

Four new species of *Cletocamptus* Schmankeiwitsch, 1875, closely related to *Cletocamptus deitersi* (Richard, 1897) (Copepoda: Harpacticoida)

SAMUEL GÓMEZ†, JOHN W. FLEEGER‡, AXAYÁCATL ROCHA-OLIVARES§ and DAVID FOLTZ‡

†*Instituto de Ciencias del Mar y Limnología, Joel Montes Camarena s/n, Ap. postal 811, C. P. 82040, Mazatlán, Sinaloa, Mexico; e-mail: samuel@ola.icmyl.unam.mx*

‡*Louisiana State University, Department of Biological Sciences, 508 Life Sciences Building, Baton Rouge, LA 70803-1715, USA*

§*Centro de Investigación Científica y de Educación Superior de Ensenada, Km 107 Carretera Tijuana-Ensenada, A.P. 2732, Ensenada, Baja California CP 22860, Mexico*

(Accepted 17 April 2003)

In 1897, Richard presented a brief and incomplete description of *Mesochra* (= *Cletocamptus*) *deitersi* from a site in the Naposta Grande River in Argentina. Since Richard's description, *C. deitersi* has been reported from inland brines as well as coastal estuaries and mangroves from North, Central and South America, India, China, Ethiopia, Hawaii, Australia, Iran and Malaysia. However, there is ample evidence to support the hypothesis that all these records belong to new and as yet undescribed species. Erroneous identification of specimens attributed to *C. deitersi* has been due to a high degree of polymorphism within and between populations, to the incompleteness of Richard's original description, and to the fact that Richard did not archive material for future comparisons. Recently, the existence of four extremely differentiated molecular lineages in specimens of *Cletocamptus* collected from the Salton Sea (California, USA), Jackson (Alabama, USA), Port Fourchon (Louisiana, USA) and Mazatlan (Sinaloa, Mexico), all previously identified with *C. deitersi*, was observed. Morphological differences among these populations are subtle but congruent with the patterns of genetic differentiation, suggesting, in fact, that each of these lineages belongs to different species.

KEYWORDS: Copepoda, Harpacticoida, *Cletocamptus*, taxonomy, USA, Mexico.

Introduction

In 1897 Richard described *Mesochra* (= *Cletocamptus*) *deitersi* from the Naposta Grande River, presumably close to the city of the same name (Naposta, Argentina). Unfortunately, Richard did not give any other indication regarding the

exact location of the type locality. More unfortunate is the fact that he did not archive material of his *C. deitersi*. Since Richard's description, *C. deitersi* has been reported from inland brines as well as coastal estuaries and mangroves from several sites in North, Central and South America as well as in India, China, Ethiopia, Hawaii, Australia, Iran and Malaysia.

Of the 13 valid species of *Cletocamptus* (*C. retrogressus* Schmankeiwitsch, 1875, *C. confluens* (Schmeil, 1894), *C. albuquerquensis* (Herrick, 1894), *C. deitersi* (Richard, 1897), *C. kummleri* (Delachaux, 1917), *C. trichotus* (Kiefer, 1929), *C. feei* (Shen, 1956), *C. affinis* Kiefer, 1957, *C. gravihiatus* (Shen and Sung, 1963), *C. helobius* Fleegeer, 1980, *C. merbokensis* Gee, 1999, *C. axi* Mielke, 2000, *C. schmidti* (Mielke, 2000), *C. deitersi* seems to be the most problematic due to its high degree of polymorphism within and between populations. This situation was briefly analysed by Fleegeer (1980; see also Lang, 1948; Löffler, 1963; Yeatman, 1963).

Several authors (e.g. Dexter, 1995; Suárez-Morales *et al.*, 1996; Gee, 1999; Mielke, 2000, 2001) have previously suggested that *C. deitersi* consists of a number of morphologically indistinguishable sibling species, and recent evidence (personal observations by S.G.; Rocha-Olivares *et al.*, 2001; Castro-Longoria *et al.*, 2003), strongly supports the hypothesis that all these records are not of *C. deitersi* but of new and as yet undescribed species. Rocha-Olivares *et al.* (2001) observed four extremely differentiated molecular lineages in specimens collected from the Salton Sea (California, USA), Jackson (Alabama, USA), Port Fourchon (Louisiana, USA) and Mazatlan (Sinaloa, Mexico), and suggested that each of these lineages corresponds to a different species. The findings by Rocha-Olivares *et al.* (2001) instigated the morphological analysis of the known populations of *Cletocamptus* previously identified with the Argentinean *C. deitersi*. This contribution is the first of a series of papers towards the revision of the known records of *C. deitersi* worldwide.

Material and methods

Specimens used in this study were collected by S. Gómez (see Gómez Noguera and Hendrickx, 1997), A. Puello (CIAD-Mazatlan, unpublished data) and Rocha-Olivares *et al.* (2001). Briefly, sediment samples were collected at an inland brine seep in Jackson (Alabama, June 1998) and at Port Fourchon (Louisiana, December 1998). Specimens were also obtained from laboratory cultures established from collections made in the Salton Sea (California) (see Dexter, 1995), and from the mouth of El Yugo estuary in Mazatlán, Sinaloa (north-western Mexico, January 2000). Sediment samples were sieved through 500 and 63 μm sieves and fixed in 95% ethanol for molecular analyses (for more details see Rocha-Olivares *et al.*, 2001). 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 was considered as intraspecific variability. Observations and drawings were made using a Leica compound microscope equipped with drawing tube at magnifications of 1000 \times . Additional observations were made also at 1250 \times . The type material has been deposited in the National Museum of Natural History (Smithsonian Institution) (USNM) and in the collection of the Mazatlán Marine Station of the Institute of Marine Sciences and Limnology (EMUCOP). The terminology proposed by Huys and Boxshall (1991)

for morphological descriptions was adopted. The following abbreviations are used in the text and tables: P1–P6, first to sixth swimming legs; EXP, exopod; ENP, endopod.

Taxonomical account

Family CANTHOCAMPTIDAE Sars, 1906 (*incertae sedis*) *sensu* Por, 1986

Genus *Cletocamptus* Schmankeiwitsch, 1875

Cletocamptus deborahdexterae sp. nov.

(figures 1–13)

Cletocamptus deitersi (Richard, 1897) *sensu* Dexter (1995), Simpson *et al.* (1998).

Cletocamptus deitersi type IIC *sensu* Rocha-Olivares *et al.* (2001).

Cletocamptus from Salton Sea, California *sensu* Castro-Longoria *et al.* (2003).

Type material

One female holotype (USNM 1010499) and one male allotype (USNM 1010500) preserved in alcohol, 10 dissected female (EMUCOP-0799-08, EMUCOP-0799-09, EMUCOP-0799-10, EMUCOP-0799-11, EMUCOP-0799-12, EMUCOP-0799-13, EMUCOP-0799-14, EMUCOP-0799-15, EMUCOP-0799-16, EMUCOP-0799-17) and five dissected male (EMUCOP-0799-03, EMUCOP-0799-04, EMUCOP-0799-05, EMUCO-0799-06, EMUCOP-0799-07) paratypes, six female and three male paratypes (USNM 1010501) and six female (EMUCOP-0799-01) and two male (EMUCOP-0799-02) paratypes preserved in alcohol. July 1997; coll. A. Rocha-Olivares, J. W. Fleeger and D. Foltz.

Type locality

Salton Sea, California (33°13'N, 115°52'W).

Etymology

The species was named in honour of Dr Deborah Dexter (San Diego State University, Department of Biology), who provided us with *Cletocamptus* specimens from the Salton Sea (California).

Description

Female. Habitus (figure 1) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 540 to 715 μm (mean, 605 μm , $N=12$; holotype, 620 μm). Rostrum set off, triangular, with pair of setules subapically. Cephalic shield ornamented with fine and long spinules along margin dorsolaterally (figure 1A, B). Dorsal and lateral surface of free thoracic somites (P2–P4 bearing somites) ornamented with transverse rows of minute spinules, with longitudinal row of small spinules close to posterior margin and with long spinules along posterior margin (figures 1A, B, 2). 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 relatively longer spinules along posterior margin (figures 1A, B, 3). First and second genital somites distinct dorsally and laterally (figure 1A, B), completely fused ventrally (figure 4A); dorsal and lateral surface of first and second genital somite with transverse rows of minute spinules, with row of long spinules along

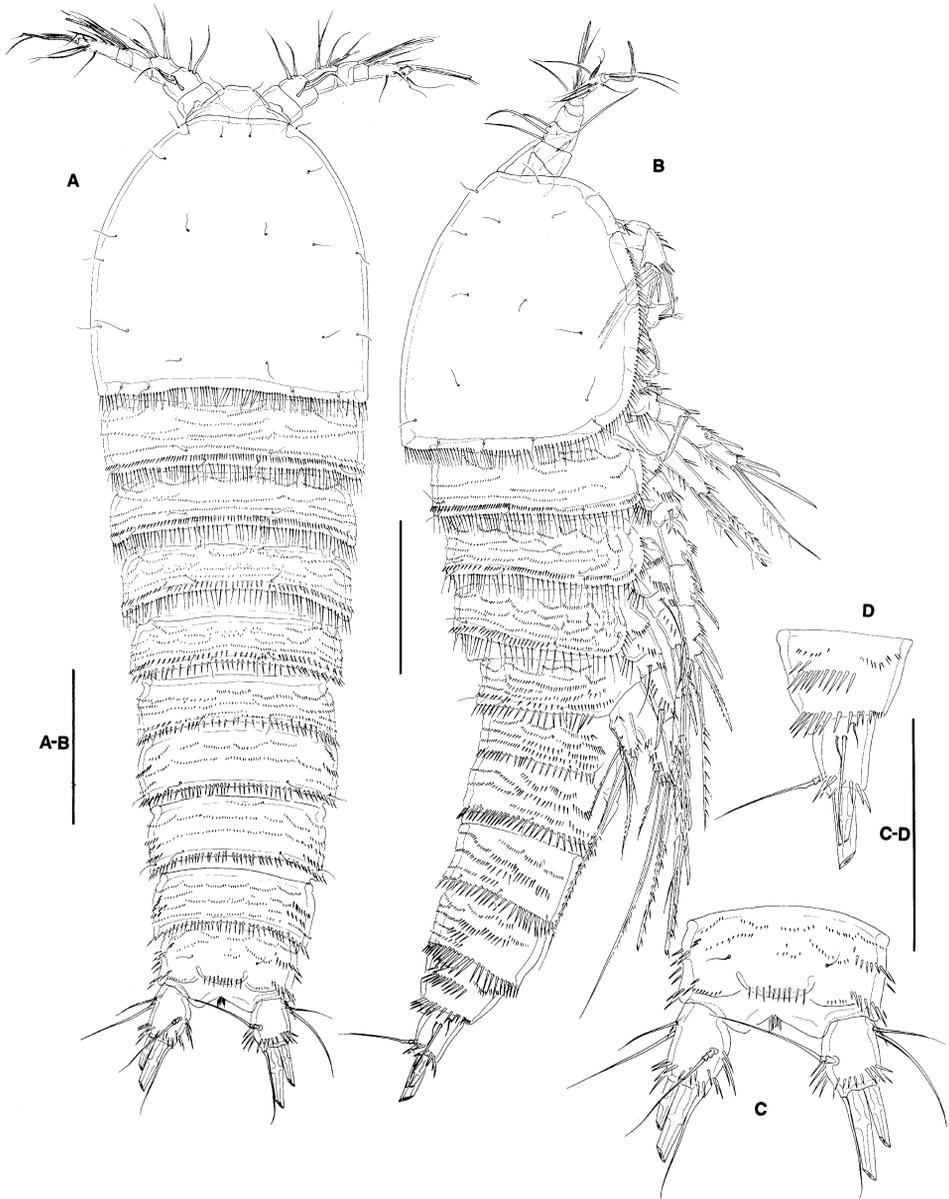


FIG. 1. *Cletocamptus deborahdexteræ* sp. nov., female. (A) Habitus, dorsal; (B) habitus, lateral; (C) anal somite and caudal rami, dorsal; (D) anal somite and right caudal ramus, lateral. Scale bars: 100 μ m.

posterior margin of both somites, and with relatively longer spinules laterally, ventrally ornamented with spinules as shown in figure 4A. Fourth and fifth urosomite as in second genital somite dorsally (figures 1A, B, 3), ventral surface ornamented with transverse rows of spinules as illustrated in figure 4A. Dorsal surface of anal somite (figure 1A, C) ornamented with transverse rows of minute spinules and with dorsolateral strong spinules close to joint with caudal rami; rounded

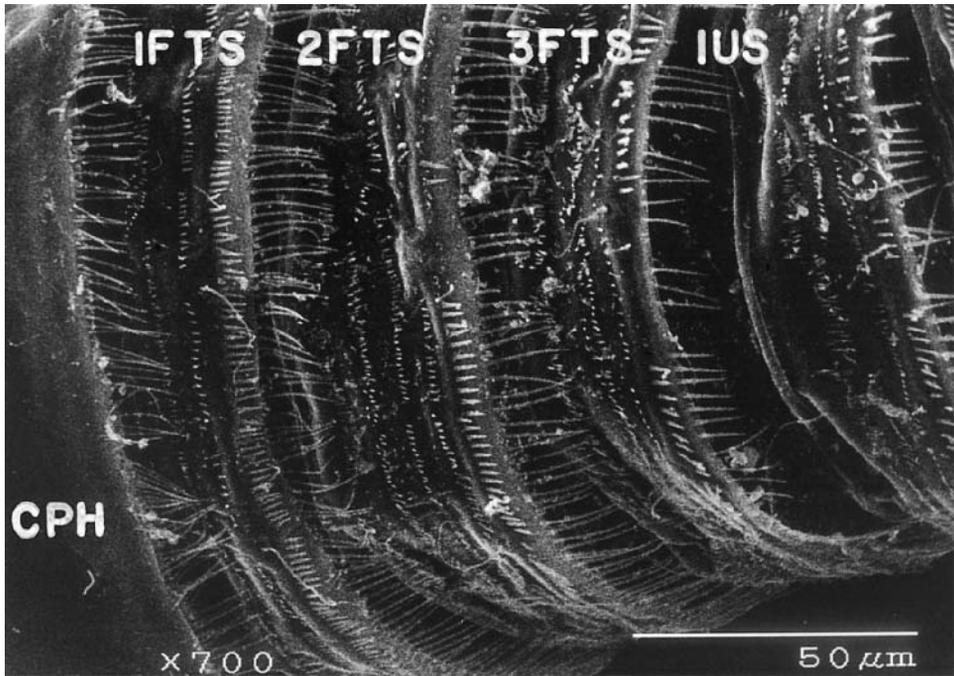


FIG. 2. *Cletocamptus deborahdexteræ* sp. nov., female. SEM microphotograph showing ornamentation along posterior margin of cephalic shield (CPH), dorsal ornamentation and ornamentation along posterior margin of first to third free thoracic somites (1-3FTS) and first urosomite (IUS).

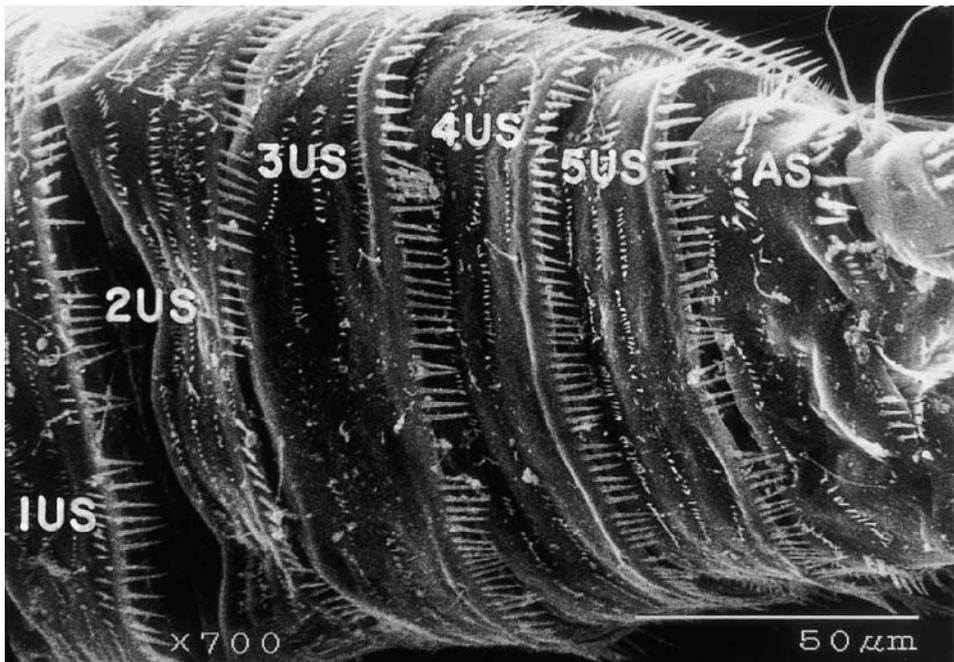


FIG. 3. *Cletocamptus deborahdexteræ* sp. nov., female. SEM microphotograph showing dorsal ornamentation and ornamentation along posterior margin of first to fifth urosomite (1-5US) and anal somite (AS).

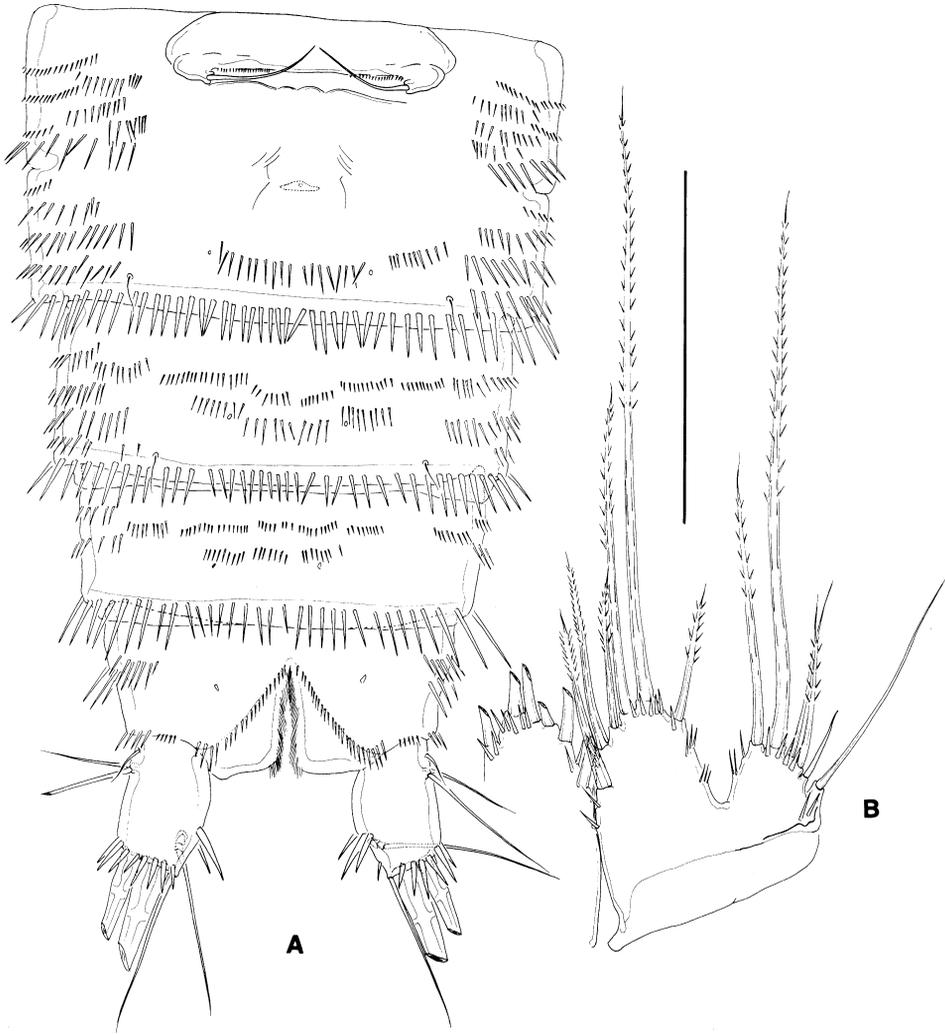


FIG. 4. *Cletocampus deborahdexterae* sp. nov., female. (A) Urosome, ventral (P5 bearing somite omitted); (B) P5. Scale bar: 100 μm .

anal operculum furnished with spinules close to posterior margin (figures 1A, C, 3, 5H); with median row of strong spinules laterally. Caudal rami (figures 1A, B, C, D, 5H, I) about 1.5 times longer than wide; dorsal and ventral surface smooth, except for inner set of spinules close to insertion site of seta VII and close to posterior margin dorsally and ventrally; with seven elements in all.

Antennule (figure 5A) six-segmented; surface of segments smooth except for two rows of spinules on first segment. Armature formula, 1-(1), 2-(8), 3-(5), 4-(1+[1+ae]), 5-(1), 6-(9+[1+ae]).

Antenna (figure 5B) 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 (the latter arrowed in figure 5B), and five distal elements. Exopod (figure 5B, C) one-segmented; about

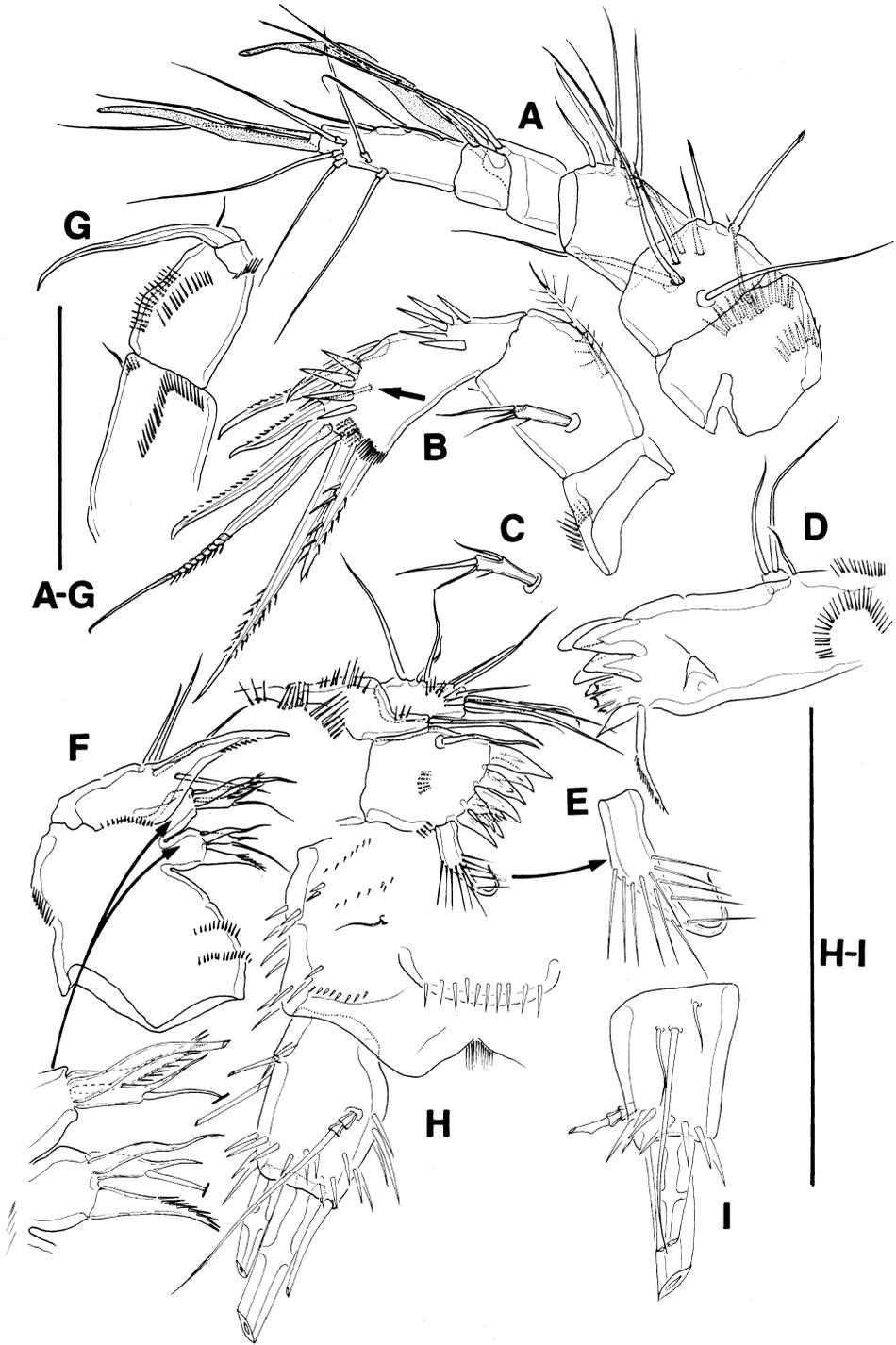


FIG. 5. *Cletocamptus deborahdexteræ* sp. nov., female. (A) Antennule; (B) antenna; (C) antennal exopod, another view; (D) mandible; (E) maxillule; (F) maxilla; (G) maxilliped; (H) anal somite and left caudal ramus; (I) right caudal ramus, lateral. Scale bars: 100 µm.

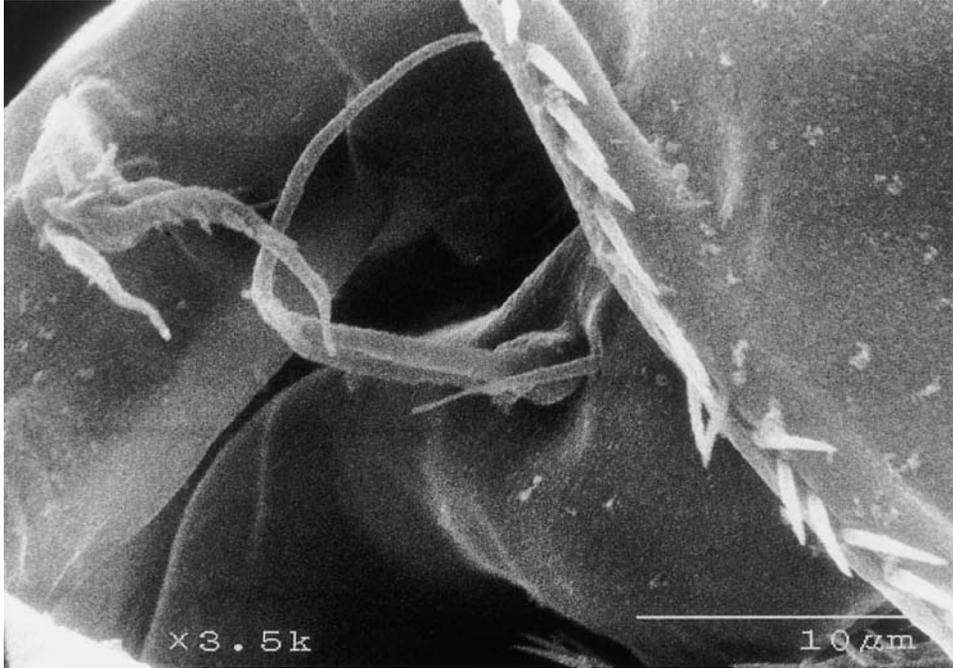


FIG. 6. *Cletocamptus deborahdexterae* sp. nov., female. SEM microphotograph showing mandibular palp with two setae and small seta arising nearby.

seven times longer than wide; ornamented with few spinules, and armed with one lateral and two apical smooth setae.

Mandible (figures 5D, 6) robust, ornamented with rows of spinules proximally; chewing edge with four strong teeth, four elements as in figure 5D, one pyriform element and one lateral pinnate strong seta. Palp (see figure 6) one-segmented, with two long setae unequal in length, with one small seta arising nearby.

Maxillule (figure 5E) robust; arthrite of praecoxa ornamented with few spinules, armed with one surface seta, seven distal spines and one lateral strong seta, the latter ornamented with long spinules (see insert in figure 5E). Coxa ornamented with some spinules and armed with two slender setae. Basis ornamented with some median spinules, and armed with three apical setae; exopod and endopod represented by three setae each.

