somites) with transverse rows of minute spinules, with longitudinal row of small spinules close to posterior margin and with long spinules along posterior margin (Figure 2A–C). Dorsal and lateral surface of first urosomite (P5-bearing somite) with transverse rows of minute spinules, with row of small spinules close to posterior margin and with long spinules along posterior margin (Figure 2D). Genital double-somite with subcuticular rib dorsally and laterally indicating former division between second and third urosomites (Figure 1A, B), but completely fused ventrally (Figure 3B); dorsal and lateral surface of second and third urosomite (first and second genital somites) with transverse rows of minute spinules, with row of long spinules along posterior margin (Figure 2E, F), and with relatively longer spinules laterally, ventrally

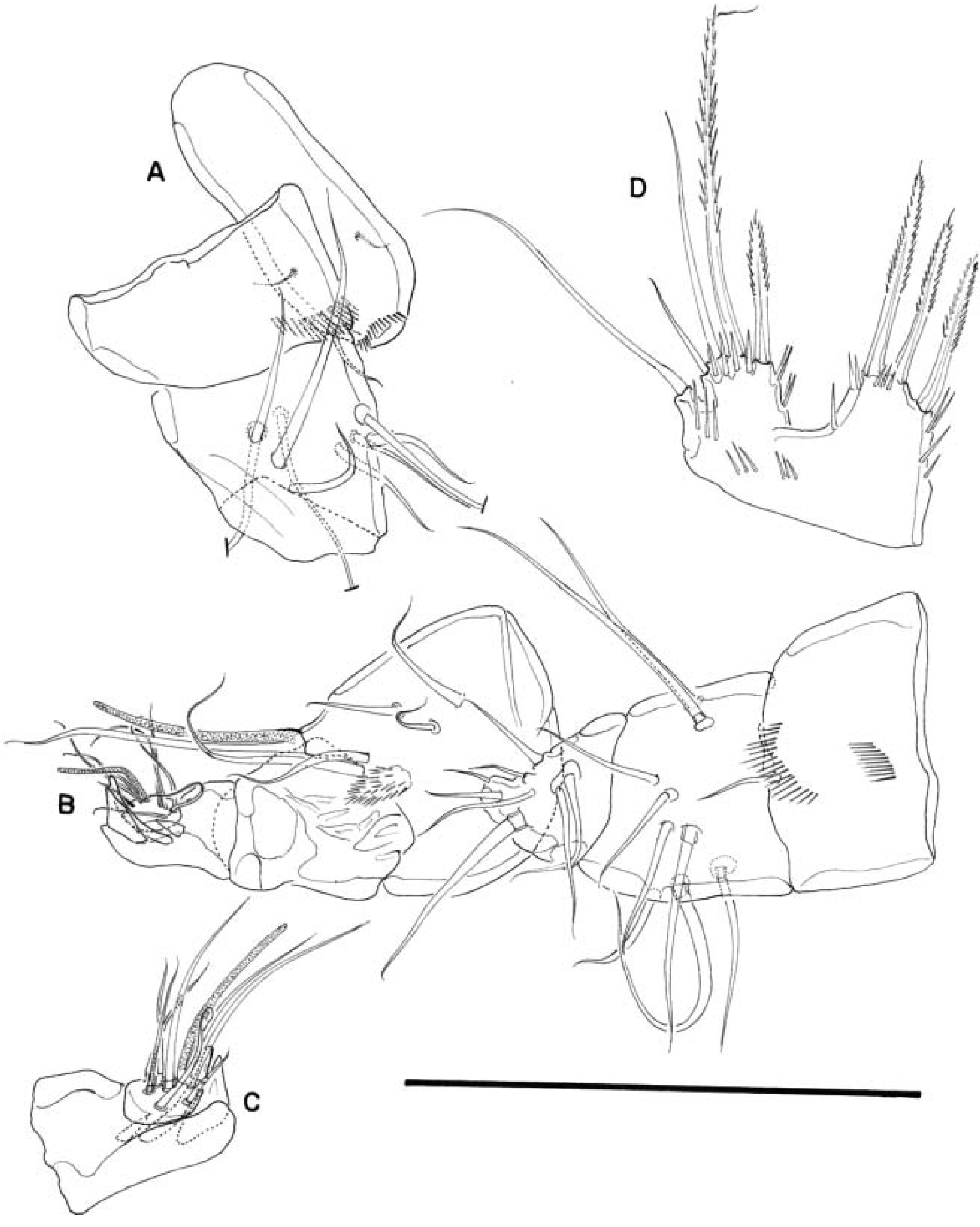

Figure 9. *Cletocamptus cecsurirensis* sp. nov. Male. (A) Rostrum, and first and second antennular segments; (B) antennule; (C) last antennular segment; (D) P5. Scale bar: 100 µm (A, B); 143 µm (C); 100 µm (D).

with spinules as figured (Figure 3B). Fourth and fifth urosomites as in previous somite dorsally, ventrally with spinular pattern (Figure 3B).

