



Redescription of *Cletocamptus albuquerquensis* and *C. dominicanus* (Harpacticoida: Canthocamptidae *incertae sedis*), and description of two new species from the US Virgin Islands and Bonaire

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Table of contents

Abstract	301
Introduction	302
Material and methods	302
Taxonomy	307
Order HARPACTICOIDA G.O. Sars, 1903	307
Family CANTHOCAMPTIDAE Brady, 1880 <i>incertae sedis</i> (Por 1986)	307
Genus <i>Cletocamptus</i> Schmankevitch, 1875	307
<i>Cletocamptus albuquerquensis</i> (Herrick, 1894)	307
<i>Cletocamptus dominicanus</i> Kiefer, 1934	320
<i>Cletocamptus tainoi</i> sp. nov.	333
<i>Cletocamptus chappuisi</i> sp. nov.	344
Discussion	345
Acknowledgements	356
References	356

Abstract

The history surrounding the identity of *Cletocamptus albuquerquensis* (Herrick, 1894) and *C. dominicanus* Kiefer, 1934 is very complex. This complexity has been exacerbated by incomplete, and in some cases erroneous, original descriptions of these two species. Also, new records from other locations did not describe the significant characters needed to clearly delineate them. This led several authors to consider *C. dominicanus* as a synonym of *C. albuquerquensis*, among other taxonomical considerations regarding, for example, the status of *Marshia brevicaudata* Herrick, 1894. Inspection of biological material from Saskatchewan (southern Canada), Wyoming (central US), Trinidad and Tobago, and the British Virgin Islands, identified by other researchers as *C. albuquerquensis*, as well as of newly collected material from Great Salt Lake (Utah, central US), Puerto Rico, Culebra Island, Vieques Island, St. John Island (US Virgin Islands), San Salvador (Bahamas), and Santa Marta (Colombia), revealed that *C. albuquerquensis* and *C. dominicanus* are distinct and identifiable species, distributed in a more restricted area than previously thought. Additionally, we describe a new species, *C. tainoi* sp. nov., from St. John Island (US Virgin Islands), and we propose another new species, *C. chappuisi* sp. nov., for two males from Bonaire previously identified as *C. albuquerquensis*. Finally, we give some observations on tube-pore-like structures, previously overlooked, on the endopod of the male leg three.

Key words: Crustacea, Copepoda, new species, North America, South America

Introduction

The identities of *Cletocamptus albuquerqueensis* and *C. dominicanus* have become blurred due, on one hand to Herrick's (1894, 1895) fragmentary and erroneous descriptions of *C. albuquerqueensis* and *Marshia brevicaudata*, and Kiefer's (1934) brief description of *C. dominicanus*, and on the other hand, to their intraspecific variability. All this led to a complex history regarding the taxonomic status of these three species. Gómez (2005) suggested that *C. albuquerqueensis* might be a complex of species, and Gómez & Gee (2009) suggested that *C. albuquerqueensis* should be relegated to *species inquirenda*. Before this study, other researchers have identified specimens of *Cletocamptus* Schmankevitch, 1875 from a variety of localities as *C. albuquerqueensis*. In an attempt to disentangle and clarify the identity of *C. albuquerqueensis* and *C. dominicanus*, we analyzed samples from Saskatchewan (Canada), Utah and Wyoming (US), and from the Caribbean islands of Puerto Rico, Culebra, Vieques, St. John Island (US Virgin Islands), San Salvador (Bahamas), Tortola (British Virgin Islands), and Santa Marta (Colombia). These samples include some recently collected by two of us (RG, JMFR) and some housed in the US National Museum. The present contribution aims to better understand the identity of *C. albuquerqueensis* and *C. dominicanus*, their intraspecific variability and distribution. We provide a complete redescription of *C. albuquerqueensis* and *C. dominicanus*, propose a neotype for the former from material recently collected from Farmington Bay (Great Salt Lake, Utah), and we designate a lectotype for the latter using Kiefer's (1934) syntypes housed in The Kiefer Collection at the State Museum of Natural History Karlsruhe, Germany.

Also, we define and describe novel paired structures, called here asprothekes, for *C. albuquerqueensis* and *C. dominicanus*. These structures have been overlooked in previous descriptions, but we confirmed their presence in some other species of the genus. Finally, two new species are described: *Cletocamptus tainoi* from St. John Island (US Virgin Islands), and *C. chappuisi* from Bonaire; the latter identified as *C. albuquerqueensis* by Chappuis (1933).