Maxilla (figure 5F): syncoxa ornamented with minute spinules along inner and outer margin, and close to joint with allobasis; with two endites, each bearing three setae (see insert in figure 5F). Allobasis drawn into strong claw bearing one accompanying seta. Endopod represented by three setae.

Maxilliped (figure 5G) subchelate. Syncoxa ornamented with two rows of spinules and armed with a small seta on inner distal corner. Basis without armature and ornamented with one anterior and one posterior row of spinules, and with few spinules close to joint with endopod. The latter drawn into long and slender claw with one accompanying small seta.

P1 (figure 7A): praecoxa ornamented with spinules close to joint with coxa. The latter ornamented with anterior transverse rows of spinules, and with posterior long

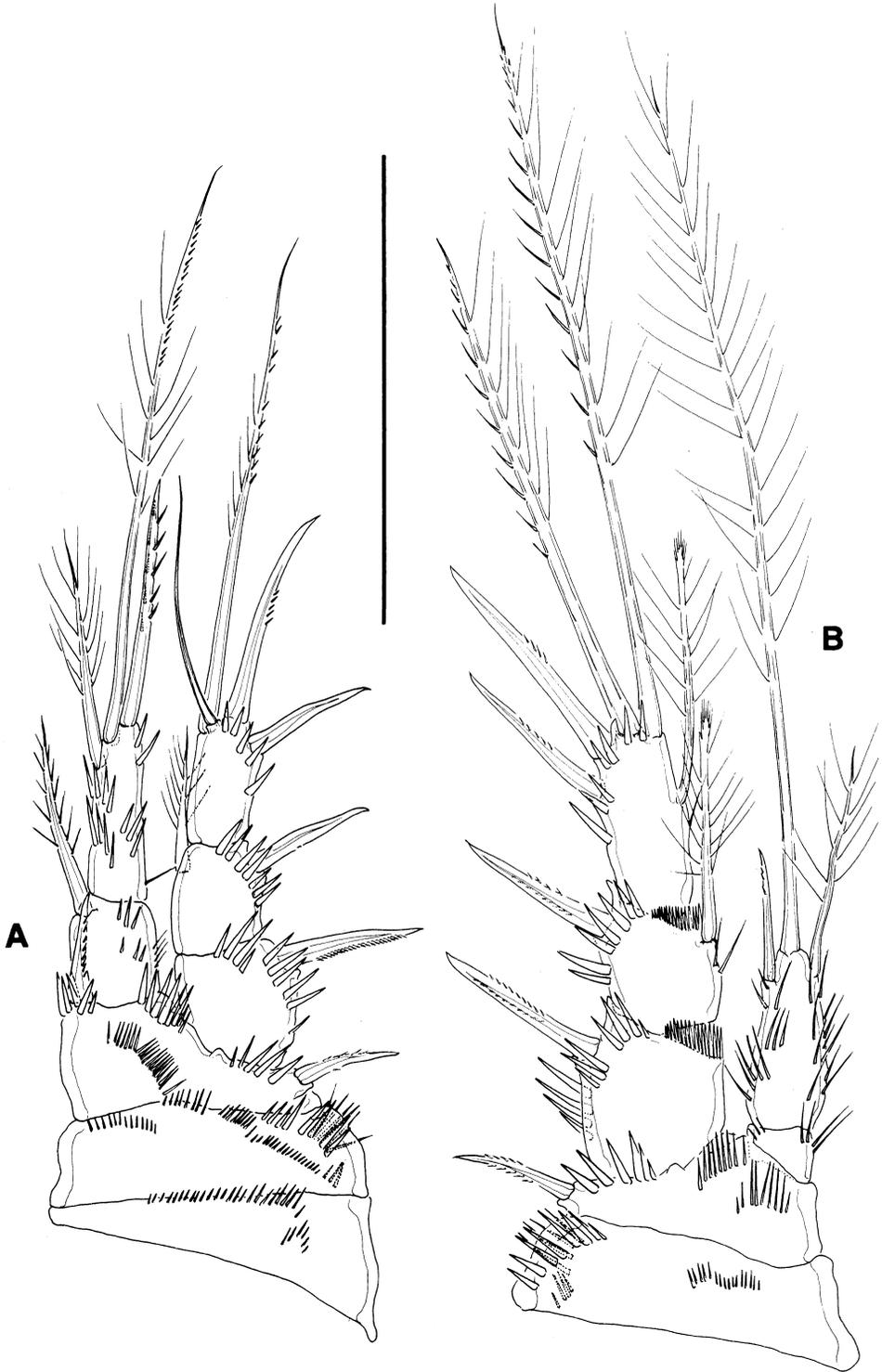


FIG. 7. *Cletocamptus deborahdexteræ* sp. nov., female. (A) P1; (B) P2. Scale bar: 100 μ m.

Table 1. Armature formula of the females of *C. deborahdexteræ* sp. nov., *C. stimpsoni* sp. nov., *C. sinaloensis* sp. nov. and *C. fourchensis* sp. nov.

	P1		P2		P3		P4	
	EXP	ENP	EXP	ENP	EXP	ENP	EXP	ENP
<i>C. deborahdexteræ</i> sp. nov.	I-0;I-1;I;II,1	0-1;0,II,1	I-0;I-1;II,2,1	0-0;I,1,1	I-0;I-1;II,2,1	0-0;I,1,1	I-0;I-1;II,2,0	0-0;0,2,0
<i>C. stimpsoni</i> sp. nov.	I-0;I-1;I;II,1	0-1;0,II,1	I-0;I-1;II,2,1	0-0;I,1,1	I-0;I-1;II,2,2	0-0;1,1,3	I-0;I-1;II,2,1	0-0;0,2,0
<i>C. sinaloensis</i> sp. nov.	I-0;I-1;I;II,1	0-1;0,II,1	I-0;I-1;II,2,1	0-0;I,1,1	I-0;I-1;II,2,1	0-0;I,1,1	I-0;I-1;II,2,0	0-0;0,2,0
<i>C. fourchensis</i> sp. nov.	I-0;I-1;I;II,1	0-1;0,II,1	I-0;I-1;II,2,1	0-0;I,1,1	I-0;I-1;II,2,1	0-0;I,1,1	I-0;I-1;II,2,0	0-0;0,2,0



FIG. 8. *Cletocamptus deborahdexteræ* sp. nov., female. (A) P3; (B) P4. Scale bar: 100 μ m.

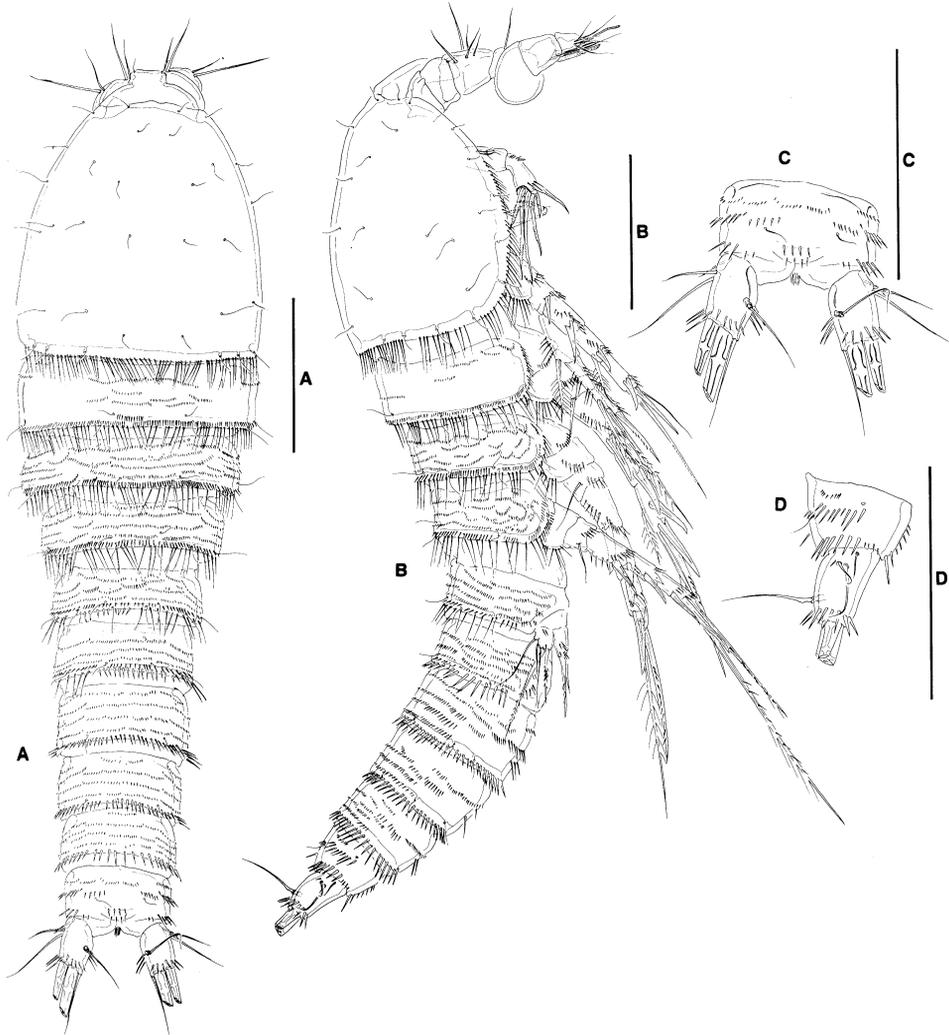


FIG. 9. *Cletocamptus deborahdexterae* sp. nov., male. (A) Habitus, dorsal; (B) habitus, lateral; (C) anal segment and caudal rami, dorsal; (D) anal segment and right caudal ramus, lateral. Scale bars: 100 μ m.

and slender spinules in outer distal corner. Basis ornamented with median row of spinules, and with stronger spinules at base of exopod, between rami and at base of inner spine of basis. Exopod three-segmented. Endopod two-segmented, nearly as long as exopod. Armature formula as in table 1.

P2 (figure 7B): coxa ornamented with median row of small spinules and with strong spinules close to outer distal corner anteriorly, and with some spinules close to outer distal corner posteriorly. Basis ornamented with spinules between rami and at base of endopod, and with stronger spinules at base of exopod; outer element spine-like. Exopod three-segmented and ornamented as in figure 7B. Endopod two-segmented, reaching about the middle of second exopodal segment; first segment

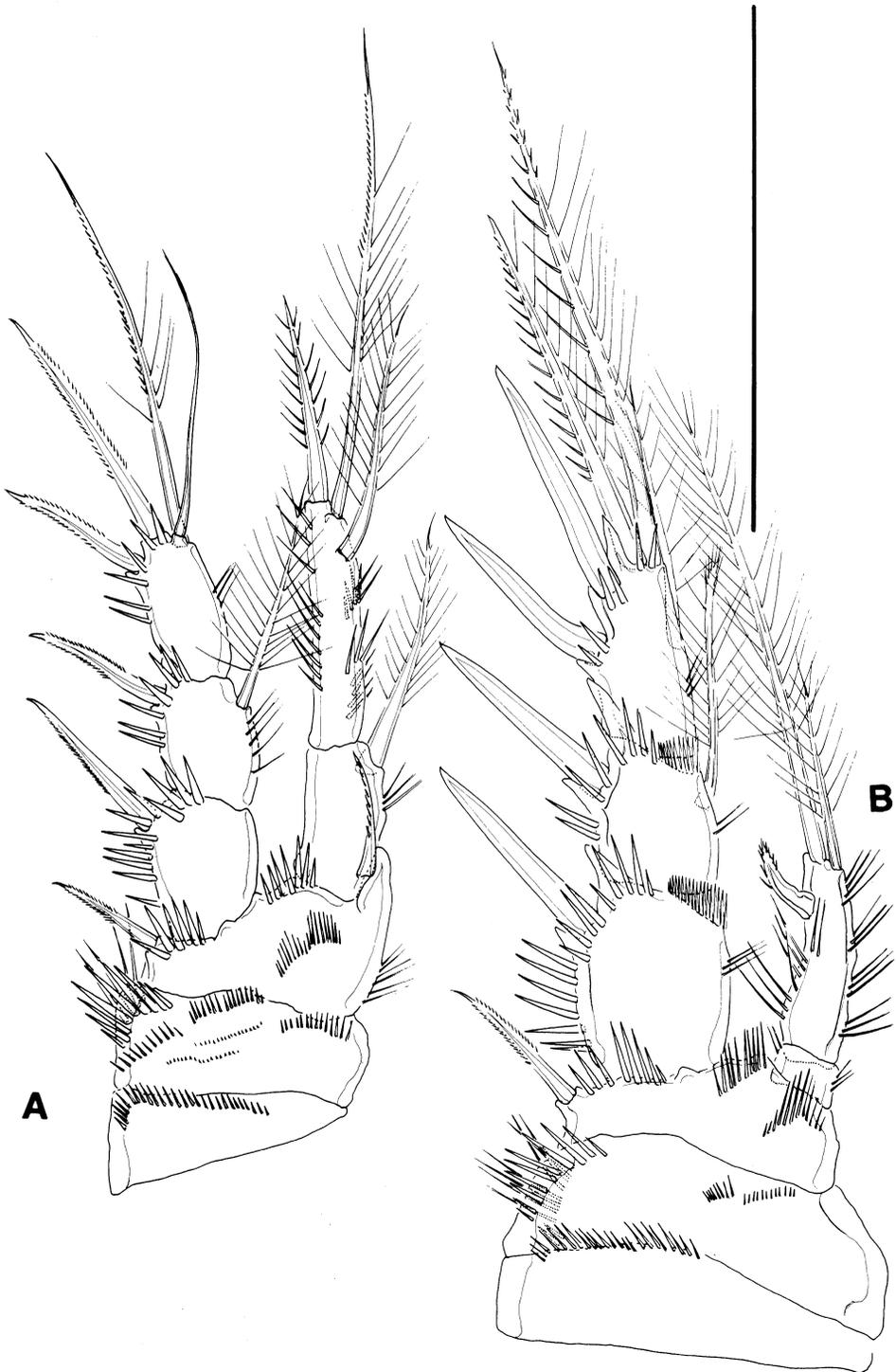


FIG. 10. *Cletocamptus deborahdexterae* sp. nov., male. (A) P1; (B) P2. Scale bar: 100 μ m.

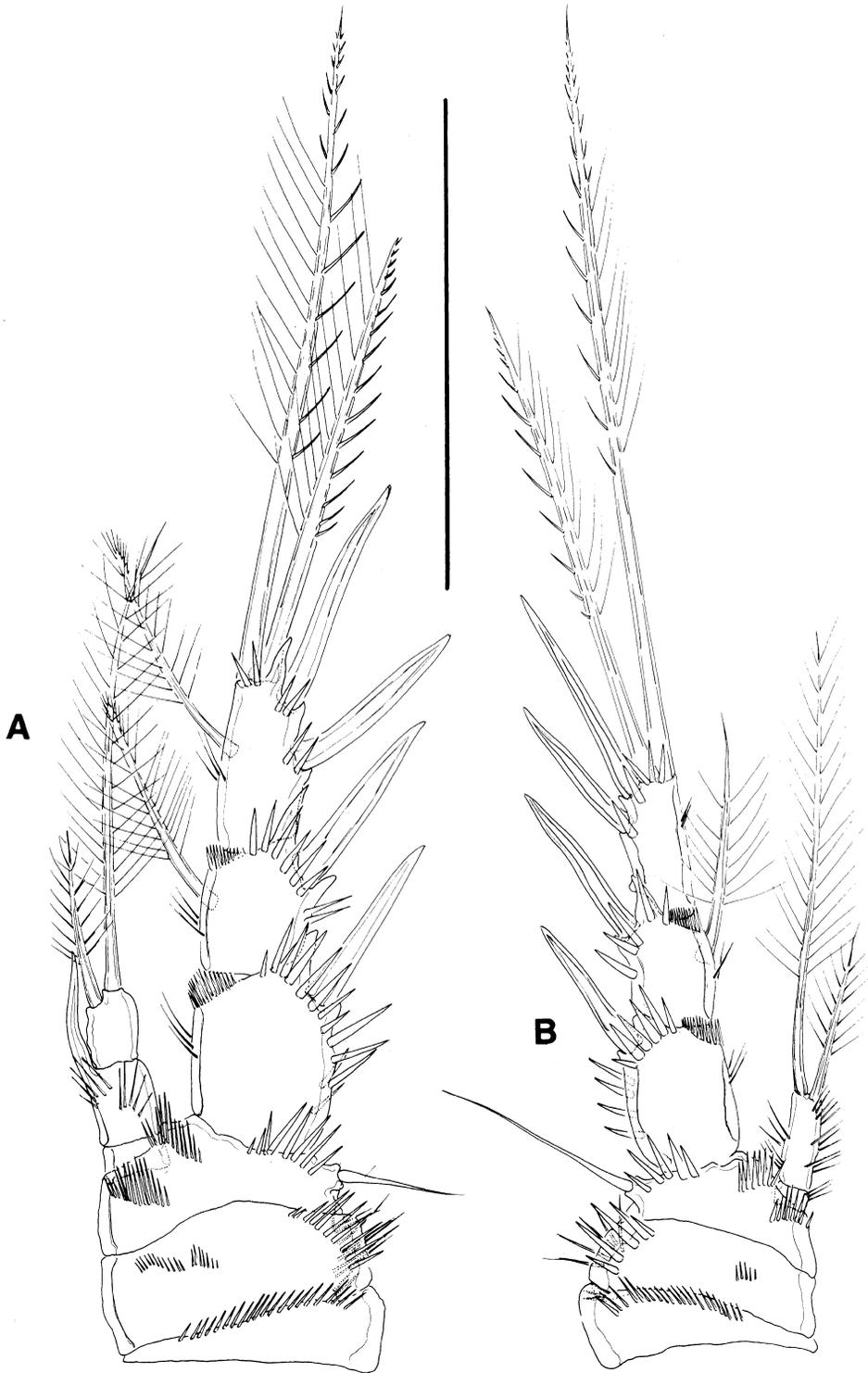


FIG. 11. *Cletocampus deborahdexteræ* sp. nov., male. (A) P3; (B) P4. Scale bar: 100 μ m.

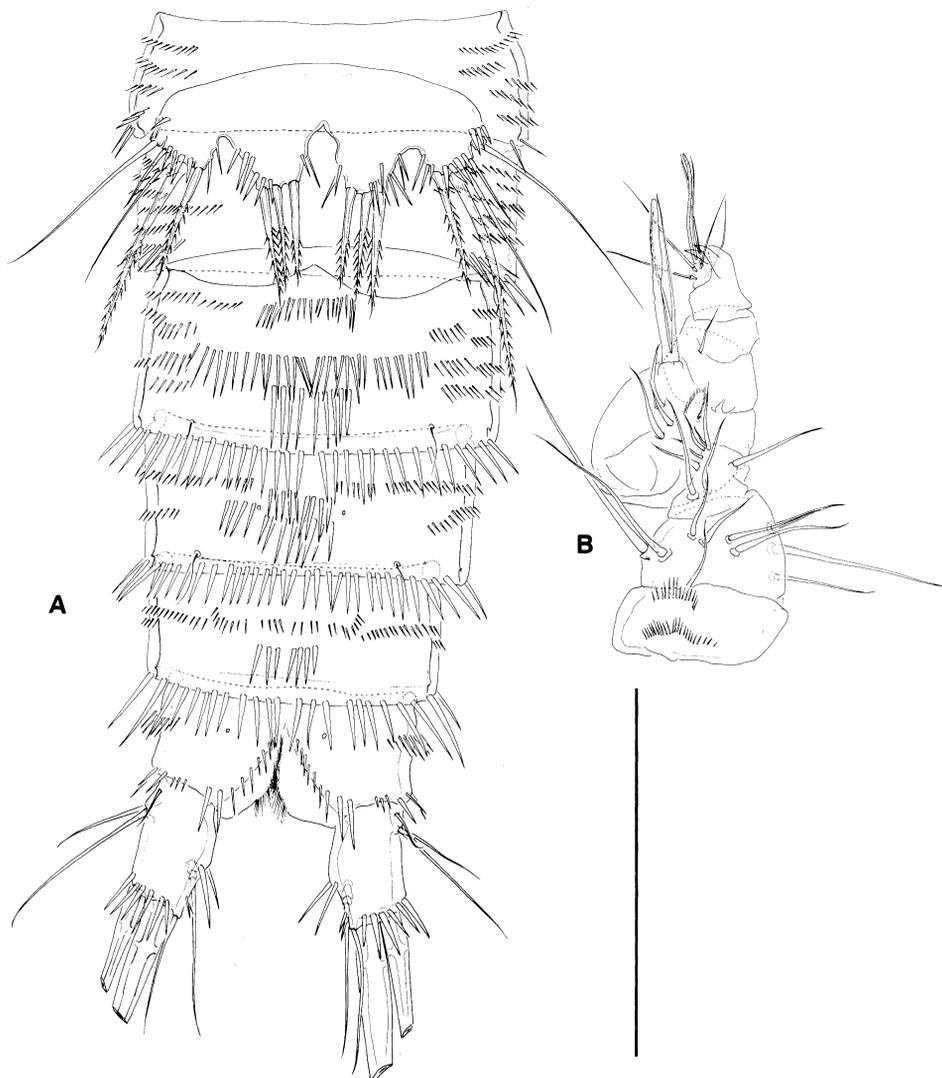


FIG. 12. *Cletocamptus deborahdexterae* sp. nov., male. (A) Urosome, ventral; (B) antennule. Scale bar: 100 μ m.

small, slightly wider than long and ornamented with outer and inner spinules; second segment ornamented with long spinules as shown in figure 7B, and armed with one inner spine, one apical and one inner seta. Armature formula as in table 1.

P3 (figure 8A): praecoxa ornamented with transverse row of spinules close to joint with coxa. The latter as in P2. Basis as in P2 except for seta-like outer element. Exopod as in P2. Endopod as in P2 except for comparatively shorter second segment. Armature formula as in table 1.

P4 (figure 8B): praecoxa, coxa and basis as in P3. Exopod as in P3, except for armature formula of third segment (without inner seta). Endopod two-segmented, barely reaching tip of first exopodal segment; first segment small, slightly wider



FIG. 13. *Cletocamptus deborahdexteræ* sp. nov., male. SEM microphotograph showing two distal teeth on last segment of male antennule.

than long; second segment ornamented with inner and outer slender spinules and armed with two apical setae.

P5 (figure 4B): exopod and baseoendopod fused. Baseoendopodal lobe longer than exopod, ornamented with sets of inner spinules, with spinules at base of apical seta and with some outer spinules; armed with one outer, one apical and four inner setae; relative length of setae as in figure 4B. Exopod ornamented with spinules as shown in figure 4B, and armed with five setae in all, plus outer seta of basis.

P6 (figure 4A) represented by median plate in anterior half of first genital somite, each vestigial leg represented by a long and slender seta. Copulatory pore in the middle of genital double segment.

Male. Total body length measured from tip of rostrum to posterior margin of caudal rami, ranging from 515 to 650 μm (mean, 562.8 μm , $N=9$; allotype, 605 μm). Habitus (figure 9A, B), anal segment and caudal rami (figure 9C, D) as in female dorsally, except for genital somite and for two rows of spinules on anal operculum. Ventral ornamentation of third, fourth and fifth urosomites (figure 12A) coarser than in female.

Antennule (figures 12B, 13) six-segmented; subchirocer. Last segment with two acute teeth (figure 13).

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

P1 (figure 10A) as in female except for dimorphic projection on inner distal corner of basis.

P2 (figure 10B) as in female except for relatively stouter outer spines of male

exopod, dimorphic inner spine on male ENP 2, and relatively shorter apical setae on second endopodal segment.

Exopod of P3 (figure 11A) as in female except for relatively stouter outer spines. Endopod three-segmented; second segment with inner distal apophysis reaching far beyond third endopodal segment; second segment barely reaching tip of first exopodal segment, with one inner and one apical seta relatively shorter than their female homologues.

P4 (figure 11B) as in female, except for stouter outer spines of exopod and relatively shorter setae of second endopodal segment.

Both P5 fused (figure 12A); exopod and baseopod fused. Exopod ornamented with spinules at base of outer seta of basis, at base of apical elements and along inner margin; with four setae. Endopodal lobe ornamented with spinules along outer and inner margin, and at base of apical setae; with three elements in all.

P6 (figure 12A) represented by plate; without armature.

Variability

Male. Paratype (EMUCOP-0799-05) possesses an aberrant right P4.

Female. Paratype (EMUCOP-0799-10) possesses two inner setae on left P3 ENP 2; paratype (EMUCOP-0799-14) possesses two inner setae on left P4 EXP 2, and five setae on right P5 BENP; paratype (EMUCOP-0799-15) possesses one inner seta on right P4 EXP 3, and five setae on right P5 BENP; paratype (EMUCOP-0799-16) possesses an aberrant outer spine on right P1 EXP 3, three setae on left P4 ENP 2, and five setae on both P5 BENP; paratype (EMUCOP-0799-09) possesses five setae on right P5 BENP; paratype (EMUCOP-0799-18) possesses a reduced inner seta on left P5 BENP (see table 2).

Cletocamptus stimpsoni sp. nov. (figures 14–23)

Cletocamptus deitersi (Richard, 1897) *sensu* Fleeger (1980), De Laune *et al.* (1984),

Decho (1986, 1988), Chandler (1986), Chandler and Fleeger (1987), Sun and Fleeger (1994), Pace and Carman (1996), Carman *et al.* (1997, 2000).

Cletocamptus deitersi type I *sensu* Rocha-Olivares *et al.* (2001).

Cletocamptus from Jackson, Alabama *sensu* Castro-Longoria *et al.* (2003).

Type material

One female holotype (USNM 1010502) and one male allotype (USNM 1010503) preserved in alcohol, 12 dissected male (EMUCOP-0698-15, EMUCOP-0698-16, EMUCOP-0698-17, EMUCOP-0698-18, EMUCOP-0698-19, EMUCOP-0698-20, EMUCOP-0698-21, EMUCOP-0698-22, EMUCOP-0698-23, EMUCOP-0698-24, EMUCOP-0698-25, EMUCOP-0698-26) and 12 dissected female paratypes (EMUCOP-0698-03, EMUCOP-0698-04, EMUCOP-0698-05, EMUCOP-0698-06, EMUCOP-0698-07, EMUCOP-0698-08, EMUCOP-0698-09, EMUCOP-0698-10, EMUCOP-0698-11, EMUCOP-0698-12, EMUCOP-0698-13, EMUCOP-0698-14), 20 female and nine male paratypes preserved in alcohol (USNM 1010504), and 13 female (EMUCOP-0698-01) and eight male (EMUCOP-0698-02) paratypes preserved in alcohol. June 1998, coll. A. Rocha-Olivares, J. W. Fleeger and D. Foltz.

Table 2. Intraspecific variability of *C. sinaloensis* sp. nov., *C. fourchensis* sp. nov., *C. stimpsoni* sp. nov. and *C. deborahdexteræ* sp. nov.

	<i>C. sinaloensis</i> sp. nov.		<i>C. fourchensis</i> sp. nov.		<i>C. stimpsoni</i> sp. nov.		<i>C. deborahdexteræ</i> sp. nov.	
	Female (<i>N</i> = 6)	Male (<i>N</i> = 5)	Female (<i>N</i> = 5)	Male (<i>N</i> = 7)	Female (<i>N</i> = 12)	Male (<i>N</i> = 12)	Female (<i>N</i> = 10)	Male (<i>N</i> = 5)
Female P4 EXP 3 with one inner setae	1 (16.7%)						1 (10%)	
Female P1 EXP 3 with five setae/spines	1 (16.7%)							
Male P1 ENP 2 with two setae				1 (14.3%)				
Male P5 BENP with four setae				1 (14.3%)		1 (8.3%)		
Male P5 BENP with two setae				1 (14.3%)				
Male P2 ENP 1 with one inner seta			2 (40%)					
Female P4 ENP 2 with reduced inner seta								
Male P2 ENP 2 with two inner setae						2 (16.7%)		
Female P2 ENP 2 with two inner setae					6 (50%)			
Female P5 EXP with six setae					1 (8.3%)			
Female P1 ENP 1 without inner seta					1 (8.3%)			
Female P3 ENP 2 with two inner setae							1 (10%)	
Female P4 EXP 2 with two inner setae							1 (10%)	
Female P4 ENP 2 with three setae			1 (20%)				4 (40%)	
Female P5 BENP with five setae							1 (10%)	
Female P4 ENP 2 with three setae							1 (10%)	

Intraspecific variability was assessed in dissected organisms only. Only the presence or lack of well-developed and/or reduced setae/spines was considered as intraspecific variability.