Dorsal surface of anal somite (Figures 1A, B, 2J) with transverse rows of spinules and with dorsolateral strong spinules close to joint with caudal rami (Figure 3I, J); rounded anal operculum furnished with two rows of strong spinules. Caudal rami (Figures 1A, B, 2I, J,

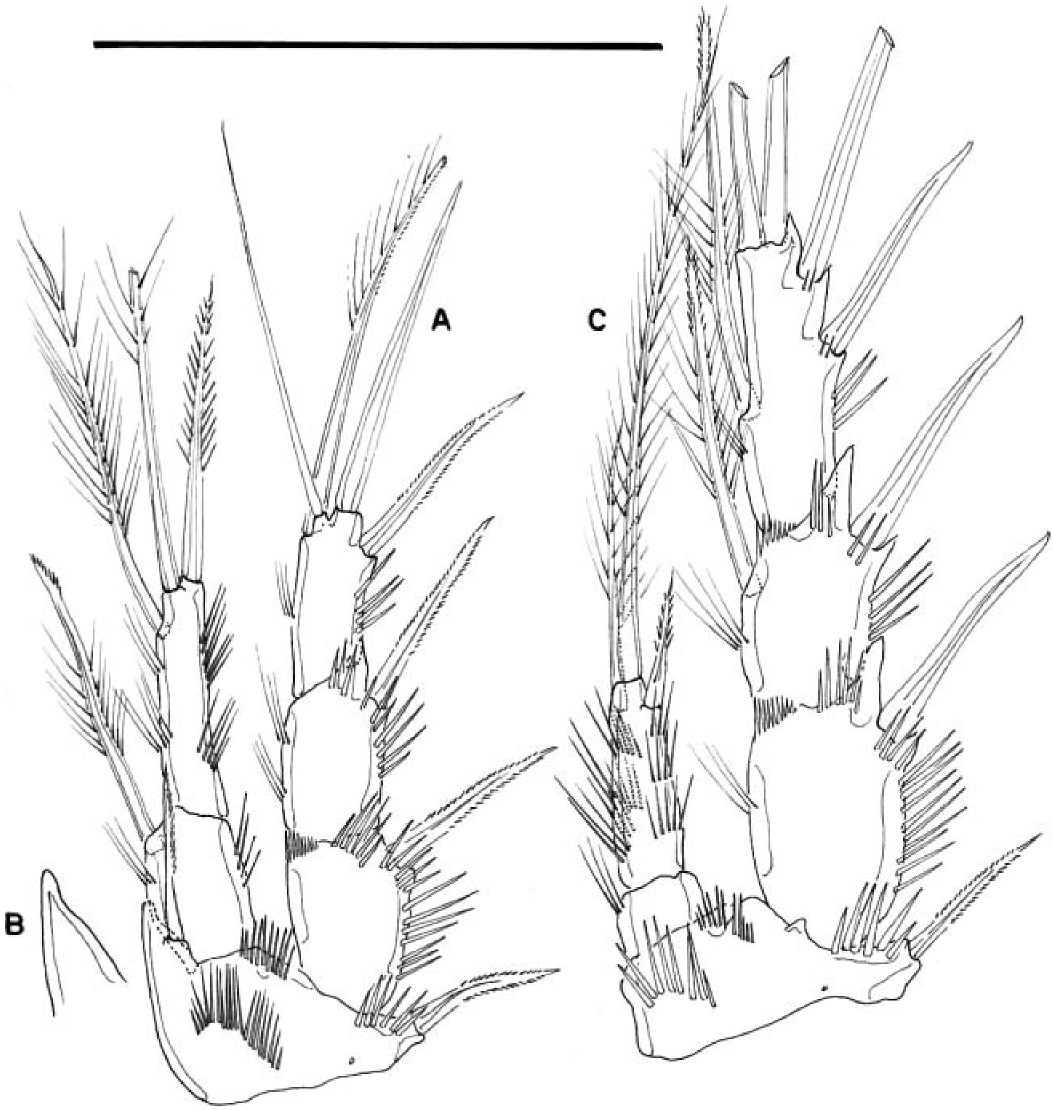

Figure 10. *Cletocamptus cecsurirensis* sp. nov. Male. (A) P1; (B) dimorphic inner projection of basis of P1; (C) P2. Scale bar: 100 μm (A); 143 μm (B); 100 μm (C).

3D) nearly as long as wide; dorsal and ventral surface smooth, except for spinules close to posterior margin; with seven elements.

Antennule (Figure 3A) six-segmented; surface of segments smooth except for two rows of spinules on first segment. Armature formula, 1-(1), 2-(10), 3-(6), 4-(1+[1+ae]), 5-(1), 6-(9+[1+ae]).

Antenna (Figure 4A) with small coxa. Allobasis armed with two abexopodal setae. Free endopodal segment ornamented with inner strong spinules proximally and subdistally; with two lateral inner spines and a slender seta and five distal elements (Figure 4C). Exopod one-segmented; about five times longer than wide; with few spinules, and with one lateral and two apical setae (Figure 4B).