Material and methods

Field samplings were made in a variety of ponds and sinkholes with a range of salinities, in southern New Mexico, southern Texas and the Rio Grande Valley (US). The aim was to re-collect *C. albuquerqueensis* near Albuquerque, New Mexico, where the species was first collected and described. Unfortunately, Herrick (1894) did not describe nor gave any other information about the exact collection site. Several colleagues made repeated attempts to collect *C. albuquerqueensis* from southern New Mexico but these were unsuccessful. However, four samples were obtained from Farmington Bay (Great Salt Lake, Utah) by Wayne Wurtsbaugh (Utah State University) on June 2, 26, 2008 and April 15, 30, 2009, that contained *C. albuquerqueensis*.

One of us (RG) collected seventy-two samples from Puerto Rico, Culebra Island, Vieques Island and St. John Island (US Virgin Islands) from 2006 to 2010. In addition, twenty-four samples from San Salvador (Bahamas Island) were collected by Douglas Barr (deceased) in 1981, 1992, 1994 and 2000, and made available for this study by Robert Knowlton (George Washington University). These ninety-six total samples were collected from a variety of aquatic habitats and locations that include enclosed coastal salt ponds, salt lagoons behind mangrove forests, and fresh and brackish water ponds. Salinities ranged from 40 to 260 ppt for the salt ponds and lagoons, and from 0 to 4.5 ppt for the fresh and brackish ponds. Sampling depths were less than a meter and most often less than half a meter. Thus, the samples contained a mix of planktonic and hyperbenthic copepods.

One of us (JMFR) collected additional material from Pozos Colorados, Santa Marta, Colombia, in August and November, 2015, using a 45 µm plankton net. This material was fixed and preserved in 70% ethanol.

Field collections from Great Salt Lake were made using a 0.5 m diameter net with 250 µm mesh from a boat. In shallow water salt ponds small plankton nets of 20 and 30 cm mouth diameters and 153 µm or less mesh size were used. These nets were towed by walking, tossed and retrieved by an attached rope or used as a filter with water poured through the net. All samples were preserved in 4% buffered formalin and later transferred to 70% ethanol.

Selected copepods were slowly transferred to 100% glycerin and dissected body parts mounted on glass slides in glycerin.

Additionally, we analyzed the following material housed in the US National Museum (Smithsonian Institution):

Cletocamptus albuquerquensis, USNM No. 310388; Canada; Saskatchewan; Dead Moose Lake; collector U. T. Hammer, 14 July 1990; identification by J. W. Reid.

Cletocamptus albuquerquensis, USNM No. 310389, Accession No. 392560; Canada; Saskatchewan; Big Quill Lake; collector U. T. Hammer, May 29, 1990; identification by J. W. Reid, 2001.

Cletocamptus albuquerquensis, USNM No. 119498, Accession No. 266592; Wyoming; Albany County; Twelve Mile Lake; collector W. W. Rice, 1966; identification by T. E. Bowman.

Cletocamptus albuquerquensis, USNM No. 128929; Trinidad; Caroni; Caroni Swamp; collector B. F. Bacon, 1966; identification by T. E. Bowman, 1969.

Cletocamptus albuquerquensis, USNM No. 278085, Accession No. 416030; Trinidad and Tobago; Chacachacare Island; surface water of salt pond; collector A. L. Kong, May 7, 1993.

Cletocamptus albuquerquensis, USNM No. 306869, Accession No. 2018756; British Virgin Islands; Anegada, Flamingo Pond; collected and identified by L. Jarecki, July 20, 2000.