N, specimens analysed.

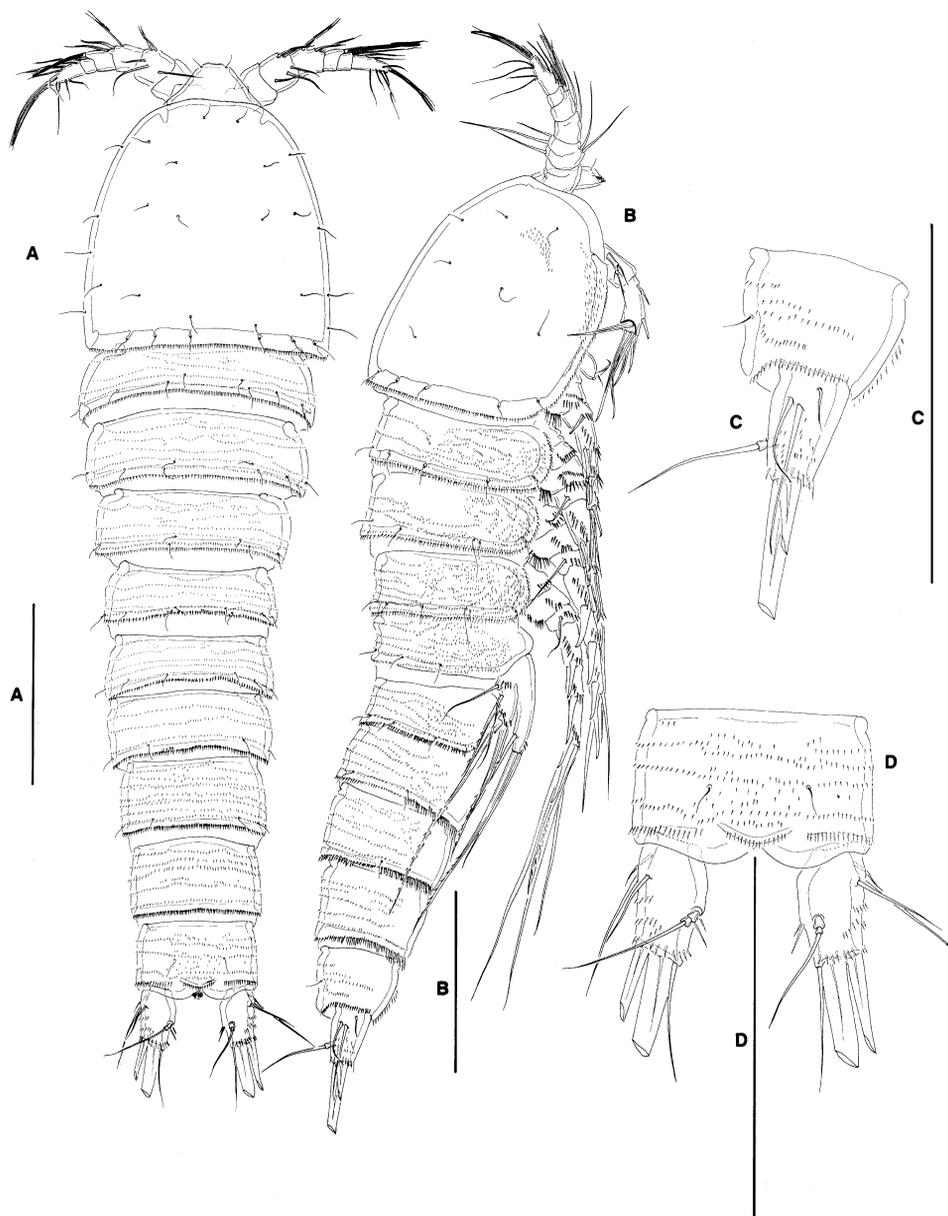


FIG. 14. *Cletocamptus stimpsoni* sp. nov., female. (A) Habitus, dorsal; (B) habitus, lateral; (C) anal somite and right caudal ramus, lateral; (D) anal somite and caudal rami, dorsal. Scale bars: 100 μ m.

Type locality

Brine seep, Fred Stimpson Wildlife Refuge, Jackson, Alabama, USA (31°23'N, 87°53'W).

Etymology

The species was named in honour of the Fred T. Stimpson Wildlife Refuge (Alabama, USA).

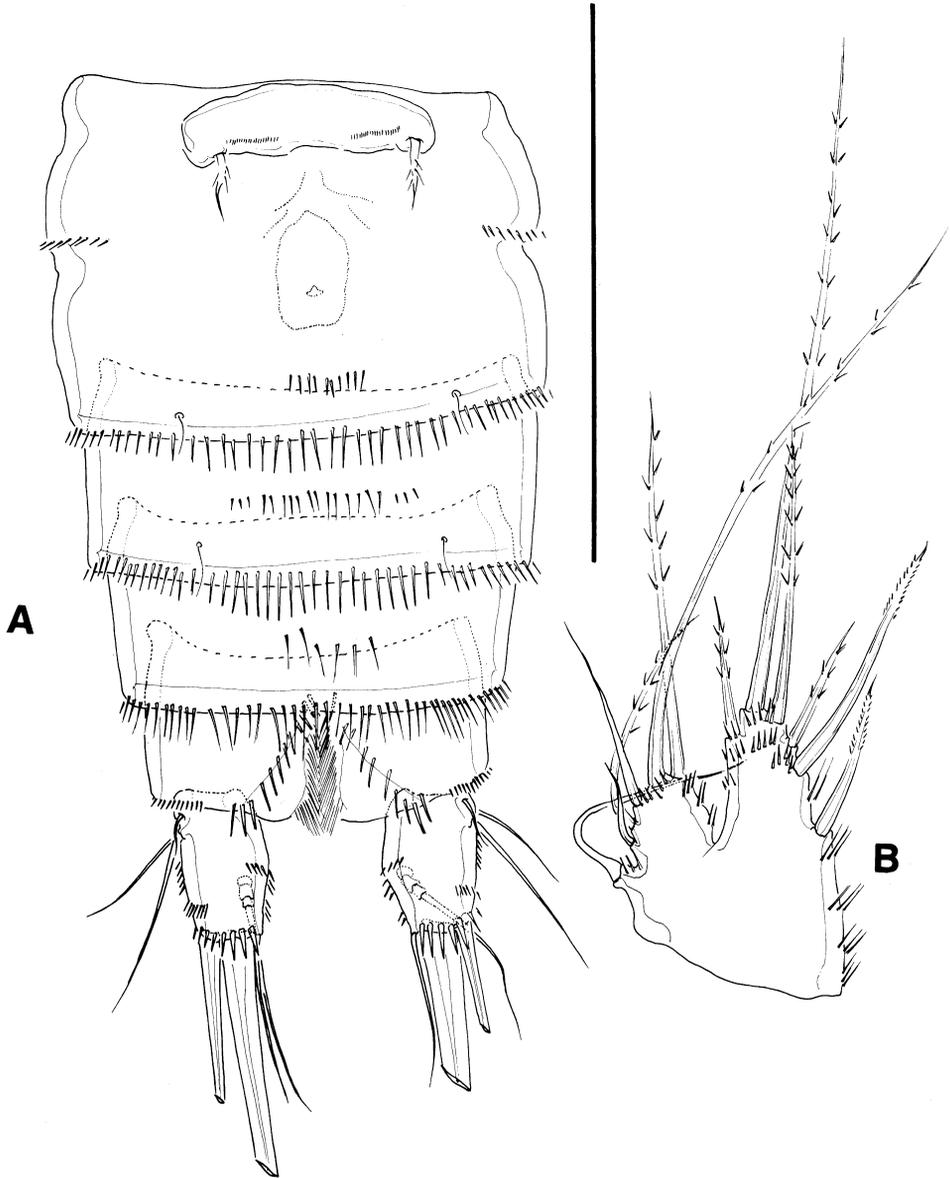


FIG. 15. *Cletocamptus stimpsoni* sp. nov., female. (A) Urosome, ventral (P5 bearing somite omitted); (B) P5. Scale bar: 100 μ m.

Description

Female. Habitus (figure 14) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 415 to 660 μ m (mean, 529 μ m, $N=26$; holotype, 550 μ m). Rostrum set off, triangular, with pair of setules subapically. Cephalic shield ornamented with small spinules along posterior margin dorsolaterally (figure 14A, B). Dorsal and lateral surface of free thoracic somites (P2–P4 bearing somites) ornamented with transverse

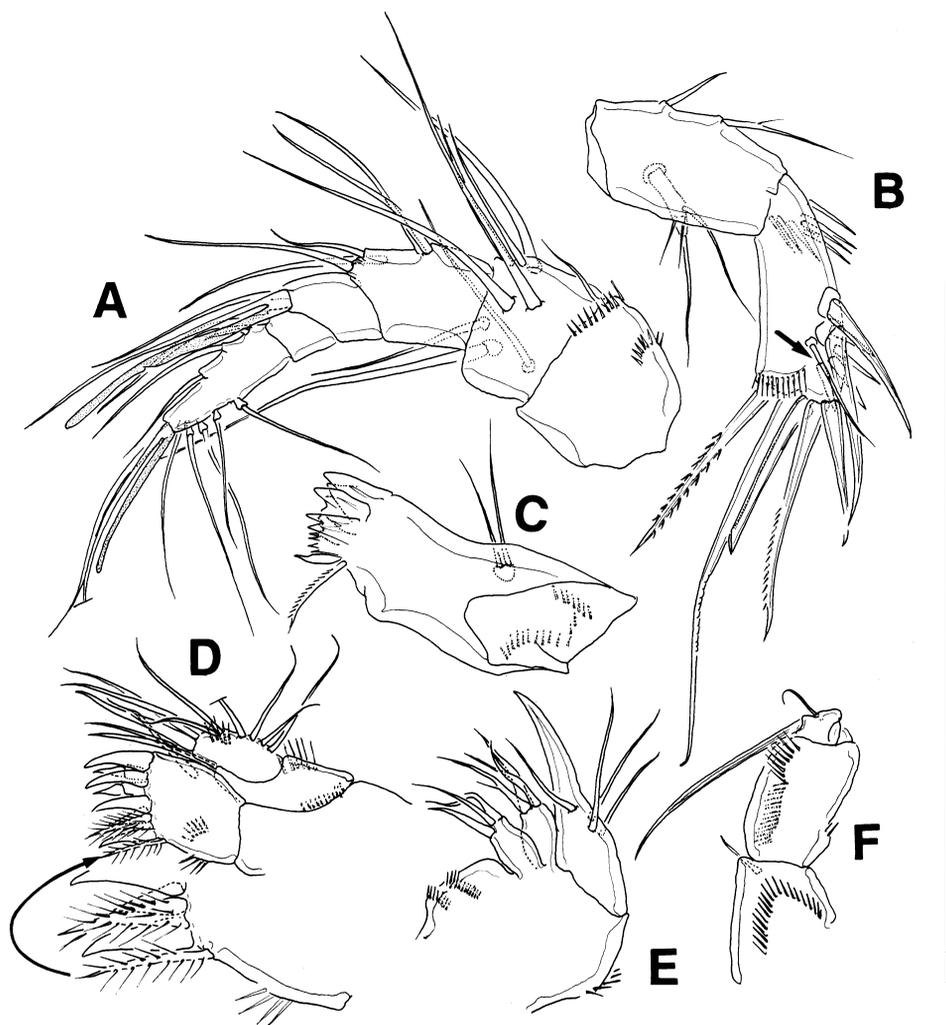


FIG. 16. *Cletocamptus stimpsoni* sp. nov., female. (A) Antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped. Scale bar: 100 μ m.

rows of minute spinules, and with very small spinules along posterior margin. Dorsal and lateral surface of first urosomite (P5 bearing somite) ornamented as preceding somite. First and second genital somites distinct dorsally and laterally, completely fused ventrally (figure 15A); dorsal and lateral surface of first and second genital somite with transverse rows of minute spinules, with row of stronger spinules along posterior margin of both somites, and with relatively longer spinules laterally; ventrally ornamented with spinules as shown in figure 15A. Fourth and fifth urosomite as in second genital somite dorsally, except for more abundant transverse spinular rows; ventral surface ornamented with few median spinules as illustrated in figure 15A, and with longer spinules along posterior margin. Dorsal surface of anal somite (figure 14A) ornamented with transverse rows of minute spinules and with dorsolateral strong spinules close to joint with

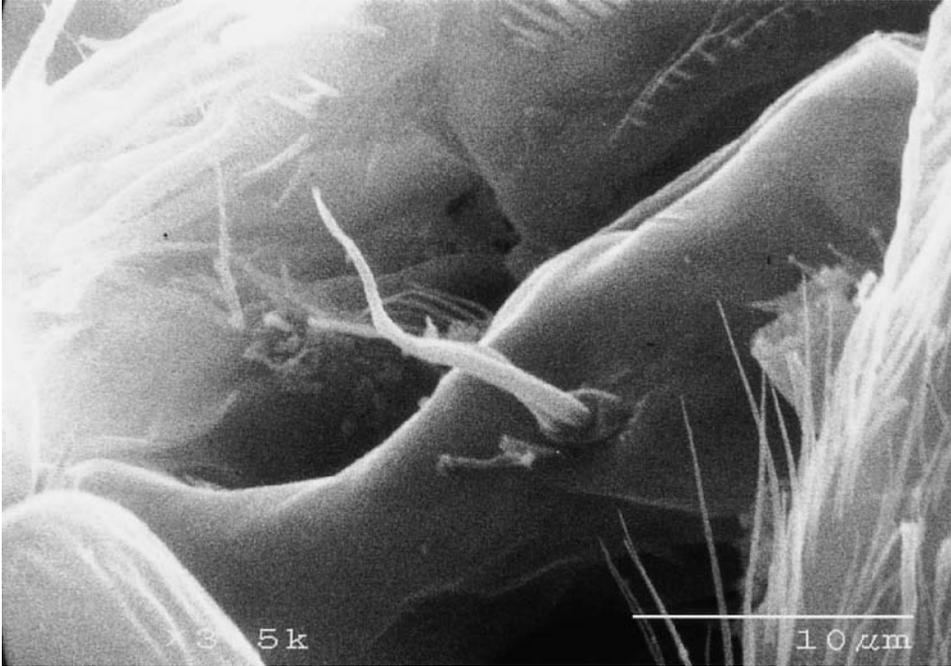


FIG. 17. *Cletocamptus stimpsoni* sp. nov., female. SEM microphotograph showing mandibular palp with two setae only.

caudal rami; rounded anal operculum furnished with small spinules close to posterior margin. Caudal rami (figure 14C, D) about 1.5 times longer than wide; with few spinular rows dorsally and ventrally (figures 14C, D, 15A); with seven elements in all.

Antennule (figure 16A) six-segmented; surface of segments smooth except for two rows of spinules on first segment. Armature formula, 1-(1), 2-(8), 3-(5), 4-(1+[1+ae]), 5-(1), 6-(9+[1+ae]).

Antenna (figure 16B) with allobasis armed with two abexopodal setae. Free endopodal segment ornamented with inner strong spinules proximally and subdistally; with two lateral inner spines and one slender seta (the latter arrowed in figure 16B), and five distal elements. Exopod one-segmented; about seven times longer than wide; ornamented with few spinules and armed with one lateral and one apical smooth seta.

Mandible (figure 16C) robust, ornamented with rows of spinules proximally; chewing edge with four strong teeth, four elements as in figure 16C, one pyriform element and one lateral pinnate strong seta. Palp small, one-segmented, with two long setae (see also figure 17).

Maxillule (figure 16D) robust; arthrite of praecoxa ornamented with few spinules, armed with a surface seta, seven distal spines and one lateral slender seta (see insert in figure 16D). Coxa ornamented with some spinules and armed with two slender setae. Basis ornamented with some median spinules, and armed with three apical setae; exopod and endopod represented by three setae each.

Maxilla (figure 16E): syncoxa ornamented with minute spinules along inner and

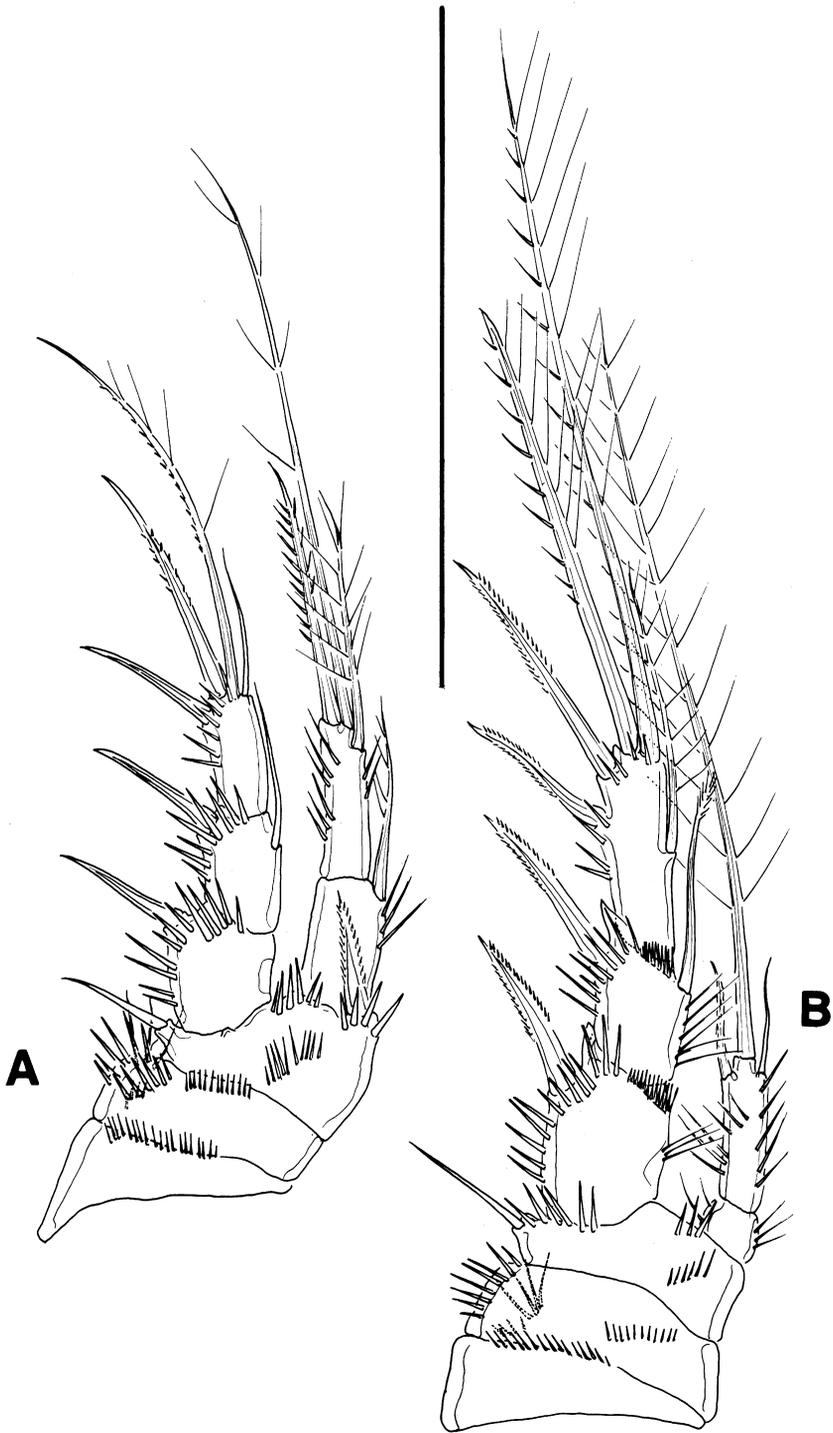


FIG. 18. *Cletocamptus stimpsoni* sp. nov., female. (A) P1; (B) P2. Scale bar: 100 μ m.



FIG. 19. *Cletocamptus stimpsoni* sp. nov., female. (A) P3; (B) P4. Scale bar: 100 μ m.

outer margin; with two endites, each bearing three setae. Allobasis drawn into strong claw bearing an accompanying seta. Endopod represented by three setae.

Maxilliped (figure 16F) subchelate. Syncoxa ornamented with spinules and armed with a small seta on inner distal corner. Basis without armature and ornamented

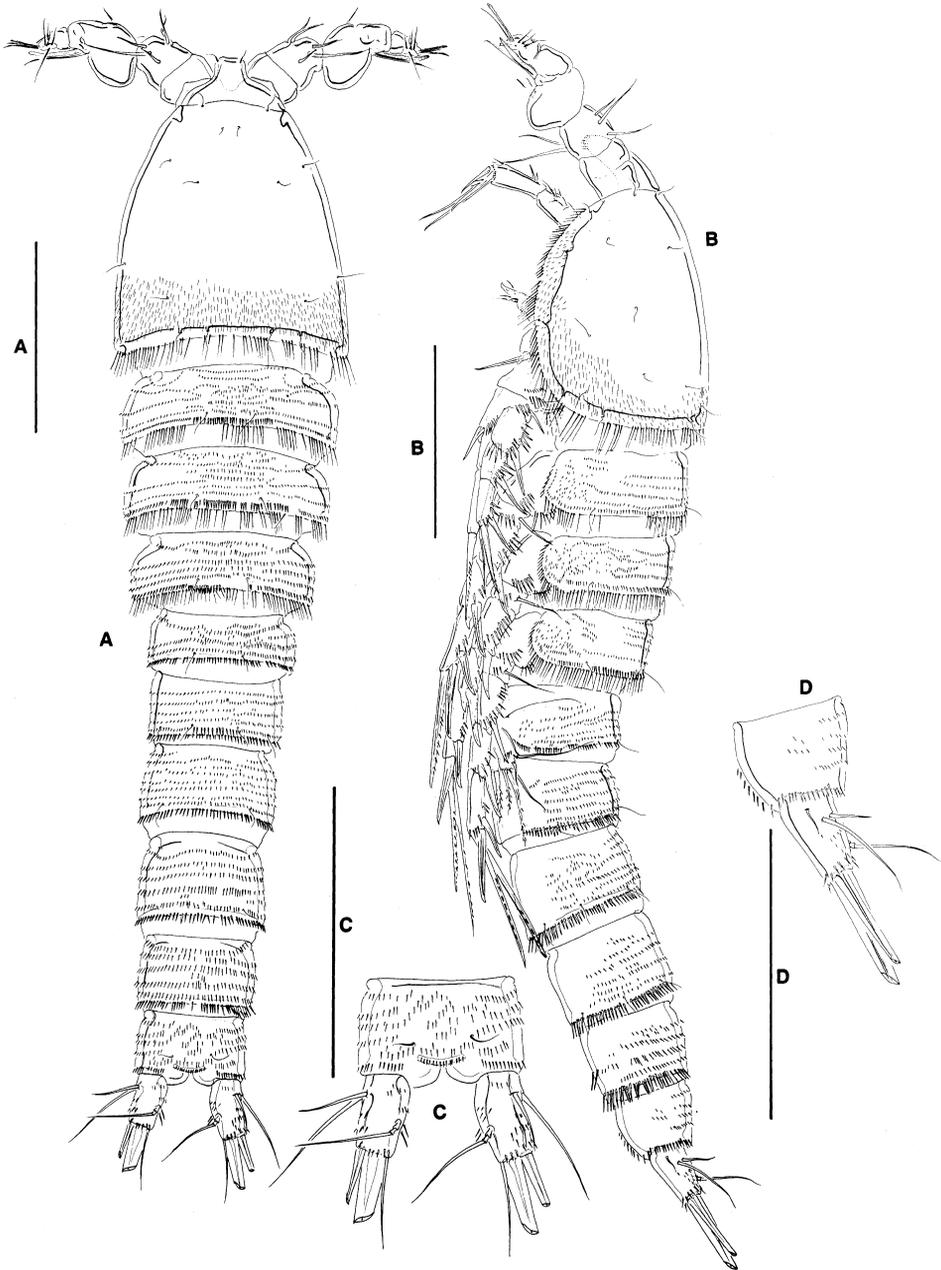


FIG. 20. *Cletocamptus stimpsoni* sp. nov., male. (A) Habitus, dorsal; (B) habitus, lateral; (C) anal somite and caudal rami, dorsal; (D) anal somite and left caudal ramus, lateral. Scale bars: 100 μ m.

with longitudinal spinules anteriorly and posteriorly. Endopod drawn into long and slender claw with one accompanying small seta.

P1 (figure 18A): praecoxa ornamented with spinules close to joint with coxa. The latter ornamented with anterior transverse rows of spinules, and with posterior

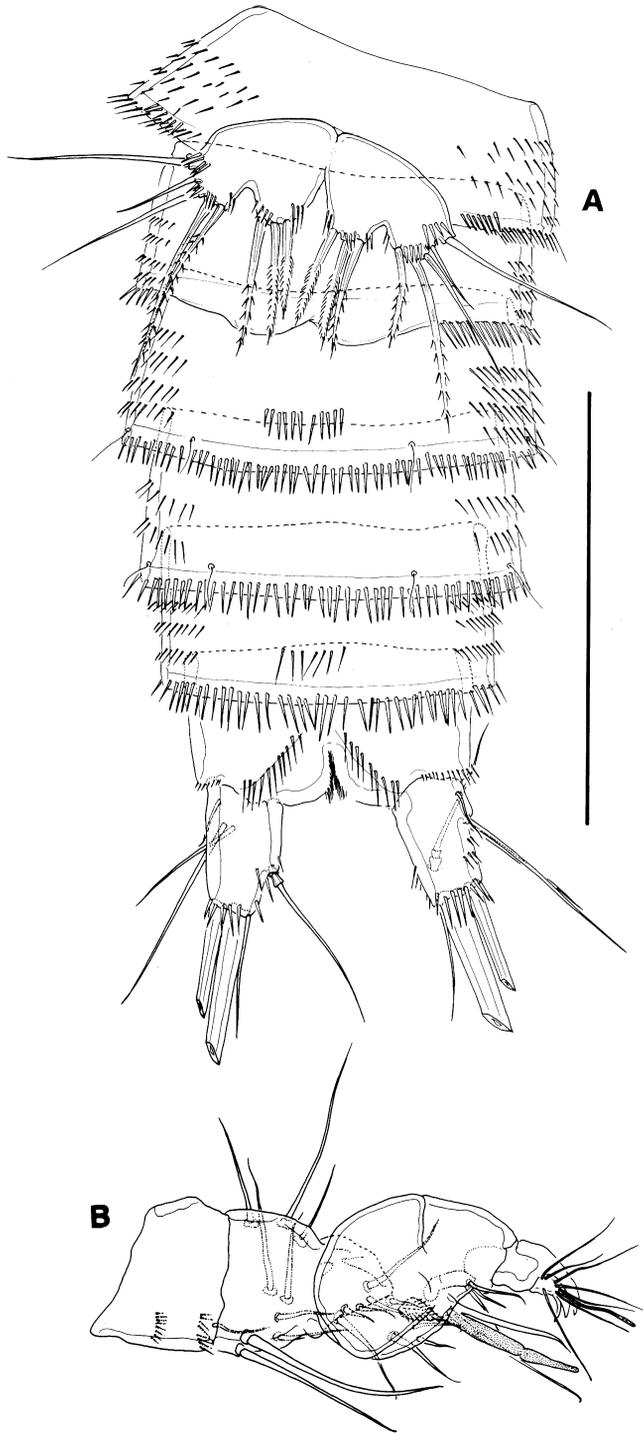


FIG. 21. *Cletocamptus stimpsoni* sp. nov., male. (A) Urosome, ventral; (B) antennule. Scale bar: 100 μ m.