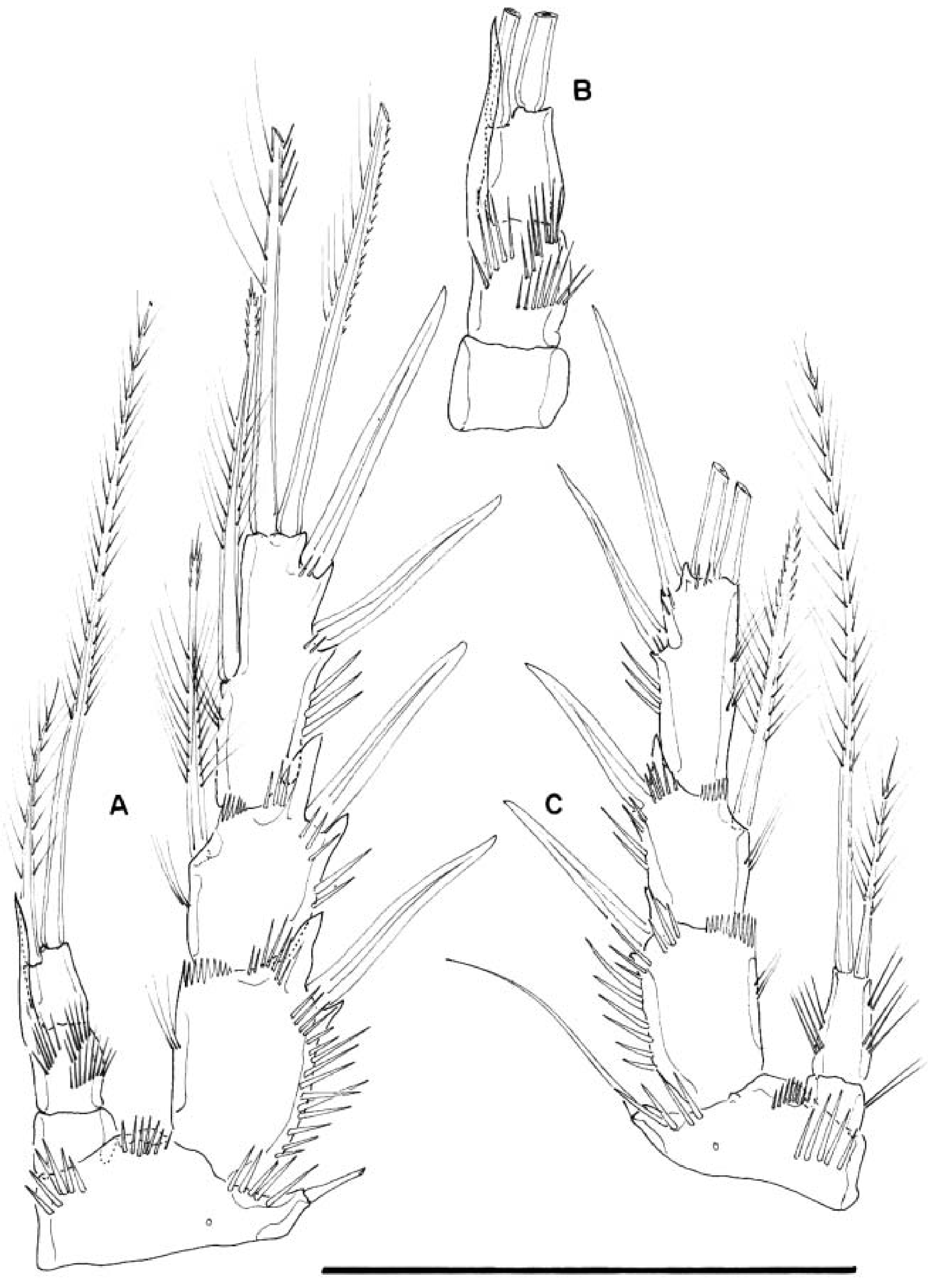

Figure 11. *Cletocamptus cecsurirensis* sp. nov. Male. (A) P3; (B) endopod of P3; (C) P4. Scale bar: 100 µm (A); 143 µm (B); 100 µm (C).

Mandible (Figure 4D) robust; chewing edge with two bicuspidate teeth, four multicuspidate teeth, one pyriform element and one lateral seta. Palp one-segmented, with two setae unequal in length and one small seta arising nearby.

Maxillule (Figure 4E) robust; arthrite of praecoxa with few spinules, with one surface seta, seven distal spines and one lateral strong seta, the latter spinulose. Coxa with some spinules and with two slender setae. Basis with some median spinules. Homology of the setae on basis, exopod and endopod difficult to assess. Basis seemingly with three apical and two lateral setae, endopod and exopod seemingly represented by three and one seta, respectively.

Maxilla (Figure 4F): syncoxa with minute spinules along inner margin; with two endites, each bearing three setae as figured. Allobasis drawn into strong claw bearing one accompanying seta. Endopod represented by three setae.

Maxilliped (Figure 5A) subchelate. Syncoxa with rows of spinules and with a small seta on inner distal corner. Basis without armature; with one anterior and one posterior longitudinal row of spinules along inner margin; with small spinules medially and subapically. Endopod drawn into long and slender claw with one accompanying small seta.

P1 (Figure 6A): praecoxa with spinules close to joint with coxa. The latter with transverse spinule rows on anterior face, and with spinule row near outer distal corner on posterior face. Basis with inner and outer spines; with median spinule row, and with stronger spinules at base of exopod, between rami and at base of inner basal spine. Exopod three-segmented. Endopod two-segmented, reaching the middle of EXP 3.

P2 (Figure 6B): coxa as in P1. Basis as in P1 except for inner spine; outer element spine-like. Exopod three-segmented and ornamented as figured; EXP 2 and 3 with inner seta. Endopod two-segmented, barely reaching beyond tip of EXP 1; ENP 1 small, slightly wider than long and with outer spinules; ENP 2 with long spinules as shown, and with one outer spine, one apical and one inner seta.

P3 (Figure 7A): coxa as in P2. Basis as in P2 except for seta-like outer element. Exopod and endopod as in P2.