For dissection we used a Zeiss Stemi SV8 dissecting microscope, with a maximum magnification of 128x. Also, for observations and illustrations, we used an Olympus BH2 compound microscope fitted with differential interference contrast optics, SPlan Apo (apochromatic) objectives and drawing tube. This system increased the effective magnifications so that illustrations were made at 575x when using the 40x objective and 1450x when using the 100x oil immersion objective. We took microphotographs using a Zeiss Supra 25 scanning electron microscope at the Bigelow Laboratory of Ocean Sciences, East Boothbay Harbor, Maine, US. For SEM observations copepods were rinsed in distilled water, dehydrated in a series of absolute alcohol and distilled water solutions (20–95%), with a final three rinses in hexamethyldisilazane (HMDS) for a minimum of 10 minutes each. The dehydrated copepods were mounted on stubs and imaged directly in the SEM with no metallic coating. Bright light microscopy was also used for microphotographs using a Kodak Easy Share C140 digital camera adapted to an Olympus CX31 compound microscope. Size measurements were made using a calibrated ocular disc. Total length measurements were made laterally from the anterior end of cephalosome to the end of the caudal rami. Since only a few specimens from each of the USNM vials could be dissected and observed, the intraspecific and geographic morphological variability is based on these few individuals. We did not consider deformed setae, spines or segments as intraspecific variability but rather as abnormalities. We considered intraspecific variability the presence or lack of well-developed and/or reduced setae and spines, presence of extra segments, and differences in spinular ornamentation of the body somites.

The type material of the new species, *C. tainoi*, is deposited in the US National Museum of Natural History at the Smithsonian Institution (USNM).

Additional material of *C. dominicanus* recently collected by Ray Gerber from St. John Island (US Virgin Islands), Puerto Rico, Culebra, Vieques and San Salvador Island (Bahamas) is deposited in his personal collection at Saint Joseph's College of Maine, Department of Biology, and in the collections of the USNM. Material of *C. dominicanus* from St. John Island (US Virgin Islands), collected by Ray Gerber, is deposited also in the Copepoda collection of the Instituto de Ciencias del Mar y Limnología at Mazatlán (ICML–EMUCOP). Material of *C. dominicanus* from Pozos Colorados (Santa Marta, Colombia), collected by Juan M. Fuentes-Reinés, is deposited in the collection of the Museo de Colecciones Biológicas de la Universidad del Atlántico (UARC) (Barranquilla, Colombia) and in the Copepoda collection of the Instituto de Ciencias del Mar y Limnología at Mazatlán (ICML–EMUCOP).

We could not trace the material upon which Herrick (1894, 1895) based his description of *C. albuquerquensis*. It appears that his material was never deposited in a collection and is most probably lost (Andrew Simons, Bell Museum of Natural History, Interim Curator, in lit.). The designation of a neotype as proposed below for *C. albuquerquensis* is based on the exceptional need of a name-bearing type of the species to define the nominal taxon objectively, and to clarify its taxonomic status and type locality. In the redescription of *C. albuquerquensis* below we give enough evidence that the neotype is consistent with what is known of the species as described by Herrick (1894, 1895) and subsequent records. The material proposed here as neotype for *C. albuquerquensis* was collected from Farmington Bay (Great Salt Lake, Utah), not far from the region where Herrick (1894) found the species for the first time, and it is deposited in the USNM, thus meeting the requirements of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999).

Friedrich Kiefer (1897–1985) deposited many of his types in the State Museum of Natural History Karlsruhe (Germany) where there is a special Copepoda collection with his name, The Kiefer Collection. Dr. Hubert Höfer,

curator of The Kiefer Collection, confirmed the existence of four slides presumably containing the syntypes of *C. dominicanus*; Kiefer (1934) did not designate any type for his material. These four slides were simply labelled as 2076, 2117, 2118 and 2119 (Fig. 1) and no other indication about what the slides contain appears in the labels. We were not able to inspect these four slides, but slide 2076 and 2119 seems to be in good condition; slide 2118 appears to have material under the broken coverslip; slide 2117 is in bad condition, the coverslip is broken and the material is probably lost. Along with the slides, Dr. Höfer found the original drawings shown in Kiefer (1934) and some others that were not included in the description of *C. dominicanus* (Figs. 2, 3). The original drawings of the female anal somite and caudal rami, female P5, and female P4ENP of *C. dominicanus* that appear in Kiefer's (1934) paper are shown in figure 2. Neither the male P2ENP, nor the aberrant spine of what seems to be the last exopodal segment of one of the swimming legs, nor the female P1 appear in Kiefer (1934). The original drawings of the male P2ENP, P2EXP3, P4 and P5, and the female P2 and P3 are shown in figure 3. Of these, only the male P3ENP and EXP1 appear in Kiefer's (1934) paper. After thorough analysis of the labels on these slides and drawings we concluded that the slides presented herein contain the material of *C. dominicanus* used for the description of the species by Kiefer (1934). Also, that there was an additional slide 2120 (not shown), making a total of five slides as follows: slide 2076, female, anal somite and caudal rami, P1, and P4; slide 2119, male, P2, P3, and P4; slide 2117, female, P2, P3, and P5; slide 2120, male, P5 (note: this slide appears to contain a dissected male based on the drawing of the male P5 in Fig. 3, but this slide seems to be missing and is lost; slide 2118, there are no drawings of what is in this slide, but pending inspection, it is considered here, along with the others, as a name-bearing type. Since this is clearly the material upon which Kiefer (1934) based the description of *C. dominicanus* and since he did not designate any type material, these five slides constitute collectively the syntypes (Arts. 72, 73; International Commission on Zoological Nomenclature 1999). Below, we propose the material of slide 2076 as the lectotype of *C. dominicanus* (Art. 74; International Commission on Zoological Nomenclature 1999). This designation is based on the need of a name-bearing type of the species, and to define the nominal taxon objectively. The remaining material becomes paralectotypes and may serve to name a neotype in case the lectotype is lost.