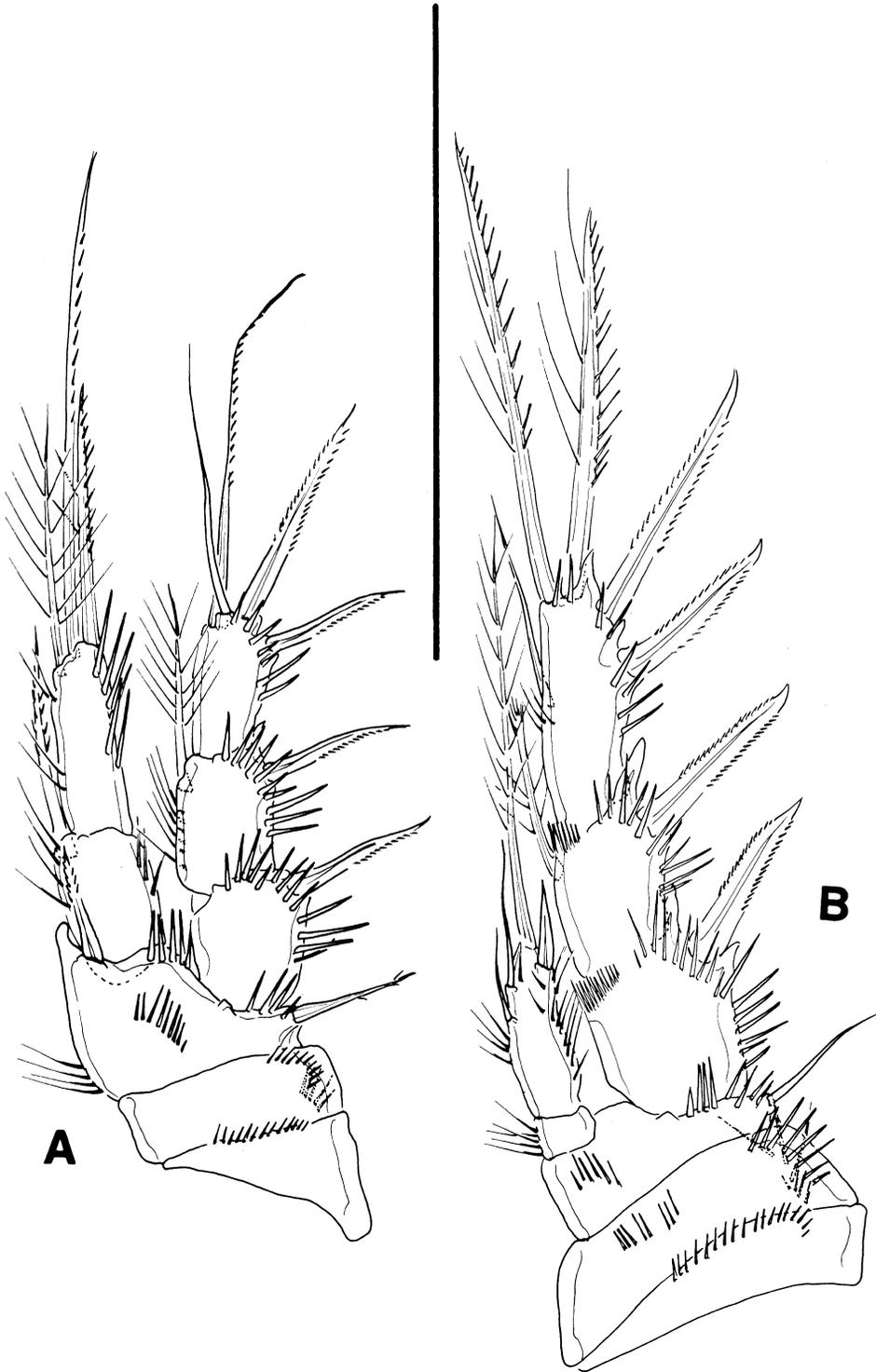


FIG. 22. *Cletocamptus stimpsoni* sp. nov., male. (A) P1; (B) P2. Scale bar: 100 μ m.

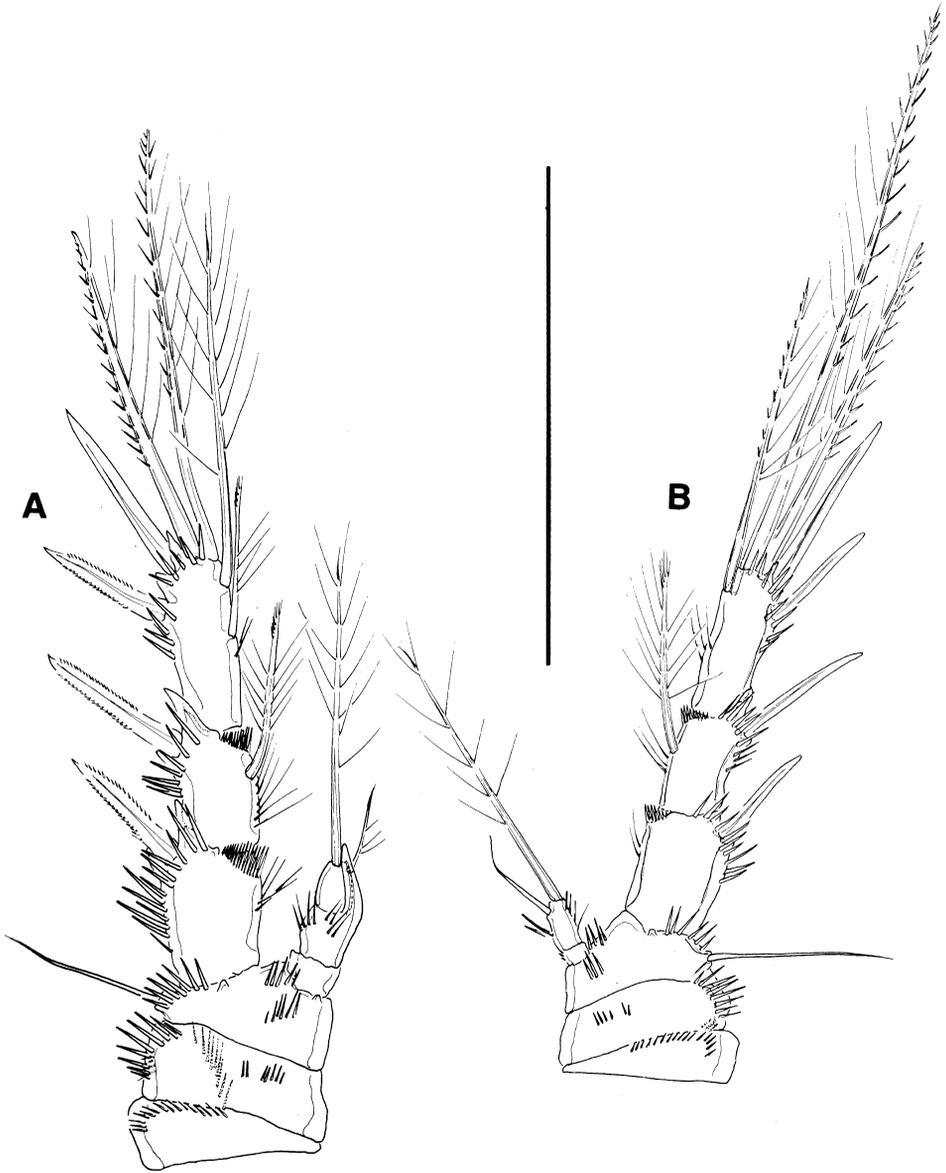


FIG. 23. *Cletocamptus stimpsoni* sp. nov., male. (A) P3; (B) P4. Scale bar: 100 μ m.

long and slender spinules in outer distal corner. Basis ornamented with median row of spinules, and with stronger spinules at base of exopod, between rami and at base of inner spine of basis. Exopod three-segmented. Endopod two-segmented, somewhat shorter than exopod. Armature formula as in table 1.

P2 (figure 18B): praecoxa as in P1. Coxa ornamented with median row of small spinules and with strong spinules close to outer distal corner anteriorly, and with some spinules close to outer distal corner posteriorly. Basis ornamented with median row of spinules close to inner distal corner, and at base of exopod; outer element of basis seta-like. Exopod three-segmented and ornamented as in figure 18B. Endopod

two-segmented, reaching proximal quarter of second exopodal segment; first segment small, about as long as wide and ornamented with outer and inner spinules; second segment ornamented with long spinules as shown in figure 18B, and armed with one inner spine, one apical and one inner seta. Armature formula as in table 1.

P3 (figure 19A): praecoxa ornamented with transverse row of spinules close to joint with coxa. The latter and basis as in P2. Exopod as in P2, except for two inner setae on third segment. Endopod as in P2, armed with three inner, one apical and one outer seta. Armature formula as in table 1.

P4 (figure 19B): praecoxa, coxa and basis as in P3. Exopod as in P3, except for armature formula of third segment. Endopod two-segmented, very small; first segment small, slightly wider than long; second segment ornamented with inner and outer slender spinules and armed with two apical setae.

P5 (figure 15B): exopod and baseoendopod fused. Baseoendopodal lobe longer than exopod, ornamented with sets of inner spinules, and with spinules on distal part of ramus; armed with one outer, one apical and four inner setae; relative length of setae as in figure 15B. Exopod ornamented with spinules as shown in figure 15B, and armed with five setae in all, plus outer seta of basis.

P6 (figure 15A) represented by median plate in anterior half of first genital somite, each vestigial leg represented by a short and thick seta. Copulatory pore in the middle of genital double segment.

Male. Total body length measured from tip of rostrum to posterior margin of caudal rami, ranging from 310 to 540 μm (mean, 406 μm , $N=18$; allotype, 540 μm). Habitus (figure 20A, B), anal segment and caudal rami (figure 20C, D) as in female dorsally, except for longer spinules along posterior margin of cephalic shield and free thoracic somites. Ventrally as in female except for genital somite and median spinules on fourth urosomite.

Antennule (figure 21B) six-segmented; subchirocer. Last segment with two acute teeth.

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

P1 (figure 22A), as in female except for dimorphic projection on inner distal corner of basis.

P2 (figure 22B): praecoxa, coxa, basis and exopod as in female, except for somewhat stouter outer spines of male exopod. Endopod two-segmented; first segment small; second segment reaching about proximal third of second exopodal segment, ornamented with spinules along inner and outer margin, and armed with one outer dimorphic spine, one apical seta and two inner slender setae.

P3 (figure 23A) as in female except for somewhat stouter outer spines of male exopod and for dimorphic three-segmented endopod. First endopodal segment small; second segment with inner distal apophysis reaching slightly beyond third endopodal segment; second segment barely reaching tip of first exopodal segment, with one inner and one apical seta comparatively shorter than their female homologues.

P4 (figure 23B) as in female, except for somewhat stouter outer spines of exopod and relatively shorter setae of second endopodal segment.

Both P5 fused (figure 21A); exopod and baseoendopod fused. Ornamented with spinules at base of outer seta of basis, at base of exopodal and endopodal setae. Exopod with four, endopod with three setae.

P6 (figure 21A) represented by plate; without armature.

Variability

Male. Paratype (EMUCOP-0698-16) was found with an aberrant outer seta of left P2 ENP 2, and right P2 ENP 2 possesses two inner setae; paratype (EMUCOP-0698-20) possesses two setae only on right P5 BENP; paratype (EMUCOP-0698-15) possesses two inner setae on right P2 ENP.

Female. Paratype (EMUCOP-0698-13) was found with inner setae of left P5 BENP closer to adjoining seta than in right ramus; four female paratypes (EMUCOP-0698-10, EMUCOP-0698-12, EMUCOP-0698-03, EMUCOP-0698-06) possess one inner seta on left P2 ENP 2 and two inner setae on right P2 ENP 2; two paratypes (EMUCOP-0698-05, EMUCOP-0698-14) possess one inner seta on right P2 ENP 2 and two setae on left P2 ENP 2; paratype (EMUCOP-0698-07) possesses an aberrant left P1 EXP 3; paratype (EMUCOP-0698-08) possesses six setae on P5 EXP; paratype (EMUCOP-0698-11) lacks inner seta on P1 ENP 1 (see table 2).

Cletocamptus sinaloensis sp. nov.

(figures 24–33)

Cletocamptus deitersi (Richard, 1897) *sensu* Gómez (2001).*Cletocamptus deitersi* type IIM *sensu* Rocha-Olivares *et al.* (2001).*Type material*

One female holotype (EMUCOP-300392-37) preserved in alcohol and one dissected male allotype (EMUCOP-300392-38) from Ensenada del Pabellón lagoon, five dissected female (EMUCOP-300491-42, EMUCOP-030192-69, EMUCOP-300392-39, EMUCOP-300392-40, EMUCOP-300392-41) and four dissected male paratypes (EMUCOP-300392-42, EMUCOP-300392-43, EMUCOP-230691-44, EMUCOP-240691-41) from Ensenada del Pabellón lagoon, and one dissected female paratype (EMUCOP-0100-02) from El Yugo estuary, seven female paratypes (EMUCOP-0100-01) from El Yugo estuary preserved in alcohol, 27 female paratypes (EMUCOP-300491-40) from Ensenada del Pabellón lagoon preserved in alcohol and one male paratype (EMUCOP-300491-41) from Ensenada del Pabellón lagoon preserved in alcohol. April and June 1991 and January and March 1992 (Ensenada del Pabellón lagoon) and January 2000 (El Yugo estuary), coll. S. Gómez (Ensenada del Pabellón lagoon) and A. C. Puello-Cruz (El Yugo estuary).

Type locality

Ensenada del Pabellón lagoon, Sinaloa (24°19'–24°35'N, 107°28'–107°45'W).

Other localities

El Yugo estuary (23°18'14"N, 106°29'W) and Urías system (23°11'06"N, 106°25'06"W), Mazatlán, Sinaloa.

Etymology

The species was named after the region (Sinaloa State) where the species was found.

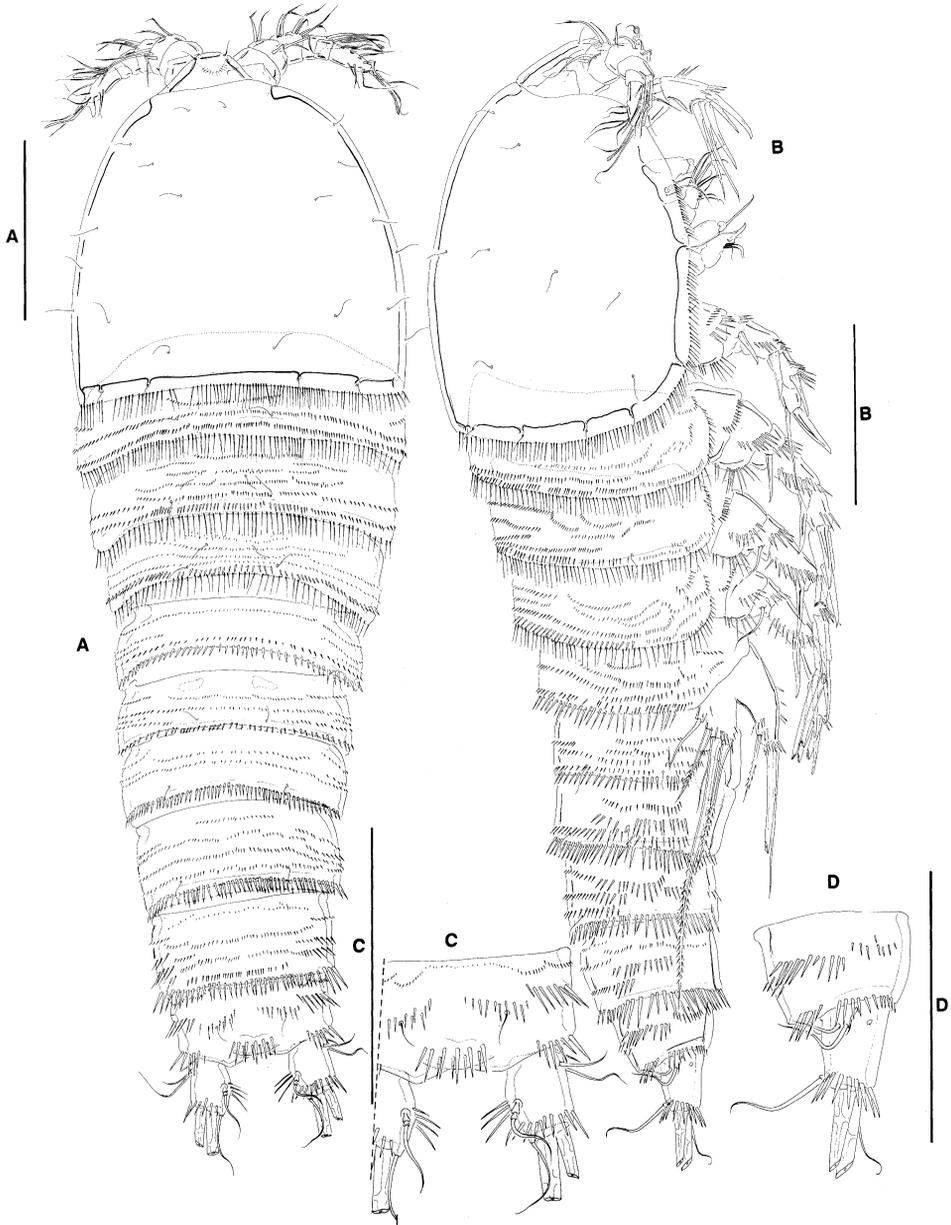


FIG. 24. *Cletocamptus sinaloensis* sp. nov., female. (A) Habitus, dorsal; (B) habitus, lateral; (C) anal somite and caudal rami, dorsal; (D) anal somite and right caudal ramus, lateral. Scale bars: 100 μm .

Description

Female. Habitus (figure 24) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 510 to 750 μm (mean, 658 μm , $N=11$; holotype, 560 μm). Rostrum set off, triangular, with pair of setules subapically. Cephalic shield ornamented with fine and long spinules

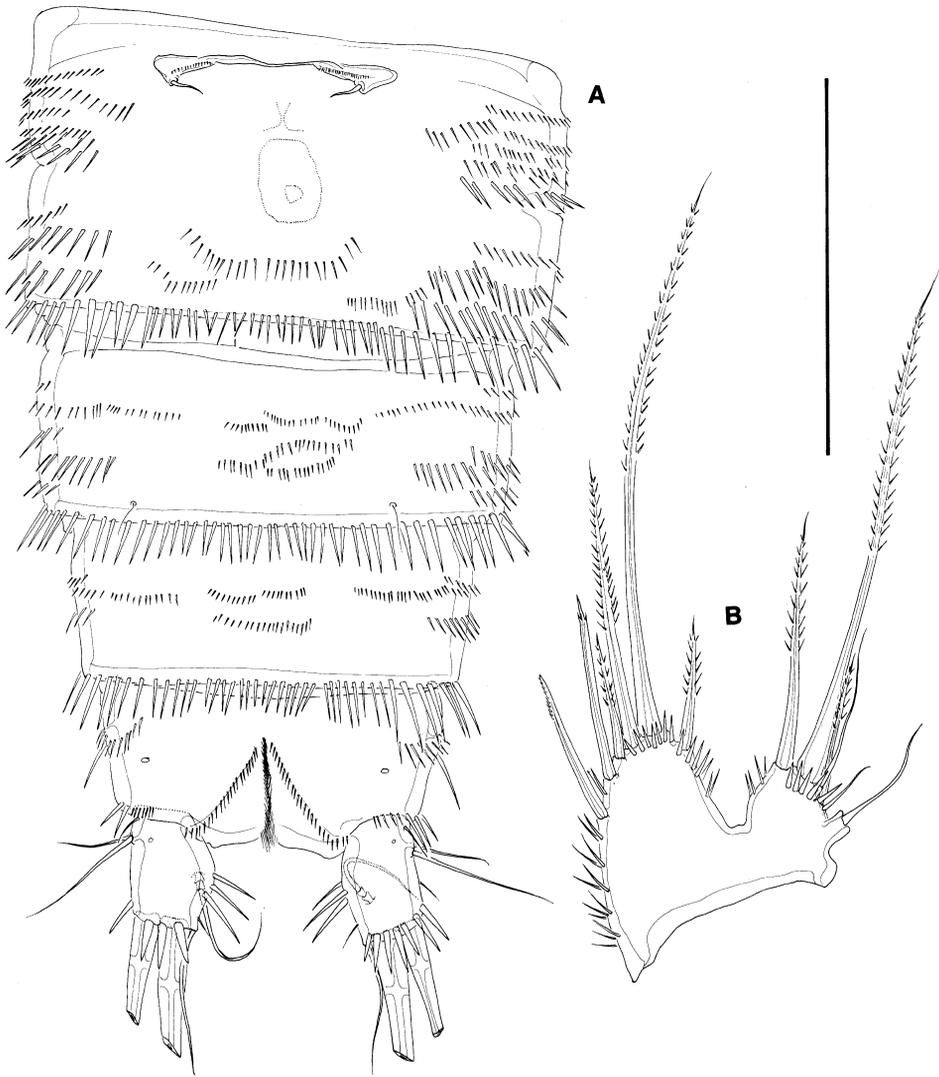


FIG. 25. *Cletocampus sinaloensis* sp. nov., female. (A) Urosome, ventral (P5 bearing somite omitted); (B) P5. Scale bar: 100 μ m.

along margin dorsolaterally (figure 24A, B). Dorsal and lateral surface of free thoracic somites (P2–P4 bearing somites) ornamented with transverse rows of minute spinules, with longitudinal row of small spinules close to posterior margin and with long spinules along posterior margin. 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 relatively longer spinules along posterior margin. First and second genital somites distinct dorsally and laterally, completely fused ventrally (figure 25A); dorsal and lateral surface of first and second genital somite with transverse rows of minute spinules, with row of longer spinules along posterior margin of both somites, and with relatively longer spinules laterally, ventrally ornamented with spinules as shown in figure 25A. Fourth and fifth urosomite

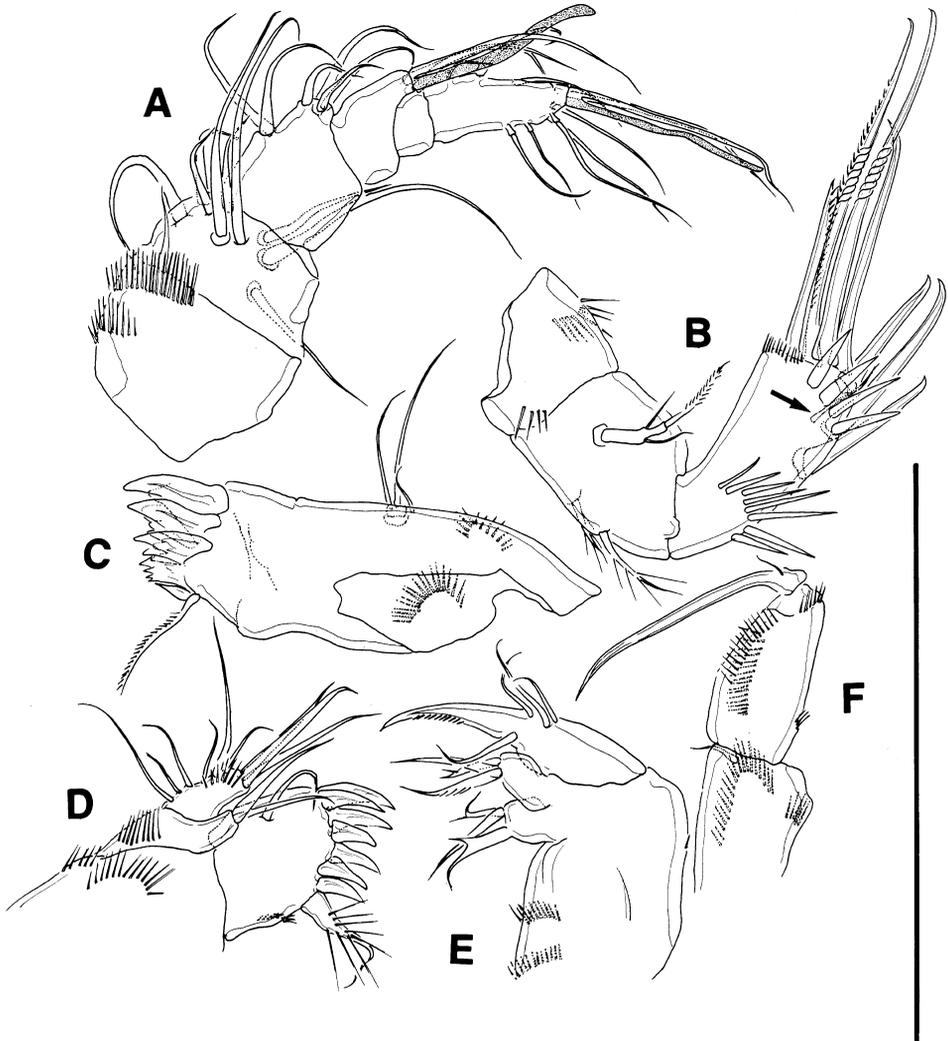


FIG. 26. *Cletocamptus sinoensis* sp. nov., female. (A) Antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped. Scale bar: 100 μ m.

as in second genital somite dorsally and laterally (figure 24A, B), ventral surface ornamented with transverse rows of spinules as illustrated in figure 25A. Dorsal surface of anal somite (figure 24A, C) ornamented with proximal transverse rows of minute spinules, with transverse rows of stronger spinules, and with dorsolateral strong spinules close to joint with caudal rami; rounded anal operculum furnished with two transverse rows of strong spinules (distalmost spinules relatively smaller) close to posterior margin (figure 24A, C). Caudal rami (figures 24A, B, C, D, 25A) about 1.5 times longer than wide; dorsal and ventral surface smooth, except for inner strong spinules close to site insertion of seta VII and close to posterior margin dorsally and ventrally; with seven elements in all.