P4 (Figure 7B): coxa and basis as in P3. Exopod three-segmented; EXP 2 with, EXP 3 without inner seta. Endopod two-segmented, barely reaching the tip of P4 EXP 1; ENP 1 small, slightly wider than long; ENP 2 with inner and outer slender spinules and armed with two apical setae (innermost shorter).

P5 (Figure 5B): exopod and baseoendopod fused. Baseoendopodal lobe about twice as long as exopod, with sets of spinules along inner and outer margin, with spinules at base of apical seta; with one outer, one apical, and four inner setae; relative length of setae as figured. Exopod with spinules as figured, with five setae, plus outer seta of basis.

Armature formula of female P1–P5 as follows:

	P1	P2	P3	P4	P5
EXP	I-0; I-1; I,I1,1	I-0; I-1; II,I1,1	I-0; I-1; II,I1,1	I-0; I-1; II,I1,0	5
ENP	0-1; 0,I1,1	0-0; I,1,1	0-0; I,1,1	0-0; 0,2,0	6

P6 (Figure 3C) represented by median plate in anterior half of second urosomite (first genital somite); each vestigial leg represented by one outer long and one slender inner seta. Copulatory pore in the middle of genital double-somite.

Male

Body (not shown) as in female except for genital double-somite (Figure 8A, B). Rostrum (Figure 9A) sexually dimorphic, elongate, with two lateral setules and set with small spinules apically on ventral surface. Second to fifth urosomites ornamented with spinules as figured. Anal somite and caudal rami (Figure 8A, B) as in female.

Antennule (Figure 9A–C) six-segmented, subchirocer; last segment as in Figure 9C and with three teeth. Armature formula difficult to define, but probably as follows 1-(1), 2-(9), 3-(8), 4-(6+[1+ae]), 5-(0), 6-(7+[1+ae]).

Antenna, mandible, maxillule, maxilla, and maxilliped (not shown) as in female.

P1 (Figure 10A) as in female except for inner projection of basis in the male (Figure 10B).

P2 (Figure 10C) as in female except for dimorphic inner spine of ENP2, and stronger and bare outer dimorphic spines of EXP 1–3.

P3 exopod (Figure 11A, B) as in female except for stronger and bare outer dimorphic spines; endopod dimorphic, three-segmented, second segment with apophysis reaching far beyond ENP 3.

P4 (Figure 11C) as in female except for stronger outer dimorphic spines.

P5 (Figure 9D): both legs distinct; baseoendopod and exopod fused; exopod with four setae plus basal seta; baseoendopod with three setae.

P6 (Figure 8B) represented by a plate, without armature.

Variability

Females (13 females analysed). The second and third innermost setae of the P5 baseoendopod of about the same length in four specimens; the anal operculum of one female possesses one row of spinules; the left P4 endopod of one female possesses three instead of two setae on the last segment; the left P3 endopod of one female possesses four instead of three setae on the last segment.

Males (10 males analysed). One male was observed without spinular ornamentation on the anal operculum; the ventral spinular rows of urosomites are longer in two males; the anal operculum of one male is furnished with only one row of spinules; the inferior spinules on the anal operculum of one male are very small; one male was found with a two-segmented left exopod of P2 (the second and third segments partially fused); the last segment of the left exopod of P2 of one male is shorter; the left P4 ENP 3 of one male possesses three instead of two setae and the right P3 EXP 3 of the same animal possesses two instead of one inner setae; the outermost spine of the P5 baseoendopod of one male is shorter; the P5 baseoendopod of one male possesses four instead of three setae.

Discussion

Specimens of *Cletocamptus* were found in sediment samples taken in Salar de Surire (Chilean Andean plateau). Upon preliminary inspection, Dr W. Mielke suggested that the Chilean material could belong to, or be very close to, *C. axi* known from the Lagoon of Puerto Núñez (Santa Cruz, Galapagos Islands). Mielke (in litt.) noted that, in the Chilean material, the antennal exopod, the inner seta of the second endopodal segment of P1, and the first endopodal segment of P2 and P3 are somewhat longer, that the caudal rami are somewhat shorter, and that the outer seta of the male P2 ENP 2 is more slender. He also noted some slight differences in the spinular ornamentation of the body somites and anal operculum, and suggested, on one hand, the possibility of finding some more slight differences, and on the other hand, that it could be rather difficult to separate the Chilean material from *C. axi* based solely on morphological evidence.

Mielke (2000) noted some intraspecific variability in *C. axi*. Such variability was found in the number of spinules on the anal operculum (five to six), armature formula (with two or three setae) and spinular ornamentation (with or without spinules) of the antennal exopod, relative length of the innermost but one setae of the male P5 exopod, armature of male P6 (with or without a small seta), and relative length of the setae of swimming legs. He also noted that one female possessed four setae on the distal endopodal segment of P3, and that the distance between the insertion points of the inner terminal seta and the seta on inner margin of the distal exopodal segment of P2 could also differ. Later, Gómez et al. (2004, p 2726) suggested a need for describing in detail the dorsal and ventral spinular ornamentation of body somites of *C. axi*. Dr Mielke kindly provided one of us (S.G.) with three males and three females of *C. axi* in which the spinular ornamentation was analysed and is presented herein (Figures 12, 13B, C). It was also possible to observe the variability noted by Mielke (2000) regarding the spinular ornamentation of the anal operculum (with one or two rows of spinules, and with different number of spinules) in the females of *C. axi* (Figures 14B, C, 15A). Of these, the spinular ornamentation shown in Figure 14B, C (with two rows of strong spinules) was observed in two of the three specimens analysed. On the other hand, the spinular ornamentation shown in Figure 13A was observed in all three male specimens of *C. axi*. Of course, it should be noted that the inspection of only three females and three males of *C. axi* is not enough and more specimens are needed to assess the intraspecific variability of the species. Upon careful inspection of the same material, one of us (S.G.) noted also the variability observed by Mielke (2000) regarding the armature formula of the second endopodal segment of the female P3 (with four instead of three setae) (Figure 14F), and the difference between the length–width ratio of the caudal rami of *C. axi* (see Figures 14B, D, 15A) and the Chilean material, and was also able to show the structure of the female P6 of *C. axi* (Figure 14A), each leg being represented by one inner minute seta and a longer outer element.