Antennule (figure 26A) six-segmented; surface of segments smooth except

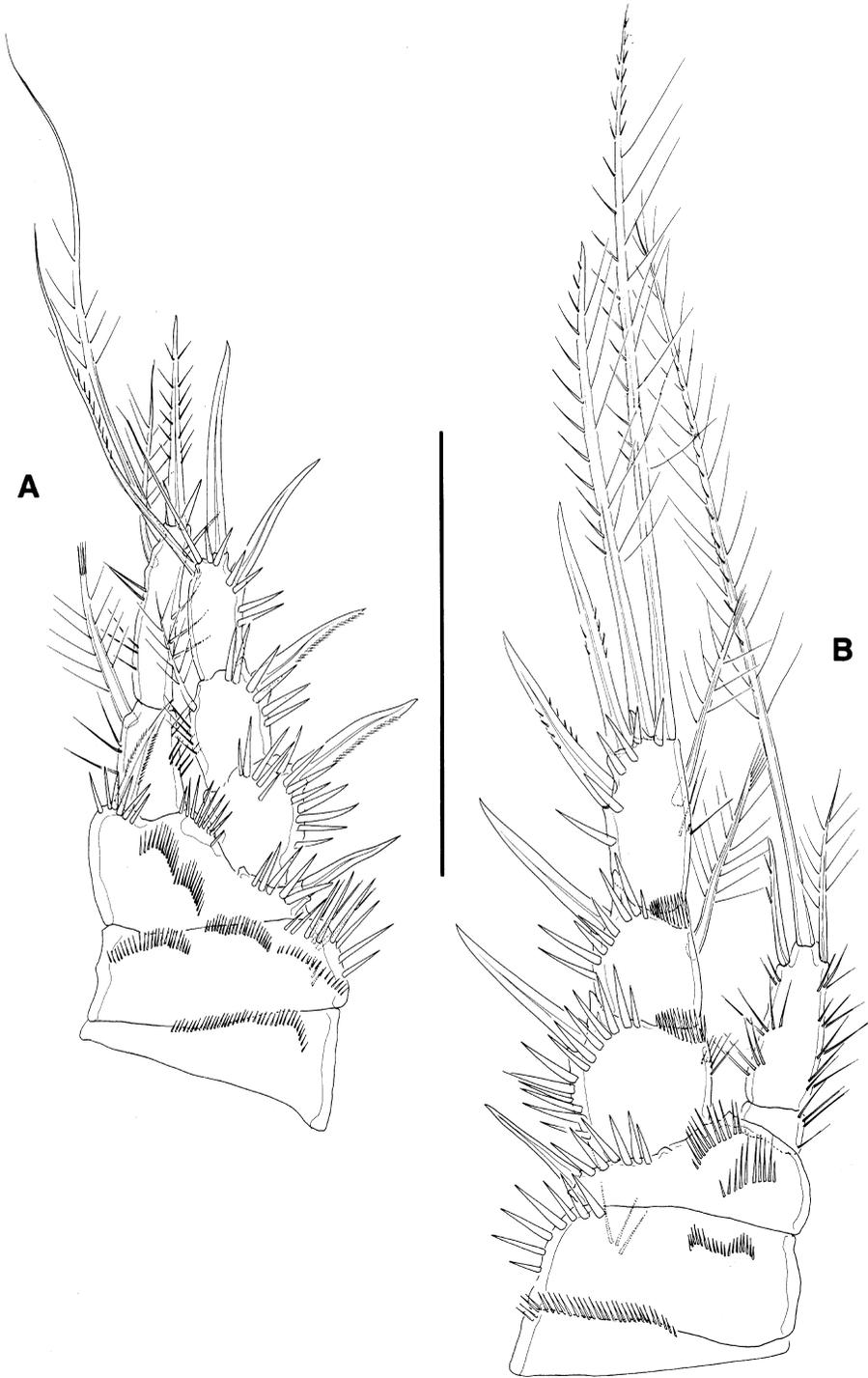


FIG. 27. *Cletocampus sinaloensis* sp. nov., female. (A) P1; (B) P2. Scale bar: 100 μ m.

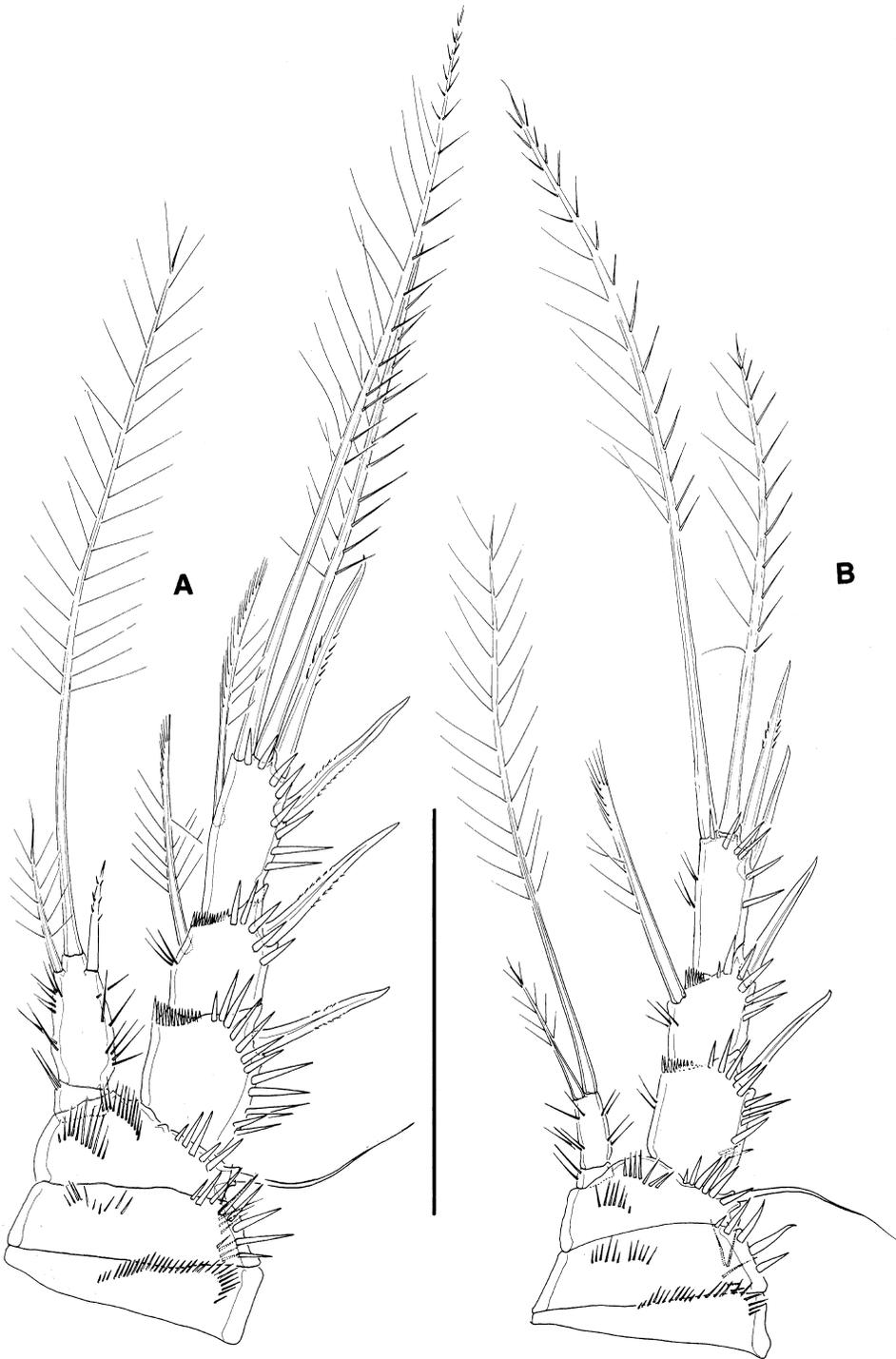


FIG. 28. *Cletocamptus sinoensis* sp. nov., female. (A) P3; (B) P4. Scale bar: 100 μ m.

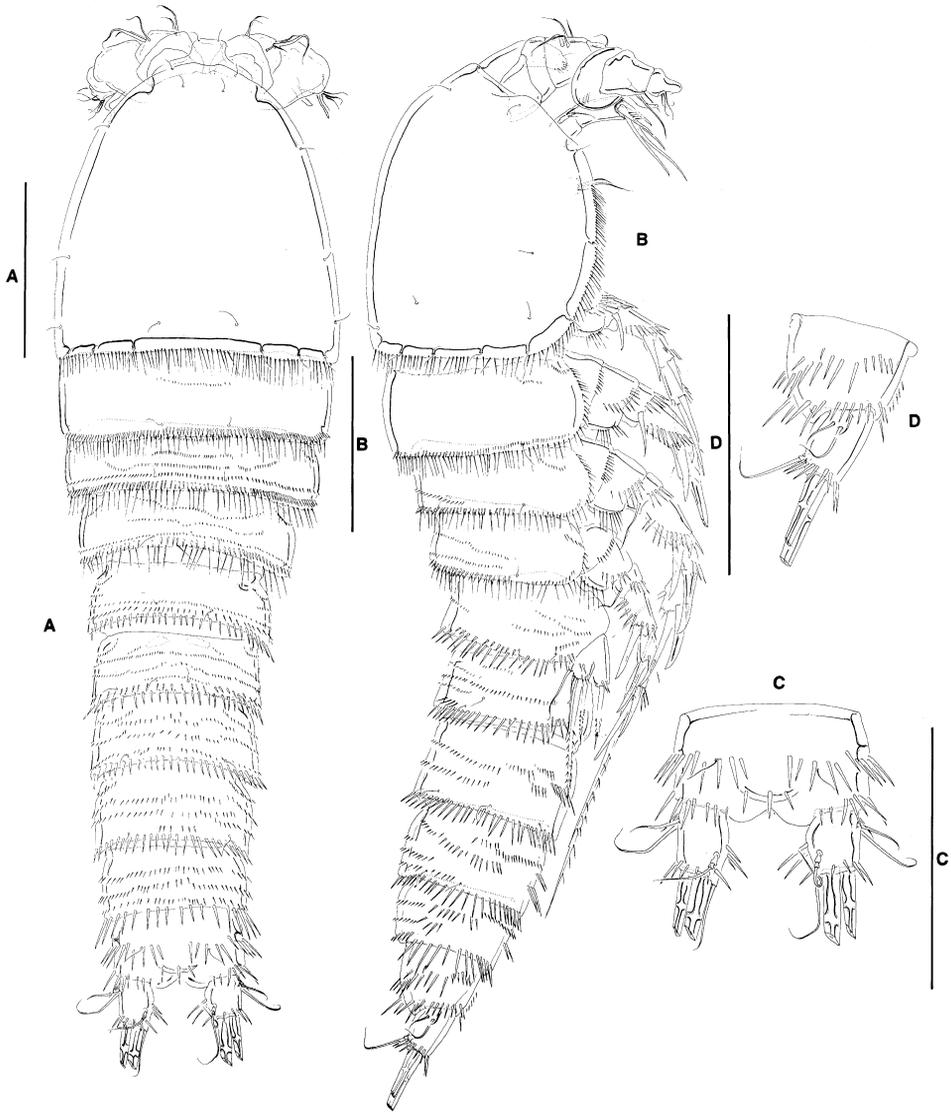


FIG. 29. *CletoCamptus sinaloensis* sp. nov., male. (A) Habitus, dorsal; (B) habitus, lateral; (C) anal somite and caudal rami, dorsal; (D) anal somite and right caudal ramus, lateral. Scale bars: 100 μ m.

for two rows of spinules on first segment. Armature formula, 1-(1), 2-(9), 3-(5), 4-(1+[1+ae]), 5-(1), 6-(9+[1+ae]).

Antenna (figure 26B) with small coxa ornamented with outer spinules and some inner spinules close to inner distal corner. 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 (the latter arrowed in figure 26B), and five distal elements. Exopod one-segmented; about seven times longer than wide; armed with one lateral and one apical smooth setae.

Mandible (figure 26C) robust, ornamented with rows of spinules proximally;

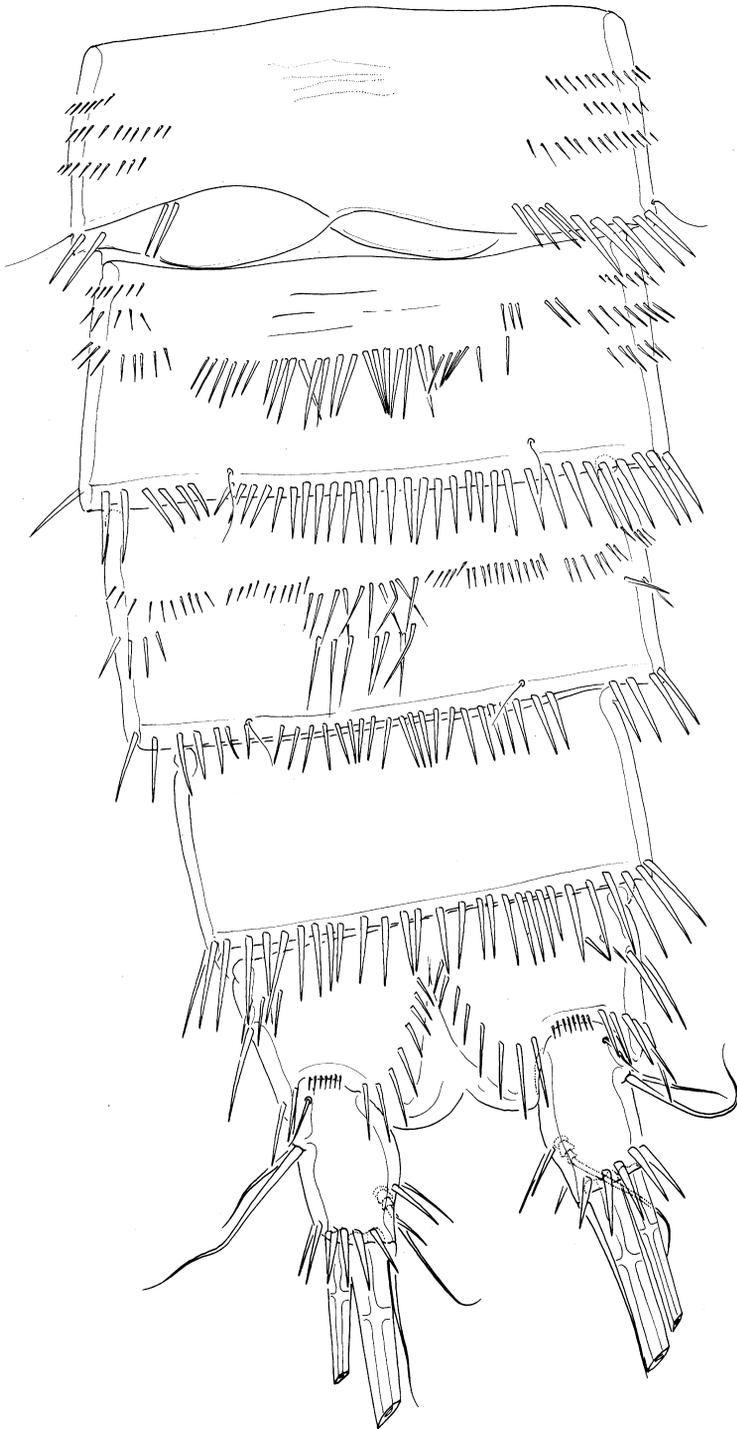


FIG. 30. *Cletocamptus sinoensis* sp. nov., male. Urosome, ventral (P5 bearing somite omitted). Scale bar: 100 μ m.

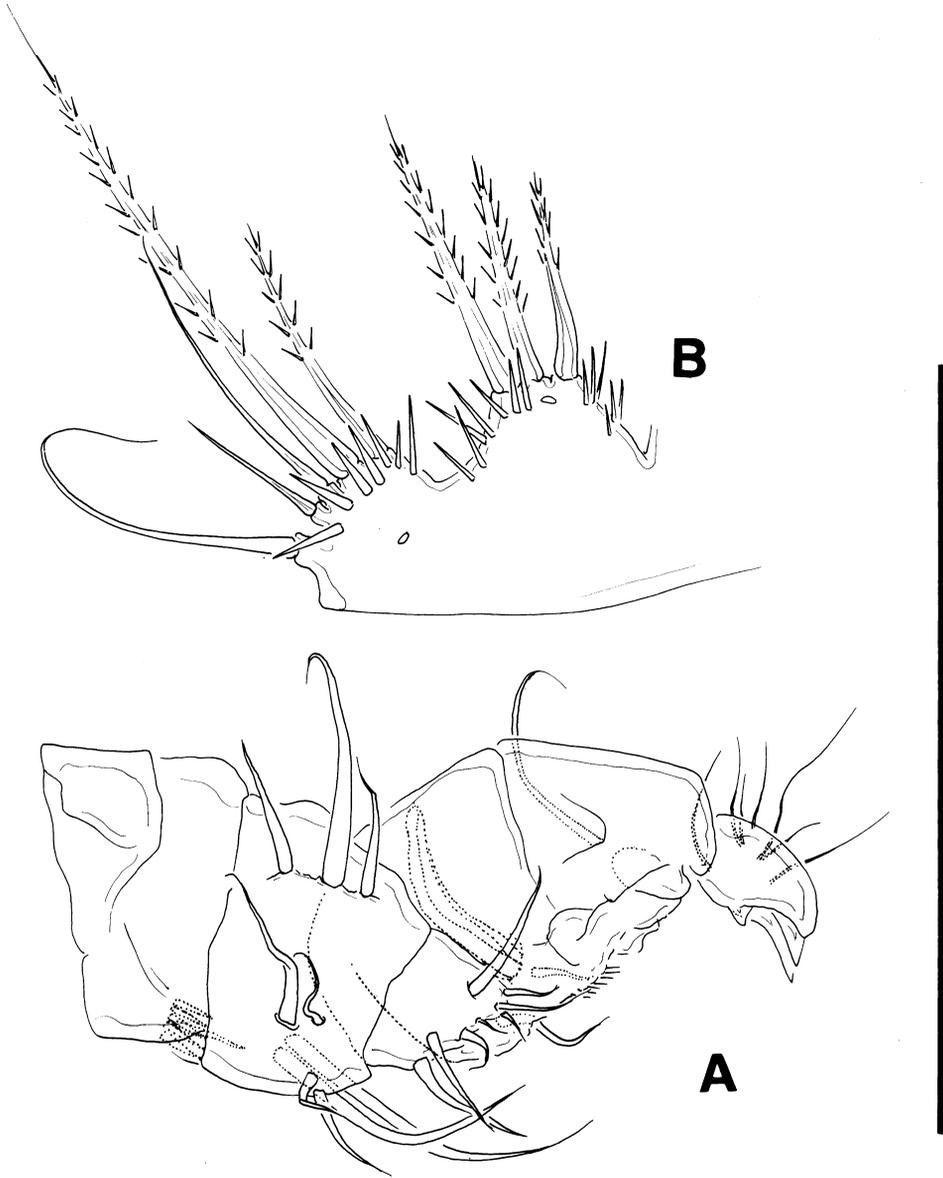


FIG. 31. *Cletocamptus sinaloensis* sp. nov., male. (A) Antennule; (B) P5. Scale bar: 100 μ m.

chewing edge with four strong teeth, four elements as in figure 26C, one pyriform element and one lateral pinnate strong seta. Palp one-segmented, with two long setae unequal in length, and a small seta arising nearby.

Maxillule (figure 26D) robust; arthrite of praecoxa ornamented with few spinules, armed with a surface seta, seven distal spines and one lateral strong seta, the latter ornamented with long spinules. Coxa ornamented with some spinules and armed with two setae. Basis ornamented with some median spinules, and armed with three apical setae; exopod and endopod represented by three setae each.

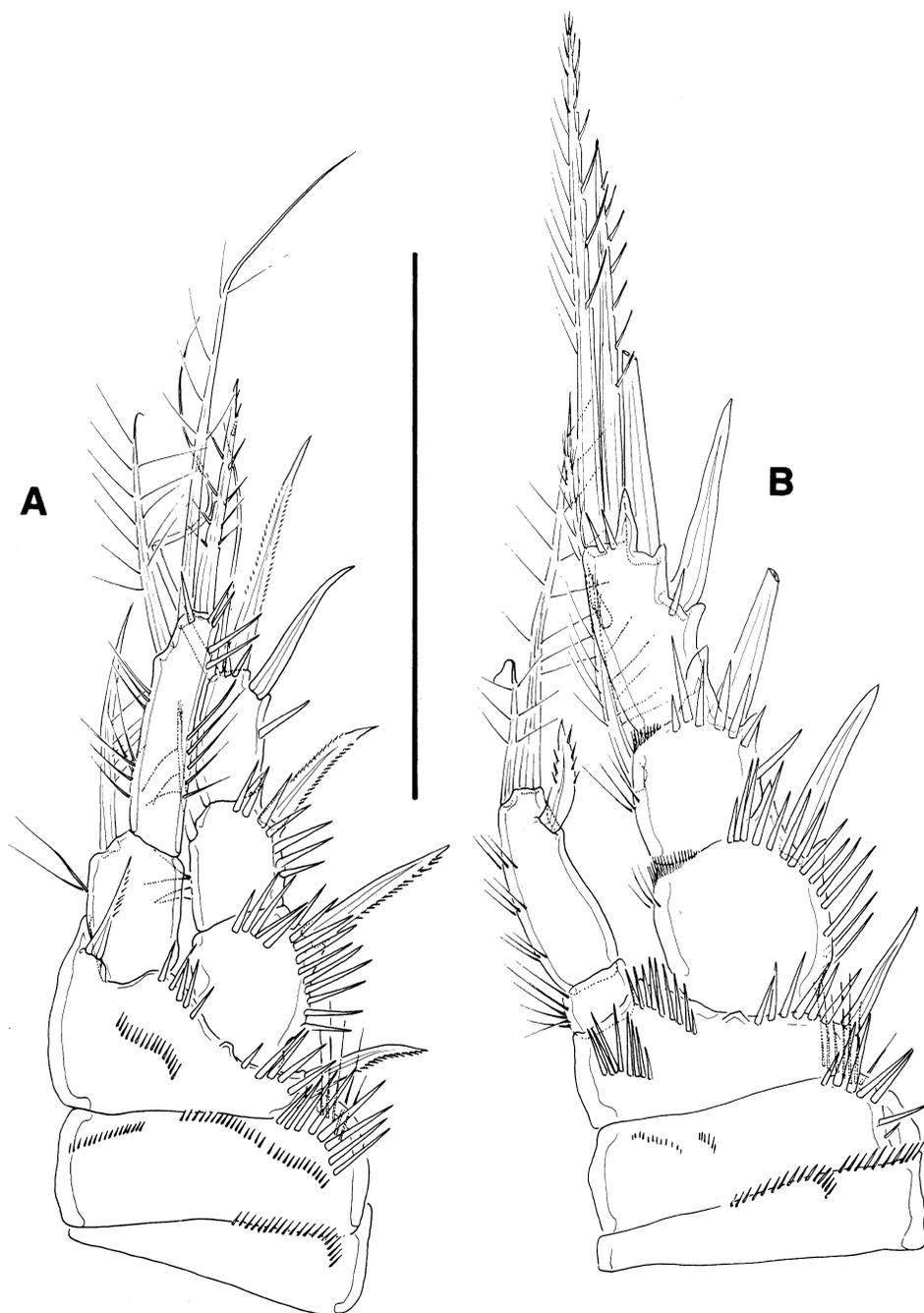


FIG. 32. *Cletocamptus sinaloensis* sp. nov., male. (A) P1; (B) P2. Scale bar: 100 μ m.

Maxilla (figure 26E): syncoxa ornamented with minute spinules along inner margin; with two endites, each bearing three setae. Allobasis drawn into strong claw bearing one accompanying seta. Endopod represented by three setae.

Maxilliped (figure 26F) subchelate. Syncoxa ornamented by two rows of

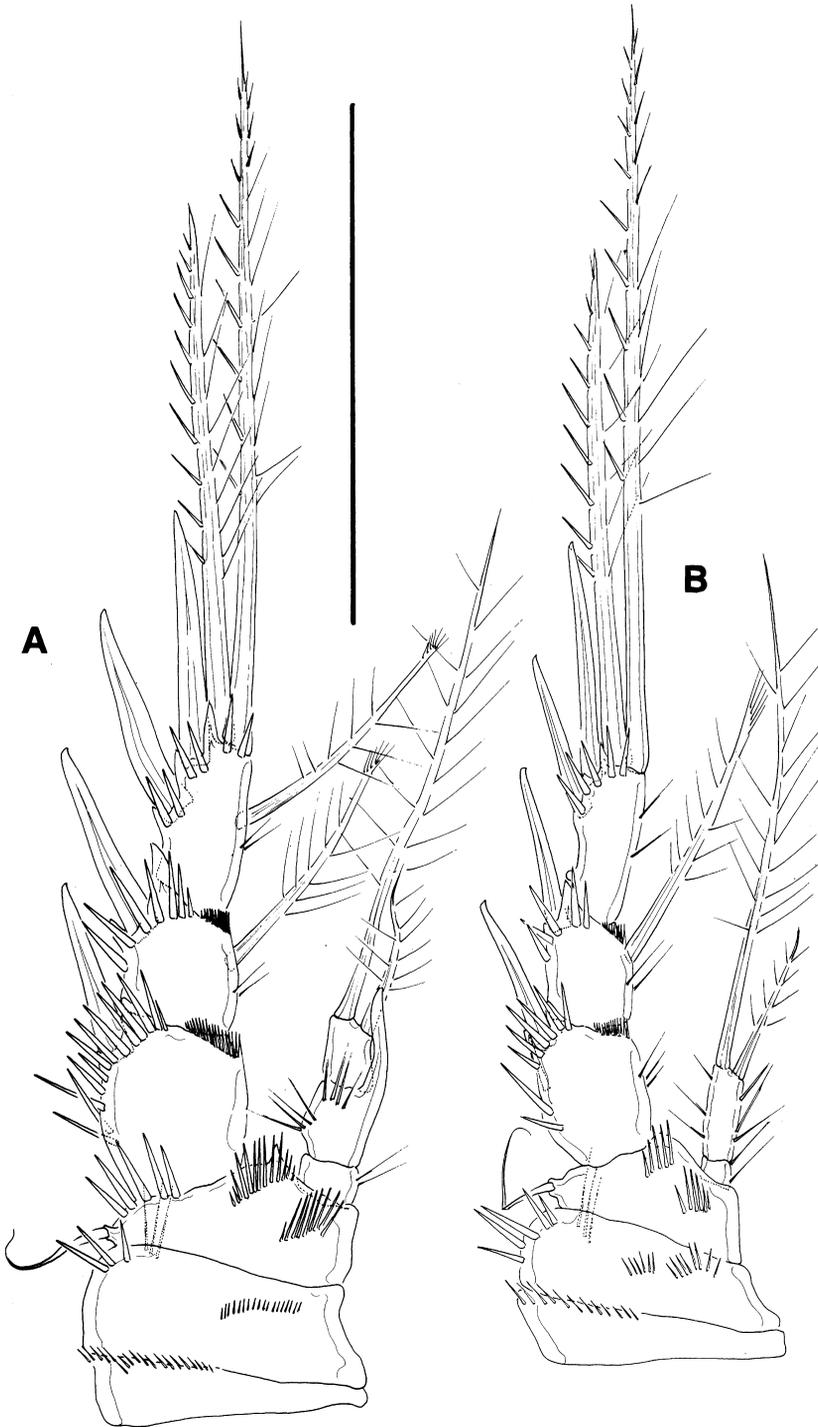


FIG. 33. *Cletocampus sinaloensis* sp. nov., male. (A) P3; (B) P4. Scale bar: 100 μ m.

spinules and armed with a small seta on inner distal corner. Basis without armature and ornamented with an anterior and a posterior row of spinules, and with few spinules close to joint with endopod. The latter drawn into long and slender claw with one accompanying small seta.

P1 (figure 27A): praecoxa ornamented with spinules close to joint with coxa. The latter ornamented with anterior transverse rows of small spinules, with strong spinules close to outer distal corner anteriorly, and with somewhat slender spinules posteriorly. Basis ornamented with median sets of spinules, and with stronger spinules at base of exopod, between rami and at base of inner spine of basis. Exopod three-segmented. Endopod two-segmented, second segment reaching far beyond third exopodal segment. Armature formula as in table 1.

P2 (figure 27B): praecoxa as in P1. Coxa ornamented with median row of small spinules and with strong spinules close to outer distal corner anteriorly, and with some spinules close to outer distal corner posteriorly. Basis ornamented with spinules between rami and at base of endopod, and with stronger spinules at base of exopod; outer element spine-like. Exopod three-segmented and ornamented as in figure 27B. Endopod two-segmented, reaching distal quarter of second exopodal segment; first segment small, somewhat wider than long and ornamented with slender inner spinules; second segment ornamented with long spinules as shown in figure 27B, and armed with one inner spine, one apical and one inner seta. Armature formula as in table 1.

P3 (figure 28A): praecoxa, coxa and basis ornamented as in P2. Exopod as in P2. Endopod as in P2 except for relatively shorter second segment. Armature formula as in table 1.

P4 (figure 28B): praecoxa, coxa and basis as in P2. Exopod as in P2, except for armature formula of third segment (without inner seta). Endopod two-segmented, barely reaching distal third of first exopodal segment; first segment small, somewhat wider than long; second segment ornamented with inner and outer slender spinules and armed with two apical setae.