Interestingly, Mielke (2000) described the endopod of P1 of *C. axi* as being shorter than the exopod (the second endopodal segment barely reaching the middle of the third exopodal segment) (see Mielke 2000, p 276, Figure 2B) and did not note any variability regarding the relative length of the endopod of P1 in any of the eight animals dissected. From our examination of the material provided by Dr Mielke, all the specimens of *C. axi*, except for one female, were found to possess a P1 endopod as long as or slightly longer than the entire exopod (Figures 14E, 15B). In this respect, it remains uncertain which condition (either the endopod as long as or longer than the exopod, or the endopod shorter than the exopod) defines the P1 of *C. axi*. Thus, as noted above, the analysis of six specimens is insufficient to assess the variability and the most common condition of the P1 endopod of *C. axi*.

Gómez et al. (2004), after analysing the variability of four species of *Cletocamptus*, suggested that the variability observed for each species must be under genetic control since their intraspecific variability seldom overlaps. The same seems to apply for the variability of *C. axi* and the Chilean material, thus supporting the erection of a new species, *C. cecsurirensis* sp. nov.

At present, the valid species within *Cletocamptus* are *C. retrogressus* Schmankewitsch, 1875, *C. confluens* (Schmeil, 1894), *C. albuquerquensis* (Herrick, 1894), *C. trichotus* Kiefer,

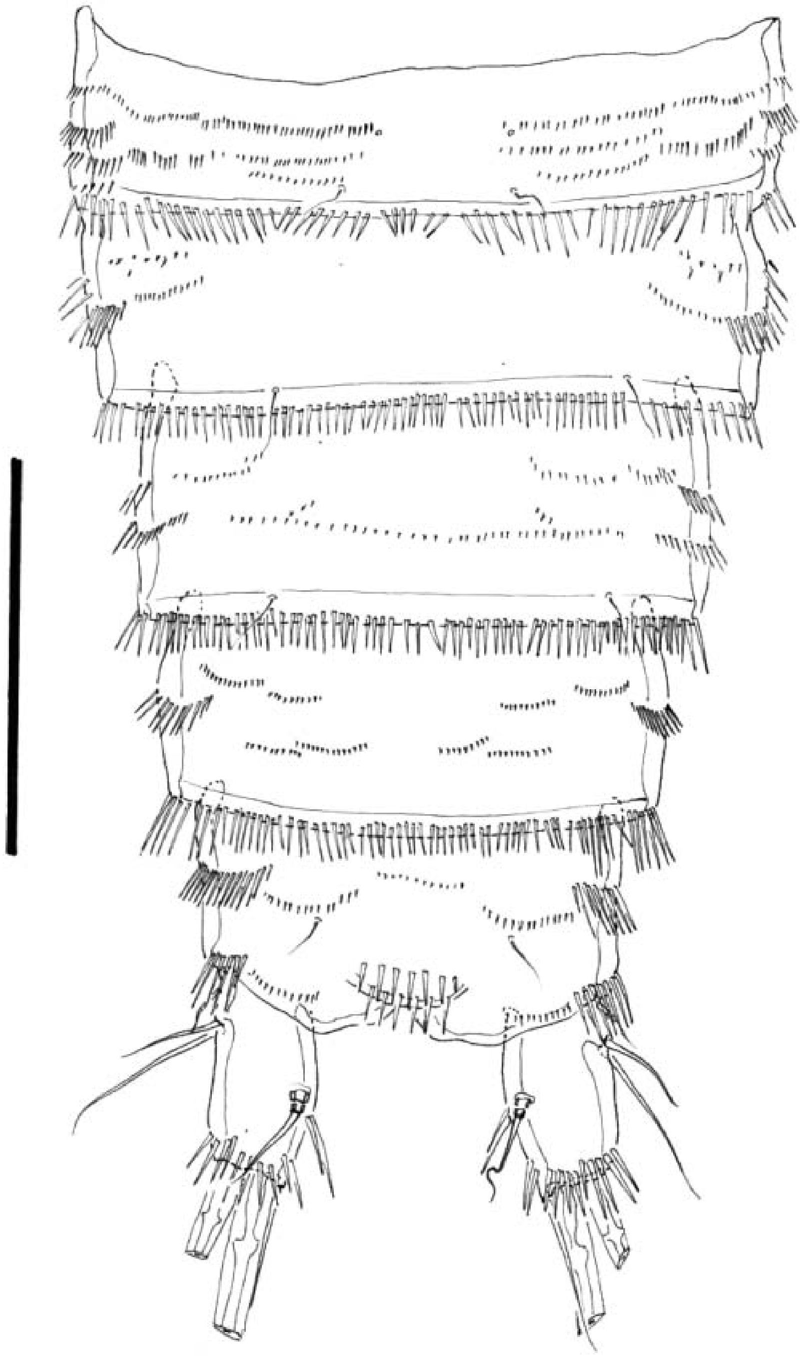

Figure 12. *Cletocamptus axi* Mielke, 2000. Female. Urosome, dorsal. Scale bar: 100 μm.

1929, *C. feei* (Shen, 1956), *C. affinis* Kiefer, 1957, *C. gravihiatus* (Shen and Sung, 1963), *C. mongolicus* Strba, 1968, *C. helobius* Fleeger, 1980, *C. merbokensis* Gee, 1999, *C. axi* Mielke, 2000, *C. schmidti* Mielke, 2000, *C. deborahdexterae* Gómez, Fleeger, Rocha-Olivares and Foltz, 2004, *C. stimpsoni* Gómez, Fleeger, Rocha-Olivares and Foltz, 2004, *C.*

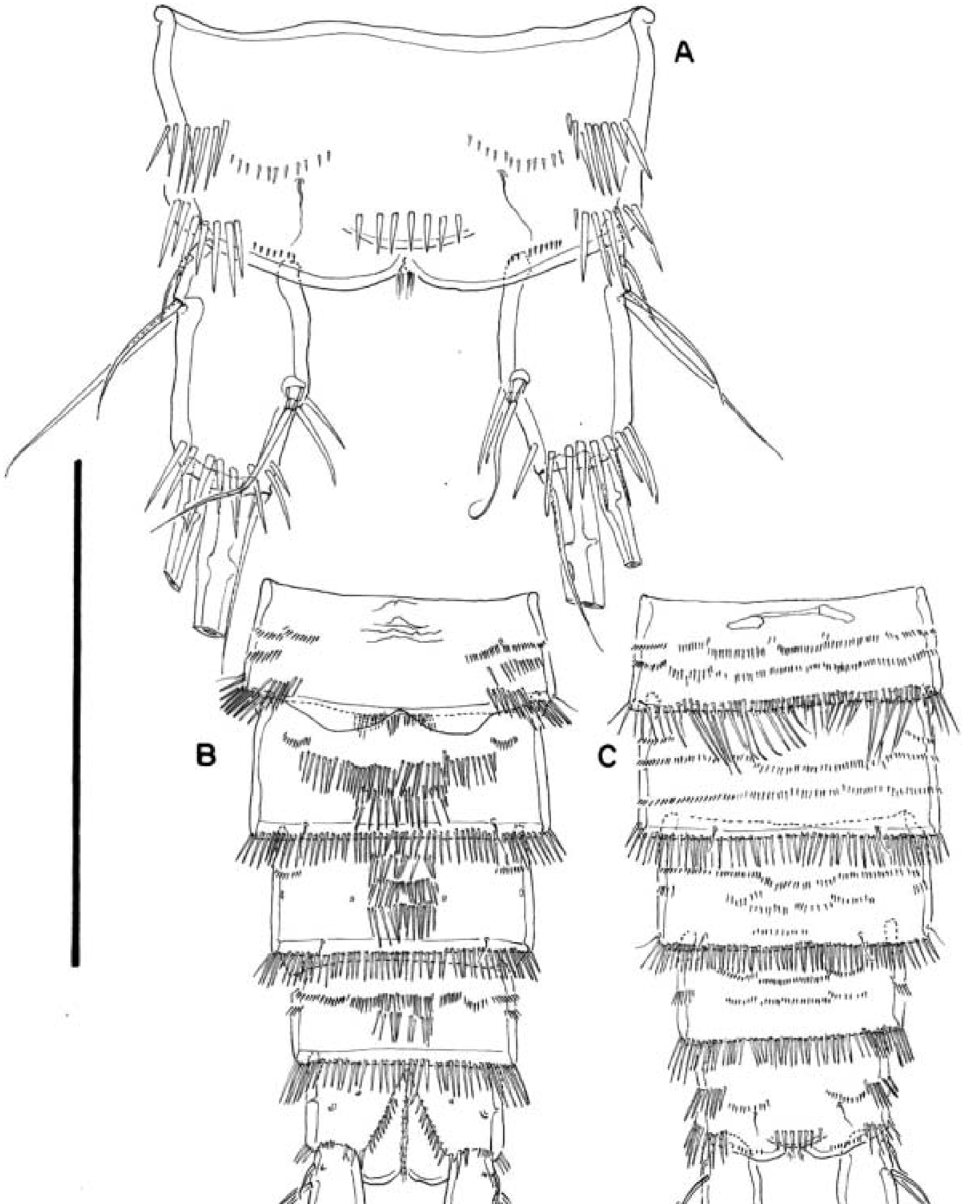

Figure 13. *Cletocamptus axi* Mielke, 2000. Male. (A) Anal somite and caudal rami, dorsal; (B) urosome, ventral (P5-bearing somite omitted); (C) urosome, dorsal (P5-bearing somite omitted). Scale bar: 100 µm (A); 240 µm (B, C).