P5 (figure 25B): exopod and baseoendopod fused. Baseoendopodal lobe longer than exopod, ornamented with sets of inner spinules, with spinules at base of apical seta and with some outer spinules; armed with one outer, one apical and four inner setae; relative length of setae as in figure 25B. Exopod ornamented with spinules as shown in figure 25B, and armed with five setae in all, plus outer seta of basis.

P6 (figure 25A) represented by median plate in anterior half of first genital somite, each vestigial leg represented by a very small and slender seta. Copulatory pore in the middle of genital double somite.

Male. Total body length measured from tip of rostrum to posterior margin of caudal rami, ranging from 570 to 610 μm (mean, 582 μm , $N=4$; allotype, 570 μm). Habitus (figure 29A, B), anal segment and caudal rami (figure 29C, D) as in female dorsally, except for fewer rows of spinules on anal operculum. Ventrally as in female except for genital somite, ornamentation of third and fourth urosomites (see figure 30) which are coarser than in female; fifth urosomite seemingly without ornamentation ventrally.

Antennule (figure 31A) six-segmented; subchirocer. Last segment with two acute teeth.

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

P1 (figure 32A) as in female except for dimorphic projection on inner distal corner of basis.

P2 (figure 32B) as in female except for relatively stouter outer spines of male exopod, dimorphic inner spine on male ENP 2 and relatively shorter apical setae on second endopodal segment.

Exopod of P3 (figure 33A) as in female except for relatively stouter outer spines. Endopod three-segmented; second segment with inner distal apophysis reaching beyond third endopodal segment; second segment reaching little beyond first exopodal segment, with one inner and one apical seta relatively shorter than their female homologues.

P4 (figure 33B) as in female, except for stouter outer spines of exopod and relatively shorter setae of second endopodal segment.

Both P5 fused (figure 31B); exopod and baseopod fused. Exopod ornamented with transverse row of strong spinules; with four setae. Endopodal lobe ornamented with sets of spinules along outer and inner margin, and at base of apical setae; with three elements in all.

P6 (figure 30) represented by plate; without armature.

Variability

No variability was observed in males.

Female. Paratype (EMUCOP-300491-42) without inner seta and with two sets of spinules on left P4 EXP 3, and with one inner seta and without spinules on right P4 EXP 3; paratype (EMUCOP-300392-40) with five setae/spines on P1 EXP 3 (see table 2).

Cletocamptus fourchensis sp. nov.

(figures 34–42)

Cletocamptus deitersi (Richard, 1897) *sensu* Fleegeer (1980), De Laune *et al.* (1984), Decho (1986, 1988), Chandler (1986), Chandler and Fleegeer (1987), Sun and Fleegeer (1994), Pace and Carman (1996), Carman *et al.* (1997, 2000).

Cletocamptus deitersi type II *sensu* Rocha-Olivares *et al.* (2001).

Cletocamptus from Port Fourchon, Louisiana *sensu* Castro-Longoria *et al.* (2003).

Type material

One female holotype (USNM 1010505) and one male allotype (USNM 1010506) preserved in alcohol, five dissected female paratypes (EMUCOP-1298-01, EMUCOP-1298-04, EMUCOP-1298-05, EMUCOP-1298-06, EMUCOP-1298-07), three female and five male paratypes (USNM 1010507), two female (EMUCOP-1298-13) and four male paratypes (EMUCOP-1298-14) preserved in alcohol, and seven dissected male paratypes (EMUCOP-1298-02, EMUCOP-1298-03, EMUCOP-1298-08, EMUCOP-1298-09, EMUCOP-1298-10, EMUCOP-1298-11, EMUCOP-1298-12). December 1998 (Port Fourchon) and January 1999 (Cocodrie), coll. A. Rocha-Olivares, J. W. Fleegeer and D. Foltz.

Type locality

Port Fourchon, Louisiana (29°05.42'N, 90°05.8'W).

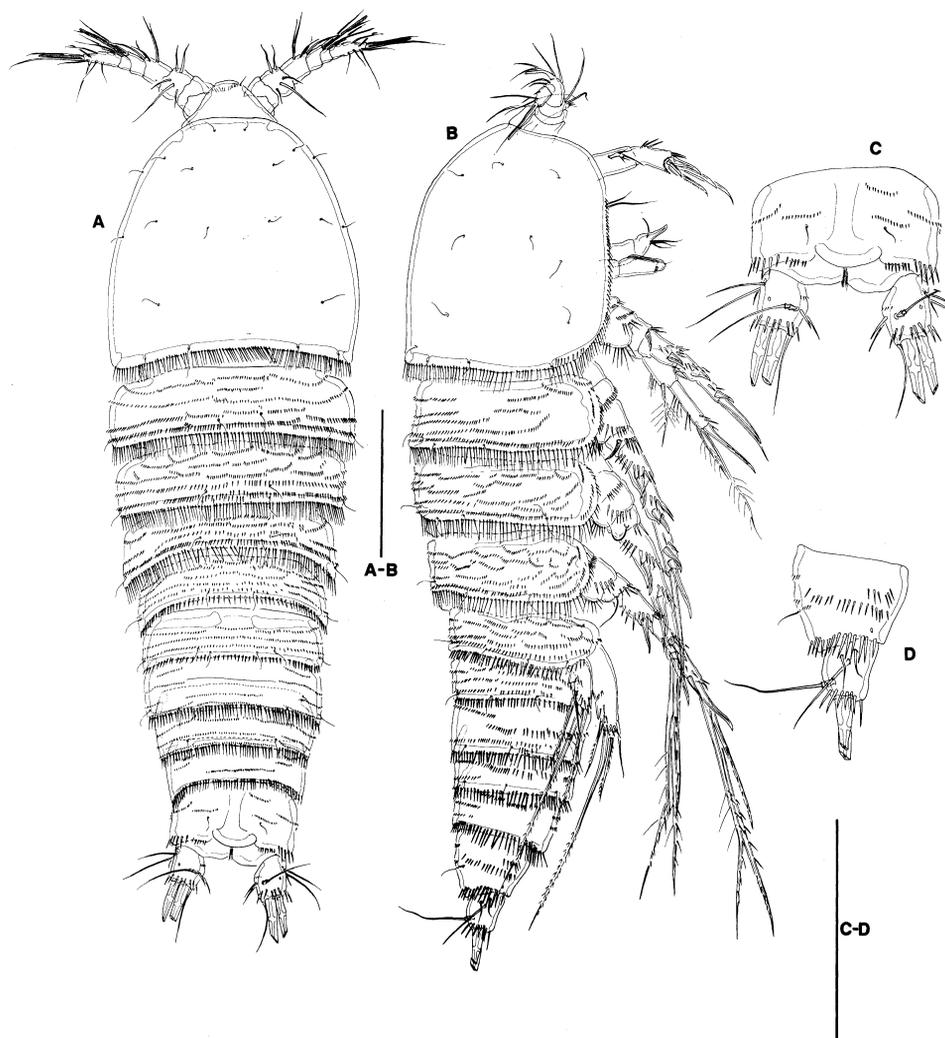


FIG. 34. *Cletocamptus fourchensis* sp. nov., female. (A) Habitus, dorsal; (B) habitus, lateral; (C) anal somite and caudal rami, dorsal; (D) anal somite and right caudal ramus, lateral. Scale bars: 100 μm .

Other sites

Cocodrie, Louisiana (29°15.2'N, 90°39.8'W); Graveline Bay, Mississippi (29°15'N, 91°21'W) (Carman *et al.*, 2000).

Etymology

The species was named after the region (Port Fourchon) where the species was found.

Description

Female. Habitus (figure 34) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 560 to 725 μm (mean, 603 μm , $N=10$; holotype, 567 μm). Rostrum set off, triangular, with

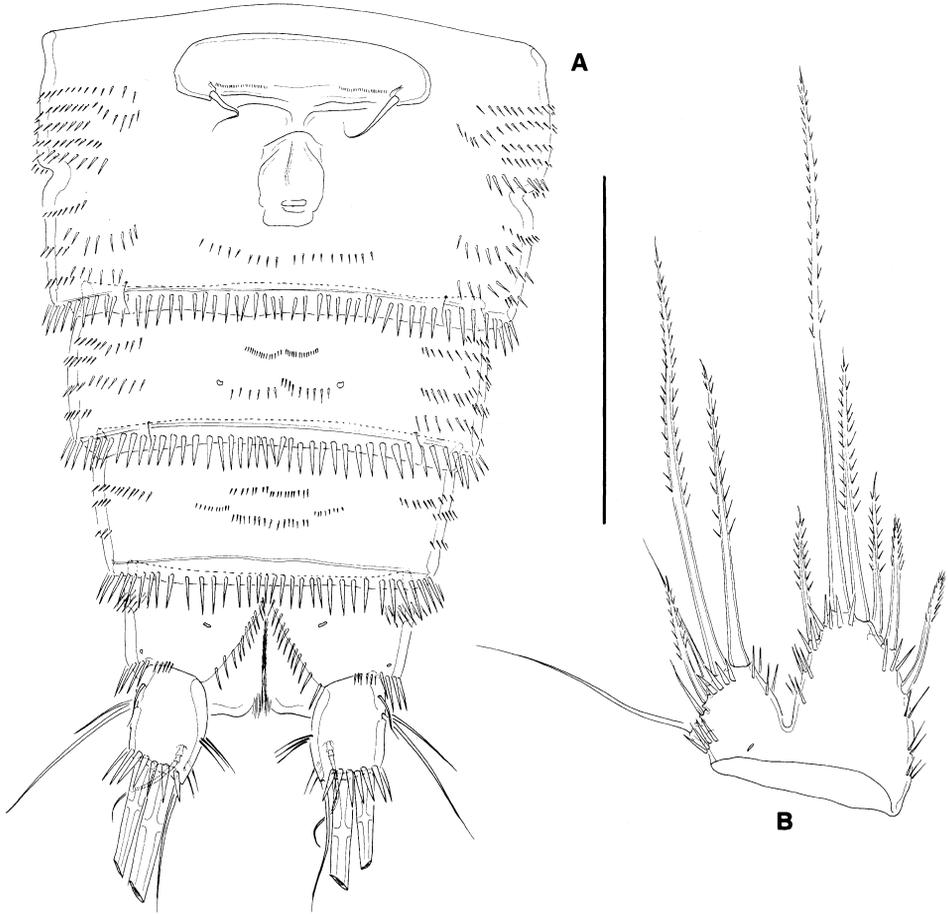


FIG. 35. *Cletocamptus fourchensis* sp. nov., female. (A) Urosome, ventral (P5 bearing somite omitted); (B) P5. Scale bar: 100 μ m.

pair of setules subapically. Cephalic shield ornamented with fine and long spinules along margin dorsolaterally. Dorsal and lateral surface of free thoracic somites (P2–P4 bearing somites) ornamented with transverse rows of minute spinules, with longitudinal row of small spinules and with long spinules along posterior margin. Dorsal and lateral surface of first urosomite (P5 bearing somite) with transverse rows of minute spinules, and with comparatively longer spinules along posterior margin. First and second genital somites distinct dorsally and laterally (figure 34A, B), completely fused ventrally (figure 35A); dorsal and lateral surface of first and second genital somite with transverse rows of minute spinules, with row of long spinules along posterior margin of both somites (spinules of second somite longer), and with relatively longer spinules laterally, ventrally ornamented with spinules as shown in figure 35A. Fourth and fifth urosomite as in second genital somite dorsally, except for fewer transverse rows on fifth urosomite, ventral surface ornamented with transverse rows of spinules as illustrated in figure 35A. Dorsal surface of anal somite (figure 34A, C) ornamented with few transverse rows of minute spinules and with dorsolateral strong spinules close to joint with caudal rami; rounded anal

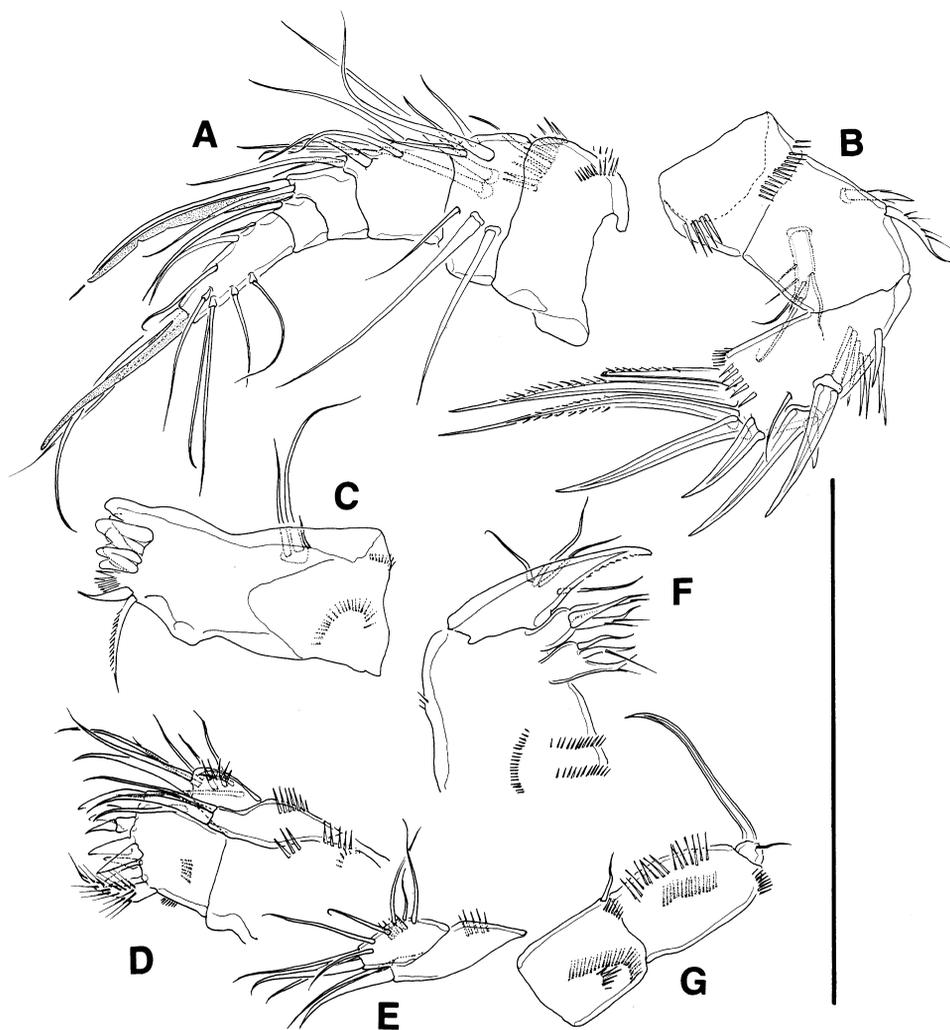


FIG. 36. *Cletocamptus fourchensis* sp. nov., female. (A) Antennule; (B) antenna; (C) mandible; (D) maxillule; (E) coxa and basis of maxillule; (F) maxilla; (G) maxilliped. Scale bar: 100 μ m.

operculum without ornamentation; with median row of strong spinules laterally (figure 34D). Caudal rami (figure 34A–D) about 1.5 times longer than wide; dorsal and ventral surface smooth, except for inner set of spinules close to insertion site of seta VII and close to posterior margin dorsally and ventrally; with seven elements in all.

Antennule (figure 36A) six-segmented; surface of segments smooth except for two rows of spinules on first segment. Armature formula, 1-(1), 2-(9), 3-(6), 4-(1+[1+ae]), 5-(1), 6-(9+[1+ae]).

Antenna (figure 36B) with small coxa ornamented with two sets of spinules. Allobasis armed with two strong abexopodal setae. Free endopodal segment ornamented with inner strong spinules proximally and subdistally, and armed with two lateral inner

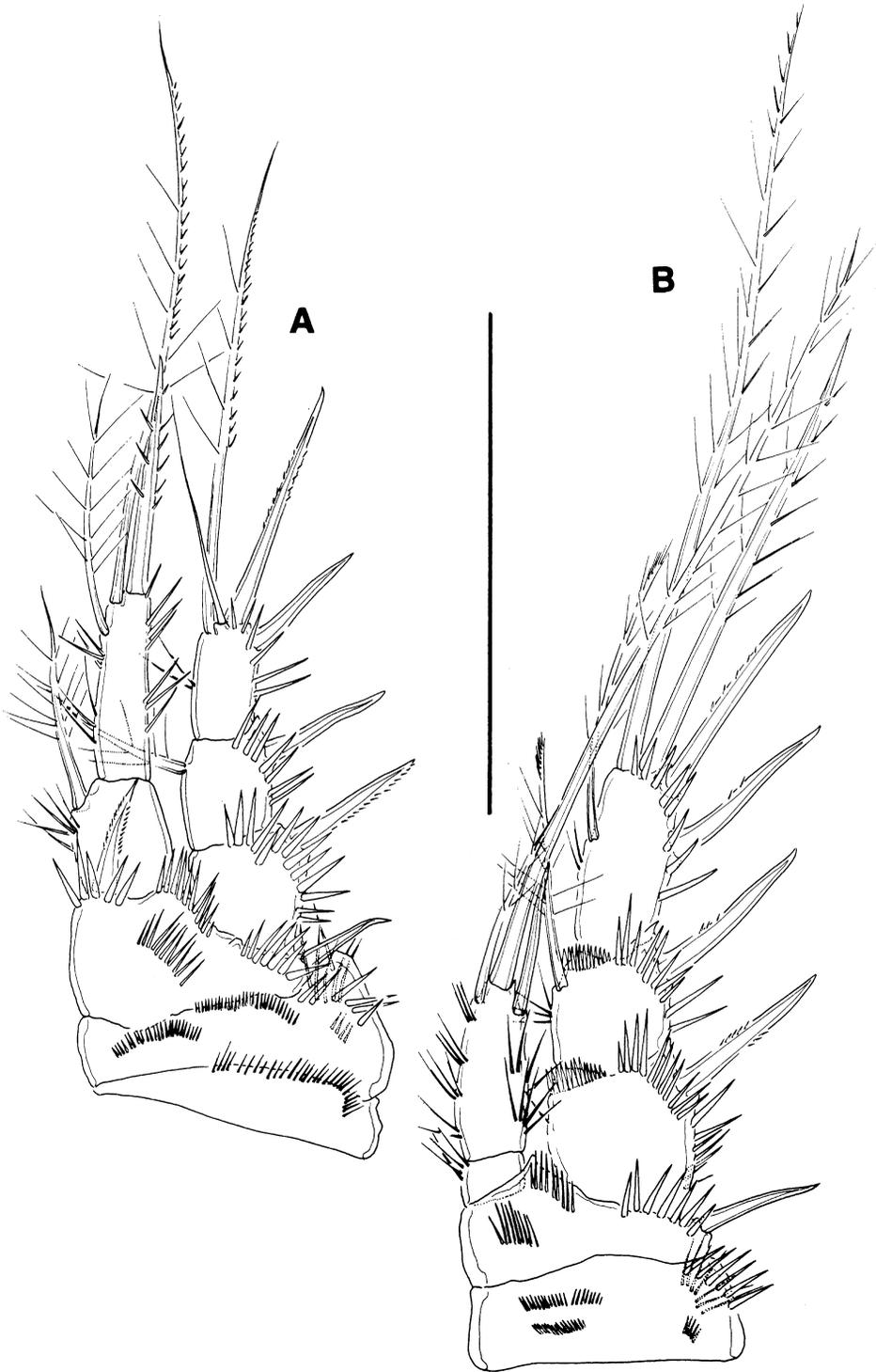


FIG. 37. *Cletocamptus fourchensis* sp. nov., female. (A) P1; (B) P2. Scale bar: 100 μ m.

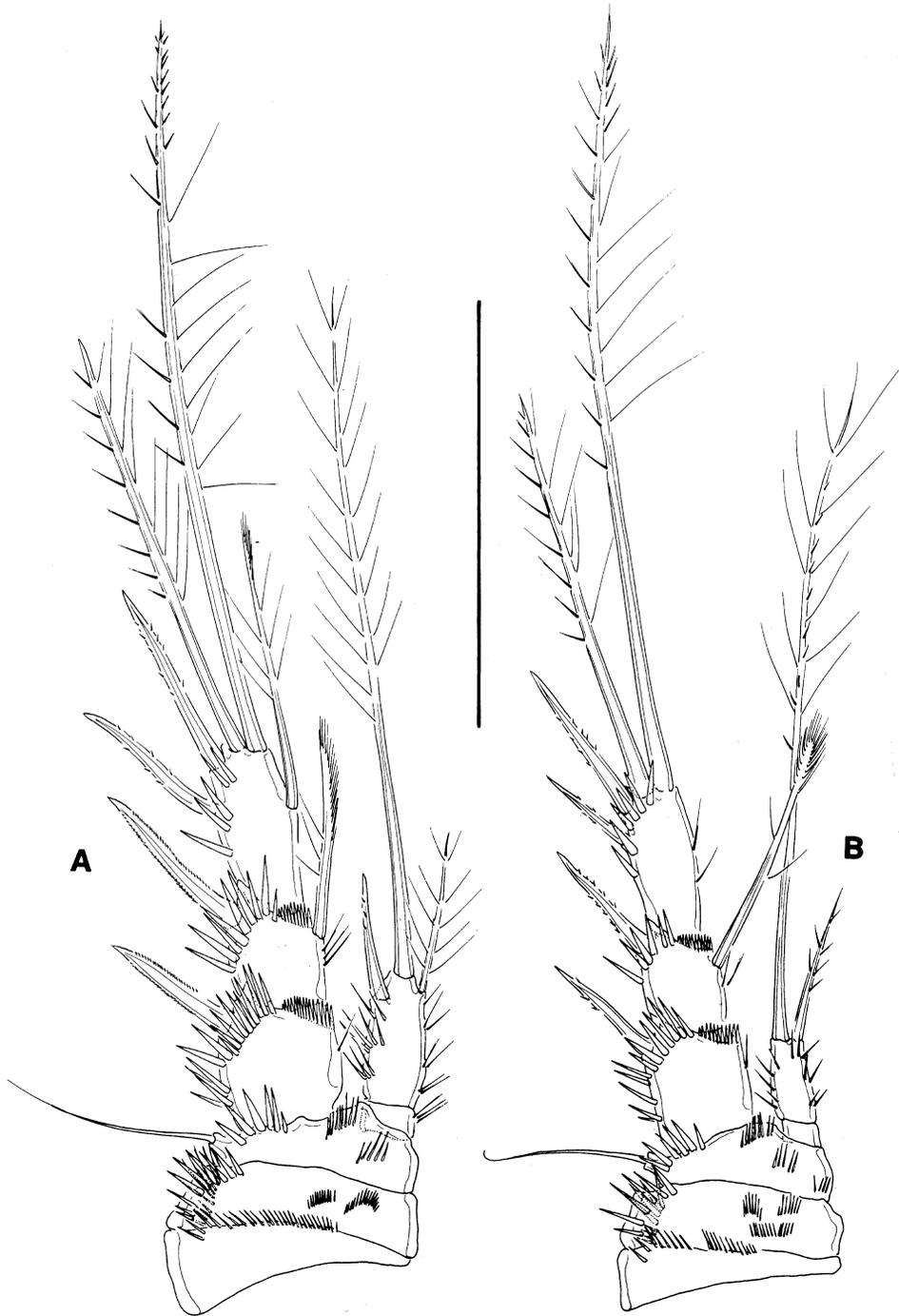


FIG. 38. *Cletocamptus fourchensis* sp. nov., female. (A) P3; (B) P4. Scale bar: 100 μ m.

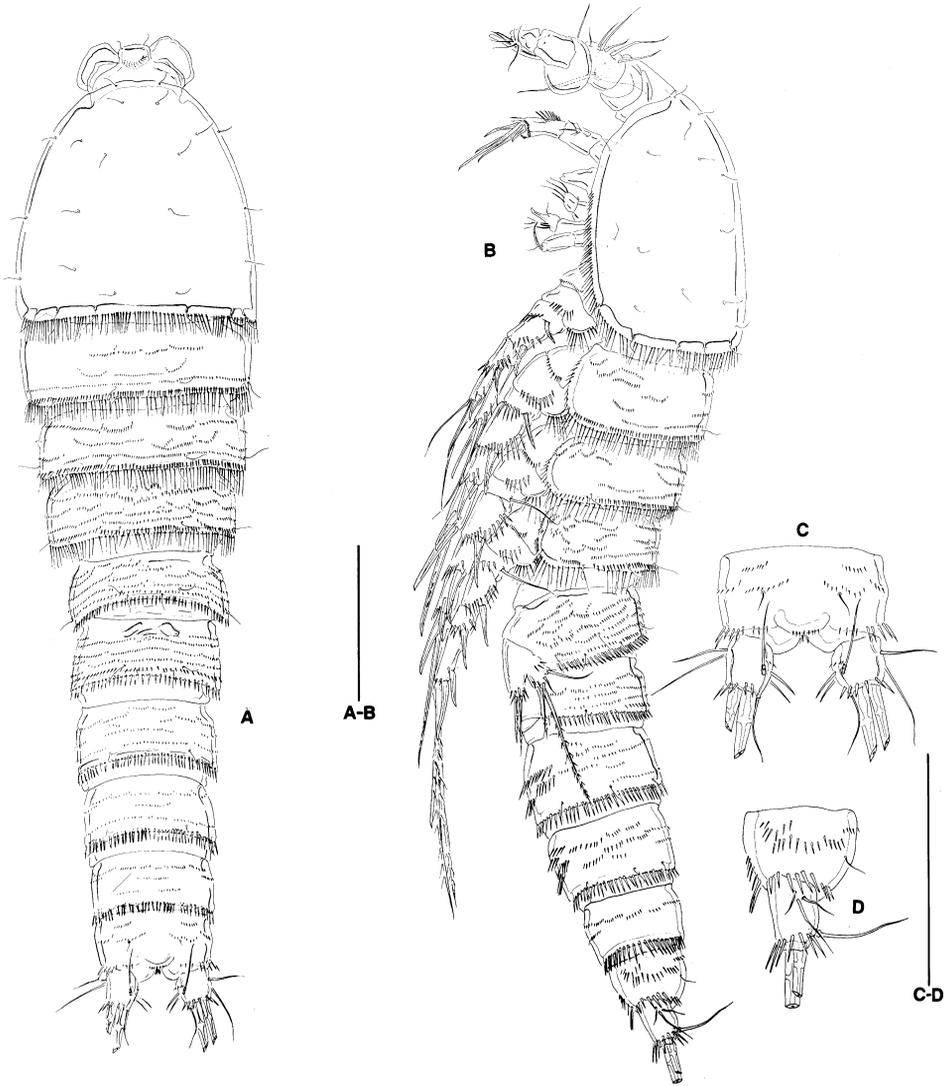


FIG. 39. *Cletocamptus fourchensis* sp. nov., male. (A) Habitus, dorsal; (B) habitus lateral; (C) anal somite and caudal rami, dorsal; (D) anal somite and left caudal ramus, lateral. Scale bars: 100 μ m.

spines and one slender seta, and five distal elements. Exopod one-segmented; about five times longer than wide; ornamented with few spinules, and armed with one lateral and two apical smooth setae.

Mandible (figure 36C) robust, ornamented with rows of spinules proximally; chewing edge with four strong teeth, a multicuspitate tooth, a pyriform element and a lateral pinnate strong seta. Palp small, one-segmented, with two long setae unequal in length, with a small seta arising nearby.