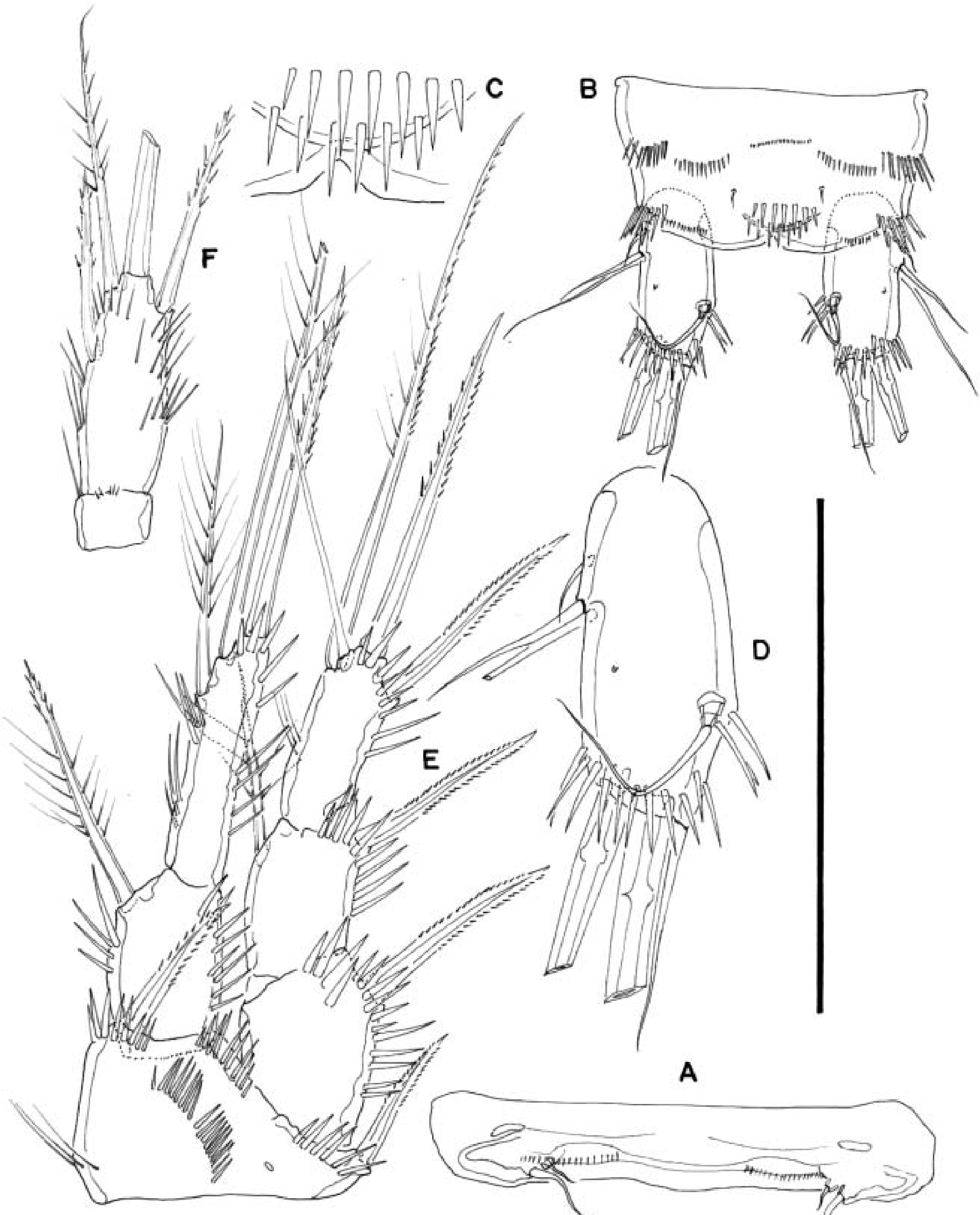

Figure 14. *Cletocamptus axi* Mielke, 2000. Female. (A) P6; (B) anal somite and caudal rami, dorsal; (C) anal operculum; (D) left caudal ramus, dorsal; (E) P1; (F) aberrant P3 ENP. Scale bar: 100 µm (A); 200 µm (B); 70 µm (C); 100 µm (D); 117 µm (E); 115 µm (F).