Maxillule (figure 36D, E) robust; arthrite of praecoxa ornamented with few spinules, armed with a surface seta, seven distal spines and one lateral strong seta,

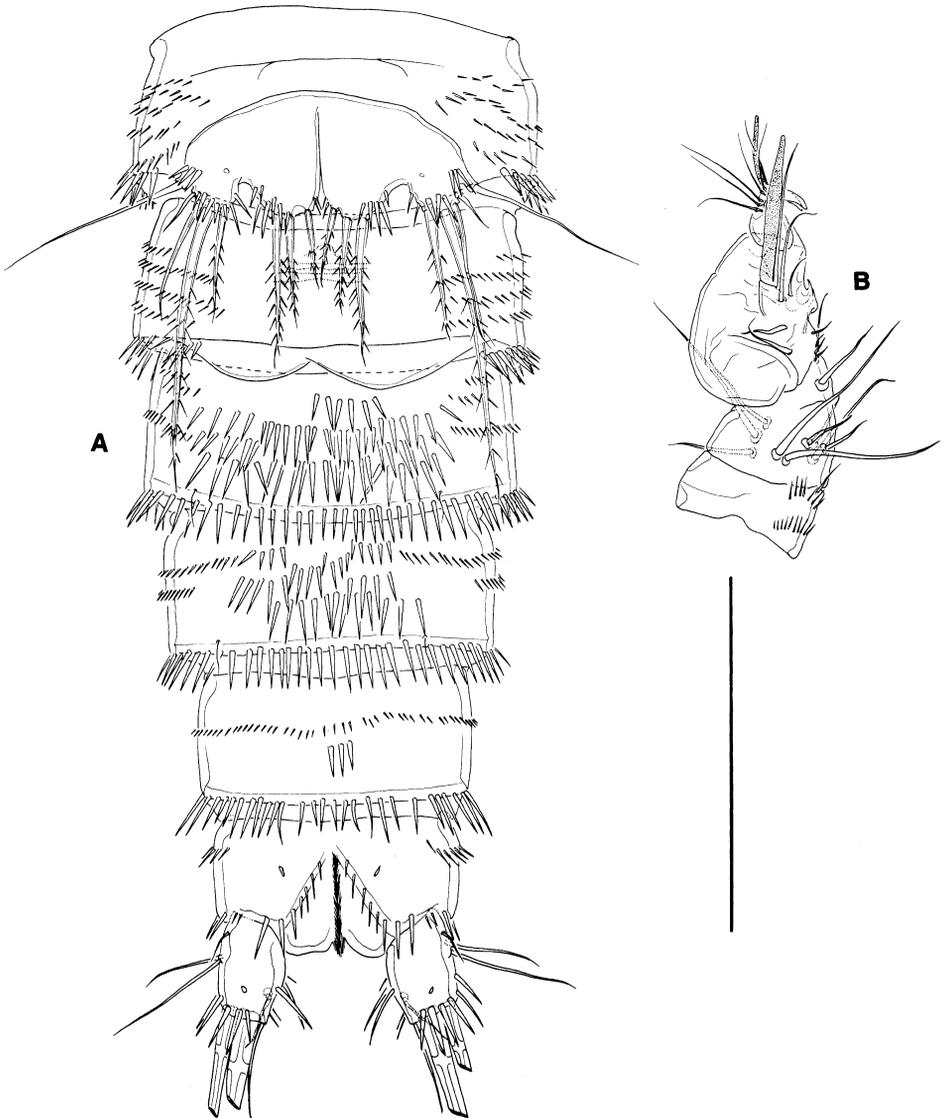


FIG. 40. *Cletocamptus fourchensis* sp. nov., male. (A) Urosome, ventral; (B) antennule. Scale bar: 100 μ m.

the latter ornamented with long spinules. Coxa ornamented with some spinules and armed with two slender setae. Basis ornamented with some median spinules, and armed with three apical setae; exopod and endopod represented by three setae each.

Maxilla (figure 36F): syncoxa ornamented with minute spinules along inner and outer margin; with two endites, each bearing three setae. Allobasis drawn into strong claw bearing one accompanying seta. Endopod represented by three setae.

Maxilliped (figure 36G) subchelate. Syncoxa ornamented by anterior and posterior rows of spinules and armed with a small seta on inner distal corner. Basis without armature and ornamented with two longitudinal rows of spinules anteriorly

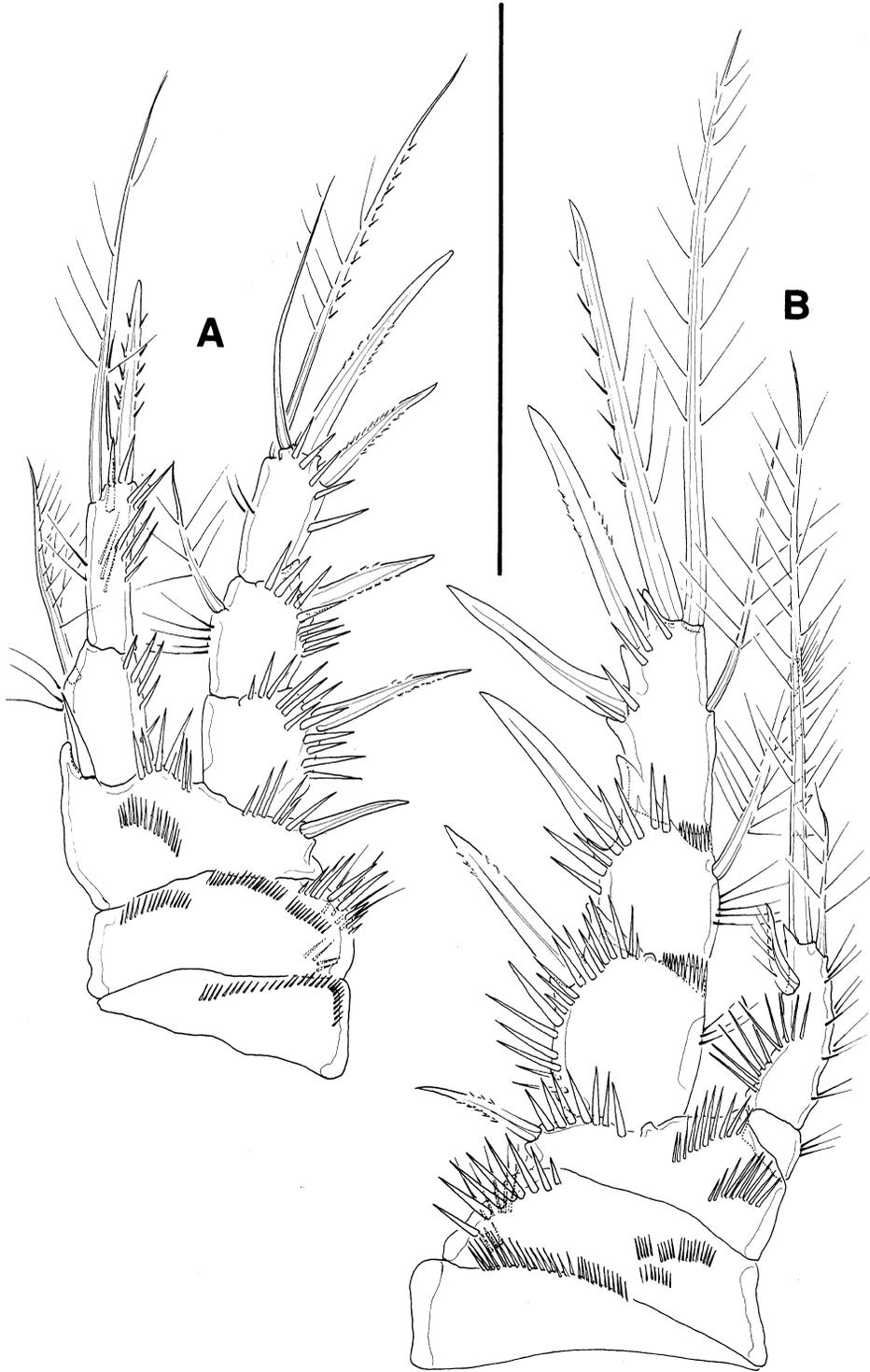


FIG. 41. *Cletocampus fourchensis* sp. nov., male. (A) P1; (B) P2. Scale bar: 100 μ m.

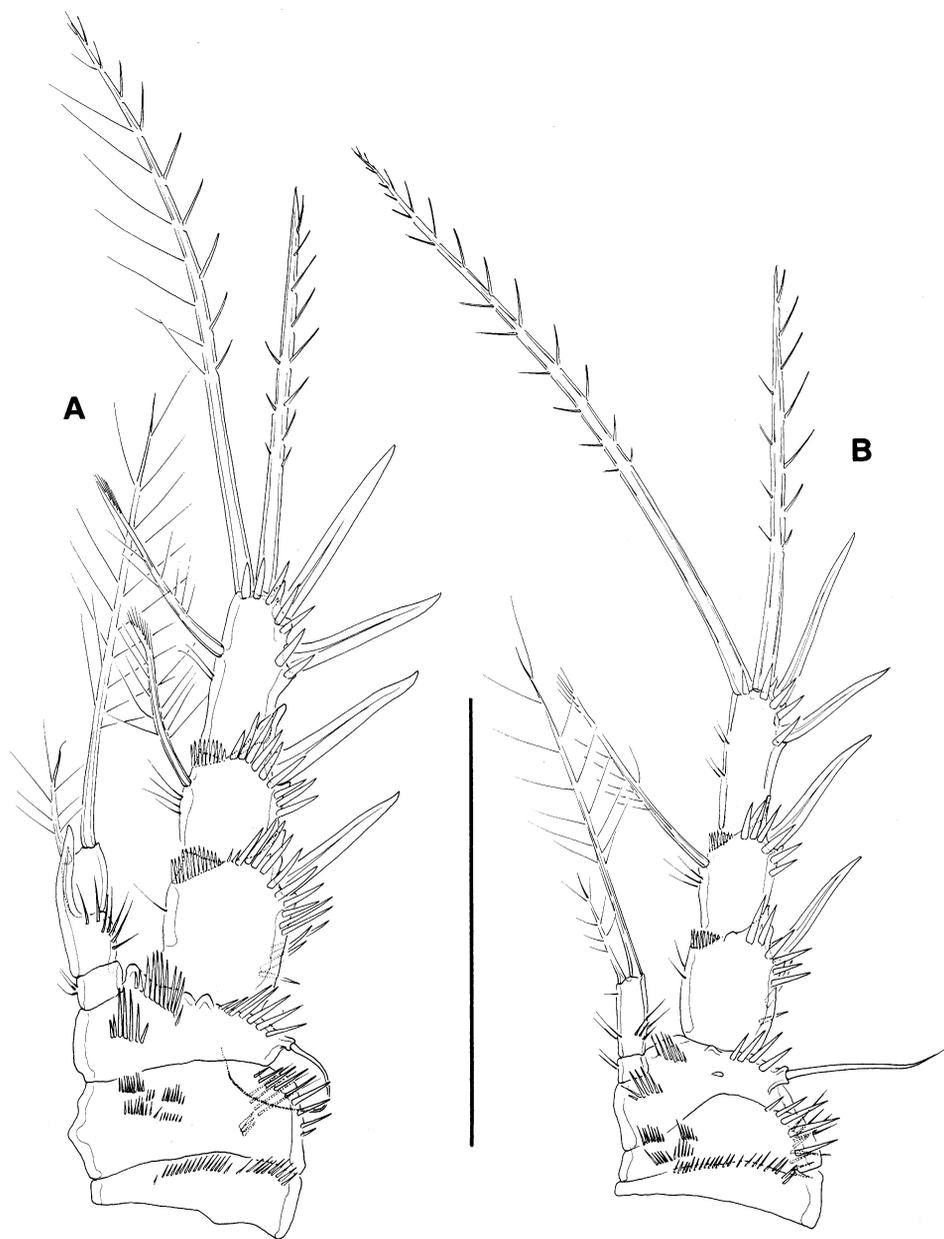


FIG. 42. *Cletocamptus fourchensis* sp. nov., male. (A) P3; (B) P4. Scale bar: 100 μ m.

and posteriorly, and with few spinules close to joint with endopod. The latter drawn into long and slender claw with one accompanying small seta.

P1 (figure 37A): praecoxa ornamented with spinules close to joint with coxa. The latter ornamented with anterior transverse rows of spinules, with comparatively stronger spinules close to outer distal corner anteriorly, and with some spinules posteriorly. Basis ornamented with median row of spinules, and with stronger spinules at base of exopod, between rami and at base of inner spine of basis.

Exopod three-segmented. Endopod two-segmented, second segment reaching beyond third exopodal segment. Armature formula as in table 1.

P2 (figure 37B): coxa ornamented with median row of small spinules and with strong spinules close to outer distal corner anteriorly, and with some spinules close to outer distal corner posteriorly. Basis ornamented with median set of spinules, with spinules between rami and with comparatively stronger spinules at base of exopod; outer element spine-like. Exopod three-segmented and ornamented as in figure 37B. Endopod two-segmented, reaching beyond the middle of second exopodal segment; first segment small, slightly wider than long and ornamented with some inner spinules; second segment ornamented with long spinules as shown in figure 37B, and armed with three elements in all. Armature formula as in table 1.

P3 (figure 38A): praecoxa as in P1. Coxa ornamented with transverse rows of spinules, with strong spinules close to outer distal corner anteriorly and with slender and long spinules on outer distal corner posteriorly. Basis as in P2 except for seta-like outer element. Exopod as in P2. Endopod as in P2 except for relatively shorter second segment reaching proximal third of second exopodal segment. Armature formula as in table 1.

P4 (figure 38B): praecoxa, coxa and basis as in P3. Exopod as in P3, except for armature formula of third segment (without inner seta). Endopod two-segmented, barely reaching tip of first exopodal segment; first segment small, slightly wider than long; second segment ornamented with inner and outer slender spinules and armed with two apical setae.

P5 (figure 35B): exopod and baseoendopod fused. Baseoendopodal lobe longer than exopod, ornamented with sets of inner and outer spinules, with spinules at base of apical seta; armed with one outer, one apical and four inner setae; relative length of setae as in figure 35B. Exopod ornamented with spinules as shown in figure 35B, and armed with five setae in all, plus outer seta of basis.

P6 (figure 35A) represented by median plate in anterior half of first genital somite, each vestigial leg represented by a long and slender seta. Copulatory pore in the middle of genital double segment.

Male. Total body length measured from tip of rostrum to posterior margin of caudal rami, ranging from 430 to 640 μm (mean, 539 μm , $N=15$; allotype, 640 μm). Habitus (figure 39A, B), anal segment and caudal rami (figure 39C, D) as in female dorsally, except for some minute spinules along posterior margin of anal operculum. Ventrally as in female except for genital somite (figure 40A). Ventral ornamentation of third, fourth and fifth urosomites (figure 40A) coarser than in female.

Antennule (figure 40B) six-segmented; subchirocer. Last segment with two acute teeth.

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

P1 (figure 41A) as in female except for comparatively shorter endopod and dimorphic projection on inner distal corner of basis.

P2 (figure 41B) as in female except for relatively stouter outer spines of male exopod, dimorphic inner spine on male ENP 2, and relatively shorter apical setae on second endopodal segment.

Exopod of P3 (figure 42A) as in female except for relatively stronger outer spines. Endopod three-segmented; second segment with inner distal apophysis reaching beyond third endopodal segment, the latter reaching tip of first exopodal

segment, with one inner and one apical seta relatively shorter than their female homologues.

P4 (figure 42B) as in female, except for stouter outer spines of exopod and relatively shorter setae of second endopodal segment.

Both P5 fused (figure 40B); exopod and baseoendopod fused. Exopod ornamented with spinules at base of outer seta of basis, at base of apical elements and along inner margin; with four setae. Endopodal lobe ornamented with spinules along outer and inner margin, and at base of apical setae; with three elements in all.

P6 (figure 40A) represented by plate; without armature.

Variability

Male. Paratype (EMUCOP-1298-03) possesses a reduced apical seta on right P1 ENP 2, and an abnormally swollen apical element on right P2 EXP 3; paratype (EMUCOP-1298-09) possesses an aberrant right P1 ENP 2, with two setae; the gap between innermost and adjoining seta of P5 BENP is larger in right P5 (EMUCOP-1298-09); paratype (EMUCOP-1298-10) possesses two and three setae on right and left P5 BENP, respectively; paratype (EMUCOP-1298-11) possesses one inner seta on left P2 ENP 1 and four setae on P5 BENP.

Female. Paratype (EMUCOP-1298-05) possesses a reduced inner seta on left P4 ENP 2; paratype (EMUCOP-1298-06) with three setae on both P4 ENP 2; paratype (EMUCOP-1298-07) possesses an abnormal inner distal seta on left P1 ENP 2 and a reduced seta on right P4 ENP 2.

Discussion

Taxonomic status of nominal species

In 1897 Richard described *Mesochra* (= *Cletocamptus*) *deitersi* from the Naposta Grande River, Argentina. Unfortunately, Richard gave no other indication regarding the exact location of the type locality. At the time of Richard's (1897) description of *C. deitersi*, only three other species (*C. retrogressus*, *C. albuquerqueensis* and *C. confluens*) of the genus were known. Following the available identification keys and tables (i.e. Lang, 1948; Fleeger, 1980), it is clear that *C. deitersi* could be separated easily from the other three species. This ease of separation probably is the result of the incompleteness of Richard's (1897) description of *C. deitersi*.

Since Richard's (1897) description, *C. deitersi* has been reported from inland brines as well as coastal estuaries and mangroves from North America (Willey, 1930, 1932; Yeatman, 1963; Fleeger, 1980; De Laune *et al.*, 1984; Chandler, 1986; Decho, 1986, 1988; Chandler and Fleeger, 1987; Sun and Fleeger, 1994; Dexter, 1995; Pace and Carman, 1996; Carman *et al.*, 1997, 2000; Simpson *et al.*, 1998; Rocha-Olivares *et al.*, 2001; personal observations by S.G.), Central and South America (Richard, 1897; Daday, 1902; Brian, 1926; Kiefer, 1933, 1936; Brehm, 1937; Harding, 1955; Herbst, 1960; Löffler, 1963; Reid and Esteves, 1984; Sitjar, 1988; Escaravage and Castel, 1989; Zamudio-Valdéz, 1991; Suárez-Morales *et al.*, 1996; Reid, 1998; Suárez-Morales and Reid, 1998; personal observations by S.G.), India (Ranga Reddy and Radhakrishna, 1979), China (Tai and Song, 1979), Ethiopia (Dussart, 1974; Defaye, 1988), Hawaii (Chappuis, 1934), Australia (Hamond, 1973), Iran (Löffler, 1961) and Malaysia (personal observations by S.G.).

However, recent evidence (Rocha-Olivares *et al.*, 2001; Castro-Longoria *et al.*, 2003; personal observations by S.G.) strongly supports the hypothesis that all these records are not of *C. deitersi* but of new and as yet undescribed species.

Cletocamptus deitersi, as constituted above, expresses a high degree of polymorphism within and between populations, making the correct separation between species related to *C. deitersi* difficult. Discrepancies between the different descriptions forced Chappuis (1924) to consider *Godetella dadayi* Delachaux, 1917 as a synonym of *Mesochra* (= *Cletocamptus*) *deitersi*. Chappuis (1933, but see Lang, 1948: 1274) recognized the discrepancies between the different descriptions and suggested that, given the small differences that were used to separate the genera *Marshia* Herrick, 1894 and *Godetella* Delachaux, 1917 from *Cletocamptus*, the former two genera should be equated to the latter. Similarly, Chappuis (1933), Kiefer (1936) and Brehm (1937) suggested that both *C. brehmi* Kiefer, 1933 and *C. bermudae* Willey, 1930 were synonyms of *C. deitersi*. Similarly, Chappuis (1933) placed Wilson's (1932) *Attheyella bicolor* Wilson, 1932 from Massachusetts within *Cletocamptus* since 'Sie scheint *C. bermudae* sehr ähnlich zu sein, gehört also in die Nähe von *C. deitersi*'. Later, in his redescription Yeatman (1963: 201–204) concluded that Wilson's paratypes of *A. bicolor* and *C. bermudae* are the same species. Moreover, upon comparison with Kiefer's (1936) and Richard's (1897) descriptions of *C. deitersi*, Yeatman (1963) concluded that *C. bermudae* was a synonym of the latter. Having been found in the same area, *A. bicolor* and *C. bermudae* could well belong to the same species. However, since Richard's (1897) and Kiefer's (1936) descriptions of *C. deitersi* were based on highly conservative features that are not useful for species separation, their respective species are considered herein as *species inquirenda* within *Cletocamptus* (see below). In the light of current research, it is quite possible that *Godetella* (= *Cletocamptus*) *dadayi*, *C. brehmi* and *C. bermudae* belong to different species. It is suggested to consider these three species as *species inquirenda* within *Cletocamptus* pending redescription based on type or topotype material. [2]

Chappuis (1934) found some specimens of *Cletocamptus* from Oahu island (Hawaii). He identified his specimens with the Argentinean *C. deitersi* and presented only four illustrations including the male P2 ENP, P3 ENP, P4 ENP and P5 (Chappuis, 1934: 634, figures 7–10). It is suggested to consider Chappuis' (1934) *Cletocamptus deitersi* as *species inquirenda* within the genus until redescription of topotype material since Chappuis' material is not available for revision or does not exist.

Kiefer (1936) found some specimens of *Cletocamptus* in Trou Caiman (Haiti). This material was examined by Chappuis (Kiefer, 1936: 301) who was of the opinion that Kiefer's material of *Cletocamptus* from Haiti could be attributed to *C. deitersi* even though he also recognized the lack of detail of Richard's (1897) and Daday's (1902) description of the species upon which he based his conclusions. Unfortunately, Kiefer (1936) omitted the written description since 'die ... Zeichnungen ein genaueres Bild vom Aussehen der wichtigsten Merkmale zu vermitteln vermögen, als es Worte könnten'. On the other hand, Kiefer (1936) included 11 illustrations (dorsal and ventral view of the female abdomen, antennal endopod and exopod, female P1–P5, ventral view of male abdomen, male P3 and male P5), but the mandible and maxillule were omitted and nothing can be said regarding their armature formulae. Taking into account that Chappuis attributed Kiefer's (1936) material to *C. deitersi* based on Richard's (1897) and Daday's (1902) [3]

descriptions which lack the necessary detail, that nothing is said about the armature of the mandible and maxillule in Daday's (1902) and Kiefer's (1936) descriptions, and that these two descriptions and the drawings included therein lack the necessary detail for species separation, Kiefer's (1936) and Daday's (1902) material of *C. deitersi* are considered herein as *species inquirendae* within *Cletocamptus*.

Herbst (1960: 50–52, figures 63–70) found some *Cletocamptus* specimens (four females and two males) in samples taken from the Lake of Nicaragua, which he identified as *C. deitersi*. However, Herbst (1960) based his identification on four female appendages (caudal ramus, P4, P5 and antennal exopod) and three male appendages (P2 ENP, P3 ENP and P5). The structures of these appendages are highly conservative among the populations previously identified with the Argentinean *C. deitersi* worldwide, and are of minor value to separate them. Therefore, the identity of Herbst's material remains questionable and it is suggested to consider the Nicaraguan species as *species inquirenda* within *Cletocamptus* until revision of his material. In the same paper Herbst (1960) briefly described some *Cletocamptus* specimens that were suggested to be a variety of *C. bicolor*. It is suggested to consider Herbst's (1960) *Cletocamptus* cfr. *bicolor* as *species inquirenda* within *Cletocamptus*.

Löffler (1961) described a new species, *C. gabrieli* from Iran, but Fleeger (1980: 31) relegated it to a junior synonym of the Argentinean *C. deitersi* based on the fact that the armature formulae of P1–P4 and antennal exopod of the former falls into the range of variation for the latter. Based on the fact that Fleeger (1980) observed some differences in the spinular ornamentation of *C. gabrieli* and that the species was found in Iran, far from the region where *C. deitersi* could be distributed (see below), it is possible that Löffler's specimens belong to a different species. However, given the quality of Löffler's (1961) original description, *C. gabrieli* should be considered as *species inquirenda* within *Cletocamptus*.

Later, Löffler (1963) described *C. deitersi ecuadorianus* Löffler, 1963 from a site in Upano River, somewhere between Latacunga and Riobamba (Ecuador). Löffler (1963) also recognized that allocation of *Cletocamptus* specimens to new or known taxa was almost impossible due to 'sehr mangelhafter Beschreibungen', questioned Chappuis' (1924) decision to consider *Godetella dadayi* as a synonym of *C. deitersi*. He also recognized the similarity between *C. kummleri* and *C. deitersi*, and suggested to consider *C. dadayi* and *C. kummleri* as subspecies of *C. deitersi*. Löffler's (1963) *C. deitersi ecuadorianus* exhibits a set of characters suggesting that this subspecies could be a different species: (1) mandibular palp with one seta only (Löffler, 1963, remained silent about the small seta arising near the mandibular palp), (2) caudal rami three times longer than wide, (3) female P2 ENP 2 with four setae in all, (4) female P3 ENP 2 with five elements in all, and (5) female P5 with 11 elements in all. *Cletocamptus bermudae* as described by Willey (1930) was shown to possess also one seta only on the mandibular palp, but the author did not comment on the small adjacent seta. During inspection of the material of *Cletocamptus deitersi* housed in the National Museum of Natural History, one of us (S.G.) found some specimens from Embalse Nihuil (on the Atuel River) in Province of Mendoza (Argentina) (USNM264522) possessing the same armature formulae of mandibular palp, female P2 ENP 2, P3 ENP 2, P5 and width/length ratio of caudal rami as described for *C. deitersi ecuadorianus* by Löffler (1963). It is suggested to upgrade *C. deitersi ecuadorianus* to full species rank as *Cletocamptus ecuadorianus* grad. nov. Löffler, 1963. However, the description of the species lacks necessary detail and

4

should be considered as *species inquirenda* within *Cletocamptus* until redescription. It is also suggested to remove the Peruvian *C. kummleri* from its synonymy with *C. deitersi* and to consider it as *species inquirenda* within *Cletocamptus*.

Hamond (1973) reported and described *C. deitersi* from Australia for the first time. Unfortunately, he did omit a detailed description since his material 'agreed so closely with the descriptions in Lang (1948) and Yeatman (1963) as to make a detailed description unnecessary' (Hamond, 1973). From his illustrations, it can be observed that Hamond's (1973) material seems to be unique among the specimens assigned to *C. deitersi*, since it differs in the armature of antennal allobasis (with one inner seta only), presence of a slender seta on basis of maxilliped, claw of maxilliped without accompanying seta, armature formula of proximal endite of maxilla (with two setae only), armature formula of maxillary endopod (with two setae only) and armature of claw of maxillary basis (without accompanying seta). Some other features observed in the Australian specimens do not correspond to *C. deitersi* as described by Richard (1897), but with *C. simpsoni* sp. nov. from Alabama (USA): mandibular palp of mandible with two setae and without the small seta arising nearby, lateral seta of maxillary arthrite slender, and armature formula of female P1–P5. Assuming that the Australian specimens belong to a different species, it is suggested to consider Hamond's (1973) *C. deitersi* as *species inquirenda* within *Cletocamptus* until careful re-examination.

Dussart (1974) reported *C. deitersi* from Ethiopia for the first time. Some years later Defaye (1988) redescribed Dussart's material and stated that 'Cette espèce, découverte en Ethiopie par Dussart (1974) et encore inconnue ailleurs en Afrique, n'a pas été retrouvé'. Although Defaye (1988) claimed that the presented figures 5 'permettront aisément son identification', Dussart (1974) observed subtle differences between his material and Kiefer's (1936) illustrations of *C. deitersi*. Again, the appendages illustrated by Dussart (1974) and Defaye (1988) are of minor value for species discrimination. It is proposed to consider Dussart's (1974) *C. deitersi* as *species inquirenda* within *Cletocamptus* until detailed redescription of his material.

Tai and Song (1979) reported and described some *Cletocamptus* specimens which they assigned to *C. deitersi*. Tai and Song's (1979) specimens resemble *C. simpsoni* sp. nov. from Alabama (USA) in the armature formula of female P1–P5. Unfortunately, Tai and Song (1979) did not illustrate the male of their *C. deitersi* and remained silent about the morphology/armature of mouth appendages. In the light of current research and given the fact that Tai and Song's (1979) description lacks necessary detail, it is suggested to consider their *C. deitersi* as *species inquirenda* until redescription of the material upon which the description was made.