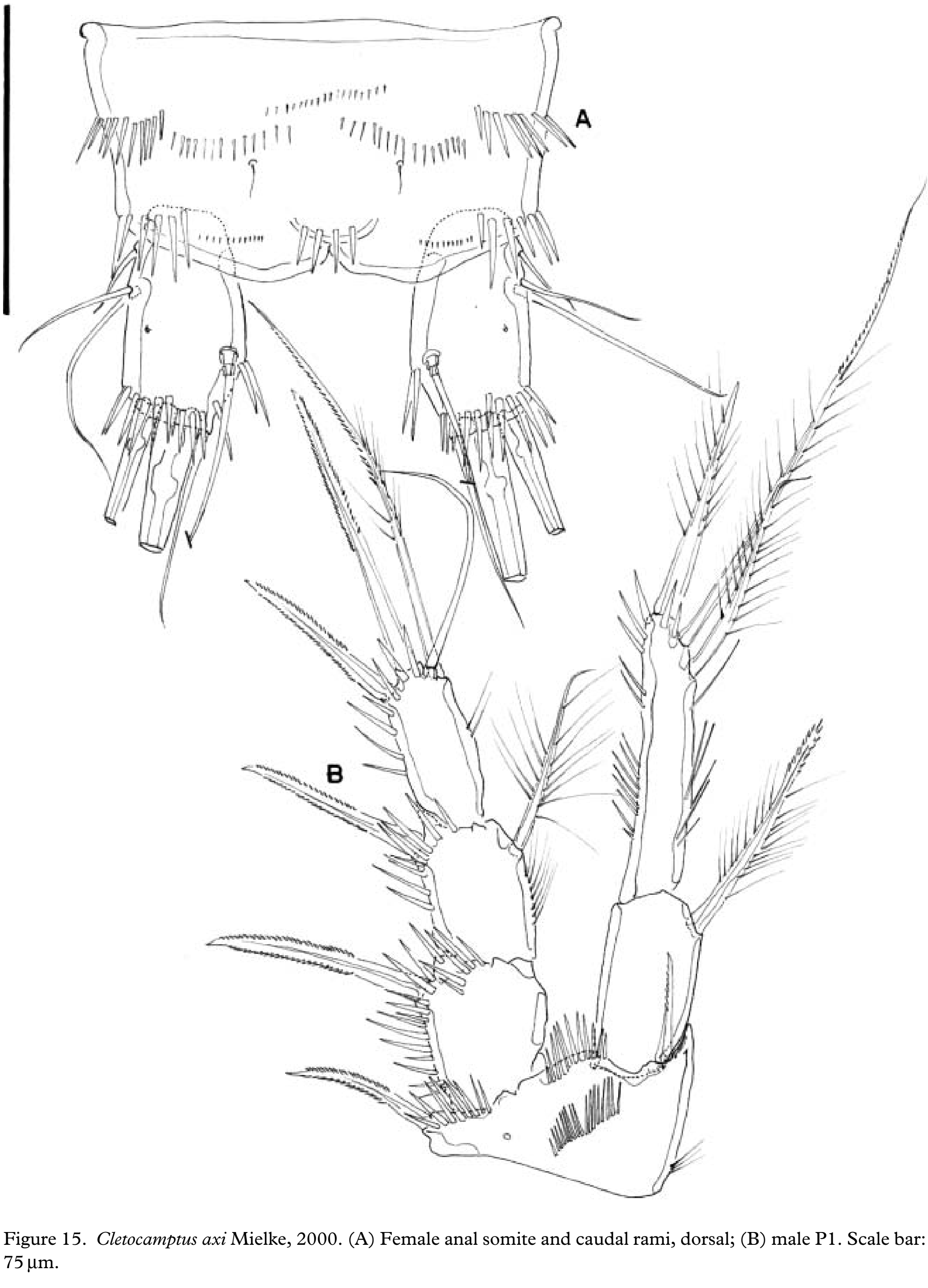

Figure 15. *Cletocamptus axi* Mielke, 2000. (A) Female anal somite and caudal rami, dorsal; (B) male P1. Scale bar: 75 μm.

sinaloensis Gómez, Fleeger, Rocha-Olivares and Foltz, 2004, *C. fourchensis* Gómez, Fleeger, Rocha-Olivares and Foltz, 2004, *C. levis* Gómez, 2005, and *C. nudus* Gómez, 2005. Of these, 10 species have been described from the Americas (*C. helobius*, *C. sinaloensis*, *C.*

fourchensis, *C. deborahdexterae*, *C. stimpsoni*, *C. axi*, *C. schmidti*, *C. albuquerquensis*, *C. levis*, and *C. nudus*).

Cletocamptus cecsurirensis sp. nov. is similar to *C. levis*, *C. sinaloensis*, *C. fourchensis*, *C. deborahdexterae*, and *C. axi* in the combination of (1) armature formula of the mandibular palp (with two setae arising from the one-segmented palp, plus a small seta arising nearby); (2) shape of the lateral spinulose element of the maxillulary praecoxal arthrite, and (3) armature formula of P1–P4. However, *C. cecsurirensis* sp. nov. and *C. levis* can be separated from *C. sinaloensis*, *C. fourchensis*, and *C. deborahdexterae* by the P1 EXP:ENP length ratio (P1 ENP longer or as long as exopod in the three later species, but P1 ENP 2 hardly reaching the middle of P1 EXP 3 in the two former species). *Cletocamptus cecsurirensis* sp. nov. and *C. levis* can be separated by the P5 baseoendopod:EXP length ratio (exopod reaching the middle of the baseoendopodal lobe, far below the insertion site of the outermost baseoendopodal seta in *C. cecsurirensis* sp. nov.—similar to that found in *C. sinaloensis*, *C. fourchensis*, and *C. deborahdexterae*—but reaching the insertion site of the outermost baseoendopodal seta in *C. levis*). Gómez (2005) noticed that *C. levis*, *C. helobius*, *C. axi*, *C. schmidti*, and *C. albuquerquensis* are the only American representatives of the genus in which the P1 ENP is shorter than the P1 EXP. Nevertheless, in the light of the present evidence, the condition of this character state for *C. axi* remains unclear, since most of the material analysed in the present study possesses a P1 ENP as long as or slightly longer than the entire exopod. Thus, this diagnostic character should be taken cautiously for *C. axi* until its variability is adequately assessed.

Cletocamptus cecsurirensis sp. nov. shows the typical sexual dimorphism for the genus in A1, basis of P1, outer spines of P2–P4 EXP, P2 ENP, P3 ENP, P5, and P6. Interestingly, *C. cecsurirensis* also showed sexual dimorphism in the rostrum, being more slender in the male than in the female. The same has been observed only for *C. retrogressus* Schmankewitsch, 1875 (Mielke 2001, p 4, Figure 2B), *C. albuquerquensis* (Herrick, 1894) (Pallares 1962, p 242, Plate I, Figure 8), and *C. levis* (Gómez 2005, p 3126, Figure 22A).

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