That same year, Ranga Reddy and Radhakrishna (1979) reported *C. deitersi* from India, but decided to omit any description 'since the species is one, already well defined, presenting no problem of identification' and 'any mention of its characters appears redundant'. Therefore, Ranga Reddy and Radhakrishna's (1979) record of *C. deitersi* is considered herein as doubtful until thorough description of the Indian material.

Dussart and Frutos (1986) reported *C. deitersi* from Pilagá River (Argentina), but they did not include any figure or comment about the *Cletocamptus* specimens. This record of *C. deitersi* is considered herein as doubtful.

Sitjar (1988) found some specimens of *C. deitersi* from the type locality. Unfortunately, Sitjar (1988) did not present any description of any appendage to

support his identification, and mentioned only that the species is restricted to Chaco, Santa Fe, Buenos Aires and Santa Cruz, having been found in Parque Mayo in June and August 1985. More unfortunate is the fact that Sitjar's material is almost certainly unavailable as it could not be traced. As mentioned before, the brief original description of *C. deitersi* and lack of voucher material for detailed comparisons have caused researchers to erroneously attribute specimens of *Cletocamptus* worldwide to the Argentinian *C. deitersi*. Consequently, this has led to an underestimated harpacticoid diversity, at least in the neotropics, where at least 24 populations of *Cletocamptus* have been erroneously identified with *C. deitersi*. Given the fact that *C. deitersi* is far from being a well-known species, and that there is not a single specimen from the type series available for detailed study, it is suggested to consider *C. deitersi* (Richard, 1897) as *species inquirenda* until rediscovery of the species from the type locality and designation of a neotype in terms of Article 75.5 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature, 1999). Due to the fact that Sitjar's (1988) material is not available for further studies, it is suggested to consider his record as unverifiable at present.

Zamudio-Valdés (1991) reported some specimens from Coahuila (central Mexico). Unfortunately, Zamudio-Valdés' (1991) material seems not to be available for it could not be traced. Therefore, Zamudio-Valdés' (1991) record of *C. deitersi* is considered herein as doubtful until rediscovery and detailed description of the Coahuilan specimens of *Cletocamptus*.

Suárez-Morales *et al.* (1996) reported *C. deitersi* from the Yucatán Peninsula. These authors stated that the species was found in Cenote Gigantes (Quintana Roo) (see Suárez-Morales *et al.*, 1996: 226). However, in their figure 125 (p. 267), *C. deitersi* is indicated to be found in northern Yucatán. Dr Tomas Iliffe assured that the species was found in Cenote Khala-Ha and Cenote Chan Hoch in central Yucatán (see Suárez-Morales *et al.*, 1996: 70, figure 15) (T. Iliffe, 2001, personal communication). On the other hand, Dr Eduardo Suárez-Morales suggested that the samples where *C. deitersi* was found could have been taken from Cenote Gigantes by someone else (E. Suárez, 2001, personal communication). Unfortunately, this material does not seem to be available for it could not be traced. It is obvious that this material was identified based on the very conservative armature formula of female P1–P5 and armature formula of mandibular palp (Suárez-Morales *et al.*, 1996: 242, figure 84). Although the high-quality illustrations of the female habitus (Suárez-Morales *et al.*, 1996: 241, figure 83) suggest that the Yucatán specimens bear a strong resemblance to *C. sinaloensis* sp. nov. and *C. deborahdexteræ* sp. nov., some other features should be redescribed in more detail (i.e. ventral ornamentation of body somites, maxillule and female antennule). Given the fact that the identity of the Yucatán specimens is uncertain, it is suggested to consider such material as *species inquirenda* within *Cletocamptus* until rediscovery and detailed redescription.

Recently, Mielke (2000) described two new species from the Galápagos, *C. axi* and *C. schmidtii*. Despite Richard's (1897) brief description, Mielke (2000) argued that 'the two new *Cletocamptus* species from the Galapagos Archipelago, *C. axi* and *C. schmidtii*, are closely related to the almost cosmopolitan *C. deitersi* (Richard, 1897)'. He also noticed that according to the intraspecific variability observed by some other authors 'both forms of Galápagos specimens could also be classed with' *C. deitersi* 'without any problems'. He goes further and noticed that 'if Richard's (1897) original description of *C. deitersi* is taken as a basis for

comparison, then *C. axi* most closely resembles this species...'. Mielke (2000) found some differences between his *C. axi* and Richard's (1897) description of *C. deitersi*. However, as suggested by Mielke (2000), the 'differences between Richard's and *C. axi* 'could be due the different interpretation of the minute body appendages'. Since *C. axi* could well be identified with the Argentinian *C. deitersi* and given the fact that Mielke (2000) did not support the creation of *C. axi* with any other argument than '...although partial populations of so-called cosmopolitan species can show morphological discrepancies, the common occurrence in the same area ... is rather an indication of the existence of two distinct species', a more detailed description of dorsal and ventral ornamentation of body somites of *C. axi* is required.

Cletocamptus schmidti is considered herein as a valid species different from *C. deitersi* based mainly on the ornamentation of the anal operculum and surface ornamentation of body somites dorsally, armature formula of P3 EXP 3 (with two inner setae), and dimorphic outermost apical spine on male P3 EXP 3. About the armature of mandibular palp and maxillary arthrite, Mielke (2000) just noticed that it agrees with those of *C. axi*. Although we are certain about the specific identity of *C. schmidti*, based on the fact that this species resembles *Cletocamptus* specimens (previously identified with *C. deitersi*) from São Luis island (Maranhao, Brazil) (USNM-250011) in the armature formula of female P1–P5 (the male of the species USNM-250011 remains unknown) (S. Gómez, 2001, personal observations), it is highly advisable to redescribe in detail the dorsal and ventral ornamentation of body somites of *C. schmidti*. Mielke (2000) observed that some specimens of *C. axi* and *C. schmidti* possess a small seta on the male P6. We have not noticed this feature in the North US species herein described, however, the presence of a small seta on male P6 on specimens from São Luis island (Jansen lagoon, Maranhao, Brazil) (USNM242172) suggests that this character may provide useful phylogenetic information.

Geographic distribution and diagnostic characters

The allegedly wide distribution of *C. deitersi* is best explained by the high intraspecific variability of *Cletocamptus* species, and by the fact that virtually all specimens attributed to this species around the globe are morphologically similar and cannot be differentiated on the basis of Richard's (1897) original description. Morphological analyses of armature formula of female P1–P5, body ornamentation, and mandible and maxillule armature formula, strongly support the erection of separate species for the specimens examined here.

Cletocamptus deborahdexteræ sp. nov. and *C. sinaloensis* sp. nov. seem to be very closely related (based on morphology). In fact, their body ornamentation is similar in that they show the typical long spinules along the posterior margin of the cephalothorax and first to third free thoracic somites. Also, the dorsal and ventral spinular pattern is similar in the female of both species, but somewhat different in the male. The only remarkable difference between these two species is the ornamentation of the anal operculum (with more and stronger spinules in *C. sinaloensis* sp. nov.). The armature of the mandible (with a one-segmented endopod armed with two long setae, and with a small seta arising nearby), maxillule and P1–P5 are also identical. *Cletocamptus fourchensis* sp. nov. from Louisiana seems to be related to some extent to *C. deborahdexteræ* sp. nov. and *C. sinaloensis* sp. nov., the only

differences being the ornamentation of the anal operculum (without spinules in the female and with tiny spinules in the male of *C. fourchensis* sp. nov.) and the ventral ornamentation of the female and male urosome. *Cletocamptus stimpsoni* sp. nov. can be easily separated from the other three species by the dorsal ornamentation of body somites (with very short spinules along the posterior margin of the cephalothorax and first to third free thoracic somites). Also, the surface spinular ornamentation of the anal somite is different, being ornamented with several transverse rows of tiny spinules. The ventral spinular ornamentation of female and male urosome is also different, being more sparse in *C. stimpsoni* sp. nov. The most striking feature observed in *C. stimpsoni* sp. nov. is the lack of the small accessory seta of the mandible, the shape of the innermost spinulose element of the maxillular arthrite, which is markedly more slender than in *C. sinaloensis* sp. nov., *C. deborahdexterae* sp. nov. and *C. fourchensis* sp. nov., and above all, the armature formula of P2–P4 (the second endopodal segment of female P3 and second endopodal segment of male P2 with three and two inner setae, respectively; the third exopodal segment of male and female P3 possesses two inner setae and the third exopodal segment of P4 possesses one inner seta). Another salient feature of *C. stimpsoni* sp. nov. is the setiform element of basis of P2. The same element is typically spiniform in the other three species.

Richard (1897) gave an incorrect interpretation of the armature formula of some swimming legs of his *C. deitersi*. Recently, Mielke (2000) presented some amendments to Richard's description. According to Mielke's (2000) amendments and to Richard's (1897) original description, *C. deitersi* could well be similar to *C. deborahdexterae* sp. nov. and *C. sinaloensis* sp. nov. in the ornamentation along the posterior margin of the cephalic shield and first to third free prosomites. Following Richard's description, *Cletocamptus deitersi* also seems to share the armature formula of the antennal exopod with *C. fourchensis*. Unfortunately, Richard (1897) remained silent about the shape of the maxillary arthrite and nothing can be said regarding the lateral strong element ornamented with long spinules. Richard (1897) described the mandibular palp as 'formé de trois courtes soies grêles insérées sur un sorte de petit bouton très difficilement perceptible...'. 6 Obviously this must be a misinterpretation. What Richard (1897) probably observed was, as in the case of other *Cletocamptus* species, a one-segmented mandibular palp with two setae and a small element arising nearby. The armature formula of the endopod of P1 of Richard's *C. deitersi* is not clear yet (P1 ENP 2 was originally described with only two apical setae and without inner armature). In his amendments to Richard's (1897) description, Mielke (2000) included also some data regarding the armature formula of female P2–P5. The anal operculum was described by Richard (1897) as having 'six dents grêles près de la naissance de la furca'. Some median spinules are shown in Richard's description (1897: 268, figure 5).

Congruence of genetic and morphological differentiation

Rocha-Olivares *et al.* (2001) analysed 121 nominal members of *C. deitersi* from North America for DNA sequence variation in two mitochondrial gene regions (cytochrome oxidase I and large subunit rDNA) and three nuclear gene regions (internal transcribed spacer region 1, 5.8S rDNA and internal transcribed spacer region 2). Four extremely differentiated molecular lineages were discovered, and

designated 'major types' I, II, IIIC and IIIM. Rocha-Olivares *et al.* (2001) suggested that the major types qualified as separate species using the genealogical concordance, phylogenetic and biological-species criteria. The morphological analysis presented here was stimulated by these findings, and specimens used in both studies were from the same collections. Morphological and molecular conclusions are completely congruent. The type I of Rocha-Olivares *et al.* (2001) corresponds to *C. stimpsoni*, type II to *C. fourchensis*, type IIIC to *C. deborahdexteræ* and type IIIM to *C. sinaloensis*. The phylogenetic and molecular clock analysis of Rocha-Olivares *et al.* (2001) suggests that *C. deborahdexteræ* and *C. sinaloensis* are most closely related and diverged 4–8 million years ago (based on the cytochrome oxidase I gene). These two species are also most similar to each other based on morphology. Further, sequence data suggest that *C. fourchensis* is most closely related to the type III lineages (*C. deborahdexteræ* and *C. sinaloensis*), and that divergence from these lineages occurred 11–29 million years ago. Finally, *C. stimpsoni* is very different from the other three types based on morphology and molecular data; *C. stimpsoni* diverged from lineages II and III 13–37 million years ago. These data further justify erection of new species for these lineages.

The distribution of genuine *C. deitersi* is, in all probability, limited to the Bahía Blanca region, with probable extensions into the Province of Buenos Aires and La Pampa (Argentina). Erroneous identifications of *Cletocamptus* have led to an underestimation of its diversity worldwide and conceivably resulted in failure to recognize species complexes at individual sites. Rocha-Olivares *et al.* (2001) reported that *C. stimpsoni* and *C. fourchensis* are sympatric both in coastal Louisiana marshes and at an inland brine seep in Alabama, isolated from the open coast. Mielke (2000) also found two species in the same general area in the Galápagos Islands. As a result of inaccurate identifications, conclusions regarding pollution effects on species diversity and genetic diversity may be biased. For example, nominal *C. deitersi* from Louisiana has been shown to increase in abundance under the influence of hydrocarbon pollutants (Carman *et al.*, 1997) but it is not known if *C. stimpsoni* and *C. fourchensis* both respond or if species-specific responses occurred. Rocha-Olivares *et al.* (in preparation) found that *C. stimpsoni* and *C. fourchensis* have similar tolerance to a hydrocarbon exposure but different tolerances to metals, suggesting that these two species may respond differently to toxicant exposure. Misidentifications may also impact studies of pollutant effects on genetic diversity (as found by Street and Montagna, 1996). Care must be taken when identifying and/or describing nominal *C. deitersi*, and special attention should be paid to the surface ornamentation of body somites both ventrally and dorsally, and armature of mandibular palp and maxillular arthrite.

Comparison of the illustrated records of *C. deitersi* (or its alleged synonyms) generates the misleading impression that this species displays a high degree of intraspecific morphological variation. As shown in table 2, intraspecific variation of *C. deborahdexteræ* sp. nov., *C. stimpsoni* sp. nov., *C. sinaloensis* sp. nov. and *C. fourchensis* sp. nov. occurs in specific appendages (i.e. the intraspecific variation of one species seldom overlaps the intraspecific variation of other species), suggesting that intraspecific variability is under genetic control.

Number of species and rates of morphological and genetic evolution

Two independent lines of evidence suggest that a combined morphological/molecular analysis of additional geographical samples of nominal *C. deitersi* will result in the segregation of more species. First, the above review of previous reports of *C. deitersi* indicates that many prior identifications were based on conserved morphological characters (primarily armature formula of swimming legs; table 1) that are generally not diagnostic for species within the *C. deitersi* complex. Second, the four widely separated North US sampling locations surveyed by Rocha-Olivares *et al.* (2001) yielded four morphologically similar but genetically divergent (and presumably geologically old) species. Depending on the biogeographic history of this species complex, additional samples from North America and other continents may yield additional divergent lineages and/or older lineages. These considerations suggest that the *C. deitersi* species complex may prove a good model system for combined morphological/molecular analyses that will improve our understanding of (1) the patterns of phylogenetic congruence between morphological and molecular characters in harpacticoid copepods and invertebrates in general, (2) the relative rates of evolution of different suites of characters, and (3) the possible evolutionary significance of morphological stasis. More pragmatically, additional morphological/molecular analyses of the *C. deitersi* complex offer the possibility of validating the taxonomic utility of particular morphological characters by using genetically identified species as a benchmark.

Acknowledgements

The first author is indebted to Dr Frank Fiers from the Koninklijk Belgisch Instituut voor Natuurwetenschappen (Brussels, Belgium) and Dr Ernest Schockaert from the Limburgs Universitair Centrum (Diepenbeek, Belgium) for their support during a stay in Belgium. We are also grateful to Ms Sc. Ana C. Puello (CIAD-Mazatlán) for providing us with specimens of *C. sinaloensis* sp. nov. from El Yugo estuary, to Mr William G. Keel and Mr Chad T. Walter (Smithsonian Institution) for providing us with the USNM catalogue numbers, and to Berenit Mendoza Garfias (Institute of Biology of the National Autonomous University of Mexico) for the scanning microphotographs. This study is a contribution to project IN202400 and project G.0086.96 and was financed by the 'Programa de Apoyo a Proyectos de Investigación y de Innovación Tecnológica (PAPIIT-UNAM)' and by the Fund of Scientific Research Flanders. This contribution was greatly improved through the thorough revision and criticism of two anonymous referees to whom we are grateful.

References

- BREHM, V., 1937, Weitere Mitteilungen über die Süßwasserfauna von Uruguay. II. Teil. Zur Variabilität der *Boeckella* Bergi Rich, *Zoologischer Anzeiger*, **120**, 301–306.
- BRIAN, A., 1926, Di alcuni copepodi d'acqua dolce dell'Argentina raccolti dal Prof. F. Silvestri, *Memorie della Società Entomologica Italiana*, **4**, 177–200.
- CARMAN, K. R., FLEEGER, J. W. and POMARICO, S., 1997, Response of a benthic food web to hydrocarbon contamination, *Limnology and Oceanography*, **42**, 561–571.
- CARMAN, K. R., FLEEGER, J. W. and POMARICO, S., 2000, Does historical exposure to hydrocarbon contamination alter the response of benthic communities to diesel contamination? *Marine Environmental Research*, **49**, 255–278.
- CASTRO-LONGORIA, E., ALVAREZ-BORREGO, J., ROCHA-OLIVAREZ, A., GÓMEZ, S. and KOBER, V., 2003, Power of a multidisciplinary approach: use of a morphological,

- molecular and digital methods in the study of harpacticoid cryptic species, *Marine Ecology Progress Series*, **249**, 297–303.
- CHANDLER, G. T., 1986, High density culture of meiobenthic harpacticoid copepods within a muddy sediment substrate, *Canadian Journal of Fisheries and Aquatic Science*, **43**, 53–59.
- CHANDLER, G. T. and FLEEGER, J. W., 1987, Facilitative and inhibitory interactions among estuarine meiobenthic harpacticoid copepods, *Ecology*, **68**, 1906–1919.
- CHAPPUIS, P. A., 1924, Sur quelques harpacticoides de la Nouvelle-Guinée et de Patagonie, *Bulletin de la Société des Sciences de Cluj (Roumanie)*, **2**, 96–103.
- CHAPPUIS, P. A., 1933, Zoologische Ergebnisse einer Reise nach Bonaire, Curaçao und Aruba im Jahre 1930. 6. Süß- und Brackwasser-Copepoden von Bonaire, Curaçao und Aruba, *Zoologische Jahrbücher Systematik, Geographie und Morphologie der Tiere*, **64**, 391–404.
- CHAPPUIS, P. A., 1934, Süßwasser Harpacticoiden aus dem Hawaiiischen Inselgebiet, *Bulletin de la Société des Sciences de Cluj (Roumanie)*, **7**, 631–635.
- DADAY, E., 1902, Mikroskopische Süßwasserthiere aus Patagonien, gesammelt von Dr. Filippo Silvestri, *Természetráji füzetek*, **25**, 201–310.
- DECHO, A. W., 1986, Water-cover influence on diatom ingestion rates by meiobenthic copepods, *Marine Ecology Progress Series*, **33**, 139–146.
- DECHO, A. W., 1988, How do harpacticoid grazing rates differ over a tidal cycle? Field verification using chlorophyll-pigment analyses, *Marine Ecology Progress Series*, **45**, 263–270.
- DEFAYE, D., 1988, Contribution à la connaissance des Crustacés Copépodes d’Ethiopie, *Hydrobiologia*, **164**, 103–147.
- DE LAUNE, R. D., SMITH, C. J., PATRICK, W. H., JR., FLEEGER, J. W. and TOLLEY, M. D., 1984, Effect of oil on salt marsh biota: methods for restoration, *Environmental Pollution*, **36**, 207–227.
- DEXTER, D. M., 1995, Salinity tolerance of *Cletocamptus deitersi* (Richard 1897) and its presence in the Salton Sea, *Bulletin Southern California Academy of Sciences*, **94**, 169–171.
- DUSSART, B. H., 1974, Contribution à l’étude des copépodes des eaux douces d’Ethiopie, *Bulletin de l’Institut Française d’Afrique Noire*, **36**, 92–116.
- DUSSART, B. H. and FRUTOS, S. M., 1986, Sur quelques copépodes d’Argentine. 2. Copépodes du Paraná Medio, *Revue d’Hydrobiologie Triopicale*, **19**, 241–262.
- ESCARAVAGE, V. and CASTEL, J., 1989, Application de la notion de confinement aux peuplements méiobenthiques des lagunes endiguées du Bassin d’Arcachon (Côte atlantique), *Acta Oecologica/Oecologia Generalis*, **10**, 1–17.
- FLEEGER, J. W., 1980, Morphological variation in *Cletocamptus* (Copepoda: Harpacticoida), with description of a new species from Louisiana salt marshes, *Transactions of the American Microscopical Society*, **99**, 25–31.
- GEE, J. M., 1999, A new species of *Cletocamptus* Schmankewitsch 1875 (Copepoda: Harpacticoida) from a mangrove forest in Malaysia, *Hydrobiologia*, **412**, 143–153.
- GÓMEZ, S., 2001, Harpacticoids from a coastal lagoon in north-western Mexico, with notes on their biogeography, in C. E. F. Rocha and J. W. Reid (eds) *Copepod Diversity in the Neotropics*. 7
- GÓMEZ NOGUERA, S. E. and HENDRICKX, M. E., 1997, Distribution and abundance of meiofauna in a subtropical coastal lagoon in the south-eastern Gulf of California, Mexico, *Marine Pollution Bulletin*, **34**, 582–587.
- HAMOND, R., 1973, The harpacticoid copepods (Crustacea) of the Saline Lakes in southeast Australia, with special reference to the Laophontidae, *Records of the Australian Museum*, **28**, 393–420.
- HARDING, J. P., 1955, The Percy Sladen Trust Expedition to Lake Titicaca in 1937. XV. Crustacea: Copepoda, *Transactions of the Linnean Society of London*, **3**, 219–247.
- HERBST, H. V., 1960, Copepoden (Crustacea, Entomostraca) aus Nicaragua und Südperu, *Gewässer und Abwässer*, **27**, 27–54.
- HUYS, R. and BOXSHALL, G. A., 1991, *Copepod Evolution* (London: The Ray Society), 468 pp.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1999, *International Code*

- of *Zoological Nomenclature* (London: The International Trust for Zoological Nomenclature 1999, c/o The Natural History Museum), 306 pp.
- KIEFER, F., 1933, Über zwei Arten der Gattung *Cletocamptus* Schmankewitsch (Copepoda Harpacticoida), *Zoologischer Anzeiger*, **105**, 141–144.
- KIEFER, F., 1936, Freilebende Süß- und Salzwassercopepoden von der Insel Haiti, *Archiv für Hydrobiologie*, **30**, 263–317.
- LANG, K., 1948, *Monographie der Harpacticiden, I and II* (Stokholm: A.-B. Nordiska Bokhandeln), 1682 pp.
- LÖFFLER, H., 1961, Beiträge zur Kenntnis der Iranischen Binnengewässer. II. Regional-limnologische Studie mit besonderer Berücksichtigung der Crustaceenfauna, *Internationale Revue der gesamten Hydrobiologie*, **46**, 309–406.
- LÖFFLER, H., 1963, Zur Ostrakoden- und Copepodenfauna Ekuadors, *Archiv für Hydrobiologie*, **59**, 196–234.
- MIELKE, W., 2000, Two new species of *Cletocamptus* (Copepoda: Harpacticoida) from Galápagos, closely related to the cosmopolitan *C. deitersi*, *Journal of Crustacean Biology*, **20**, 273–284.
- MIELKE, W., 2001, *Cletocamptus retrogressus* (Copepoda, Harpacticoida) from irrigation and drainage ditches of the Rhône Delta (Camargue, France), a redescription, *Vie et milieu*, **51**, 1–9.
- PACE, M. C. and CARMAN, K. R., 1996, Interspecific differences among meiobenthic copepods in the use of microalgal food resources, *Marine Ecology Progress Series*, **143**, 77–86.
- POR, F. D., 1986, A re-evaluation of the Cletodidae Sars, Lang (Copepoda, Harpacticoida), *Syllogeus*, **58**, 420–425.
- RANGA REDDY, Y. and RADHAKRISHNA, Y., 1979, A new record of *Cletocamptus deitersi* (Richard, 1895) (Copepoda: Harpacticoida) from India, *Current Science*, **48**, 45.
- REID, J. W., 1998, Maxillopoda-Copepoda, Harpacticoida, in P. S. Young (ed.) *Catalogue of Crustacea of Brazil* (Rio de Janeiro: Museu Nacional), pp. 75–127.
- REID, J. W. and ESTEVES, F. DE A., 1984, Considerações ecológicas e biogeográficas sobre a fauna de copépodos (Crustacea) planctônicos de 14 lagoas costeiras do Estado do Rio de Janeiro, Brasil, in L. D. de Lacerda, D. S. D. de Araújo, R. Cerqueira and B. Turq (eds) *Restingas: Origem, Estrutura, Processos* (Niterói, Brazil: CEUFF), pp. 305–326.
- RICHARD, J., 1897, Entomostracés de l'Amérique du Sud, recueillis par MM. U. Deiters, H. Von Ihering, G. W. Müller et C. O. Poppe, *Mémoires de la Société Zoologique de France*, **10**, 263–301.
- ROCHA-OLIVARES, A. J., FLEEGER, J. W. and FOLTZ, D. W., 2001, Decoupling of molecular and morphological evolution in deep lineages of a meiobenthic harpacticoid copepod, *Molecular Biology and Evolution*, **18**, 1088–1102.
- SIMPSON, E. P., GONZÁLEZ, M. R., HART, C. M. and HURLBERT, S. H., 1998, Salinity and fish effects on Salton Sea microecosystems: benthos, *Hydrobiologia*, **381**, 153–177.
- SITJAR, C. C., 1988, Crustáceos del arroyo Naposta Grande (Provincia de Buenos Aires, Argentina), *Spheniscus*, **6**, 63–72.
- STREET, G. T. and MONTAGNA, P. A., 1996, Loss of genetic diversity in Harpacticoida near offshore platforms, *Marine Biology*, **126**, 271–282.
- SUÁREZ-MORALES, E. and REID, J. W., 1998, An updated list of the free-living freshwater copepods (Crustacea) of Mexico, *The Southwestern Naturalist*, **43**, 256–265.
- SUÁREZ-MORALES, E. J., REID, J. W., ILIFFE, T. M. and FIER, F., 1996, *Catálogo de los copépodos (Crustacea) continentales de la Península de Yucatán, México* (Mexico: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) and El Colegio de la Frontera Sur (ECO-SUR), Unidad Chetumal), 296 pp. 8
- SUN, B. and FLEEGER, J. W., 1994, Field experiments on the colonization of meiofauna into sediment depressions, *Marine Ecology Progress Series*, **110**, 167–175.
- TAI, A.-Y. and SONG, Y.-Z., 1979, Harpacticoida Sars, 1903, in C.-J. Shen (ed.) *Fauna Sinica, Crustacea, Freshwater Copepoda* (Beijing: Science Press), pp. 164–300. 9
- WILLEY, A., 1930, Harpacticoid Copepoda from Bermuda. Part I, *Annals and Magazine of Natural History*, **10**, 81–114.
- WILLEY, A., 1932, Copepod phenology. Observations based in new material from Canada and Bermuda, *Archivio zoologico italiano*, **16**, 601–617.

- WILSON, C. B., 1932, Copepods of the Woods Hole Region, Massachusetts, *Bulletin of the United States Natural History Museum*, **158**, 1–635.
- YEATMAN, H. C., 1963, Some redescrptions and new records of littoral copepods for the Woods Hole, Massachusetts region, *Transactions of the American Microscopical Society*, **82**, 197–209.
- ZAMUDIO-VALDÉZ, J. A., 1991, Los copépodos de vida libre (Crustacea, Maxillopoda) del Valle de Cuatro Ciénegas, Coahuila, México. Undergraduate thesis, Autonomous University of Nuevo León, Monterrey, Mexico.

Authors Queries

Journal: **Journal of Natural History**

Title: **Four new species of *Cletocamptus* Schmankewitsch, 1875, closely related to *Cletocamptus deitersi* (Richard, 1897) (Copepoda: Harpacticoida)**

Authors: **S. Gómez *et al.***

Dear Author

During the preparation of your manuscript for publication, the questions listed below have arisen. Please attend to these matters and return this form with your proof. Many thanks for your assistance

Query Reference	Query	Remarks
1	Year OK? (as elsewhere)	
2	any translation?	
3	any translation?	
4	any translation?	
5	any translation?	
6	any translation?	
7	'Gómez, 2001' – Please supply page numbers?	
8	Suárez-Morales et al. 1996, 'Mexico' – supply city?	
9	Tai and Song, 1979 – 'Beijing' OK?	