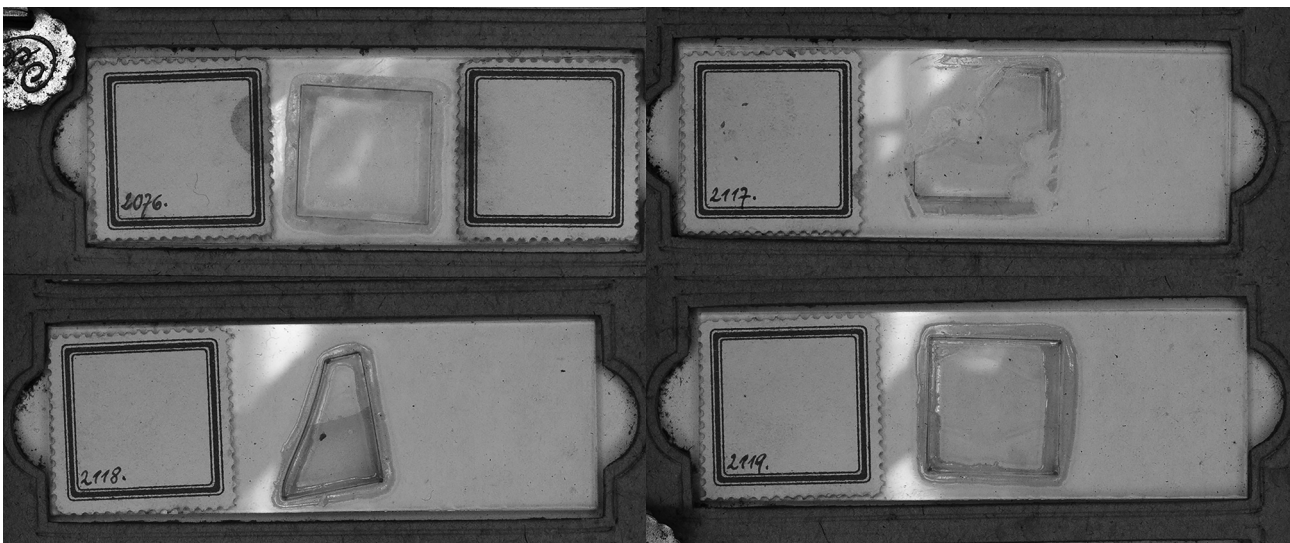


FIGURE 1. Kiefer's slides containing material of *C. dominicanus* Kiefer, 1934. Photograph by Dr. Hubert Höfer, curator of The Kiefer Collection, State Museum of Natural History Karlsruhe (Germany).

Chappuis (1933) deposited his material of *C. albuquerqueensis* from Bonaire in his personal collection (see footnote in Chappuis 1933: 391). Dr. Karen van Dorp, senior manager of the Chelicerata and Myriapoda Collections of The Naturalis Biodiversity Center (The Netherlands), confirmed that Chappuis' (1933) material of *C. albuquerqueensis* is not deposited in the Chelicerata and Myriapoda Collections, and is most probably lost. Following Art. 74.4 (International Commission on Zoological Nomenclature 1999), the specimen illustrated by Chappuis (1933) and described here as *C. chappuisi*, is herein designated as the lectotype, and the only name-bearing type of the species. Though Chappuis' (1933) material of the species no longer exists, this does not invalidate the designation above (Art. 74.4, International Commission on Zoological Nomenclature 1999).

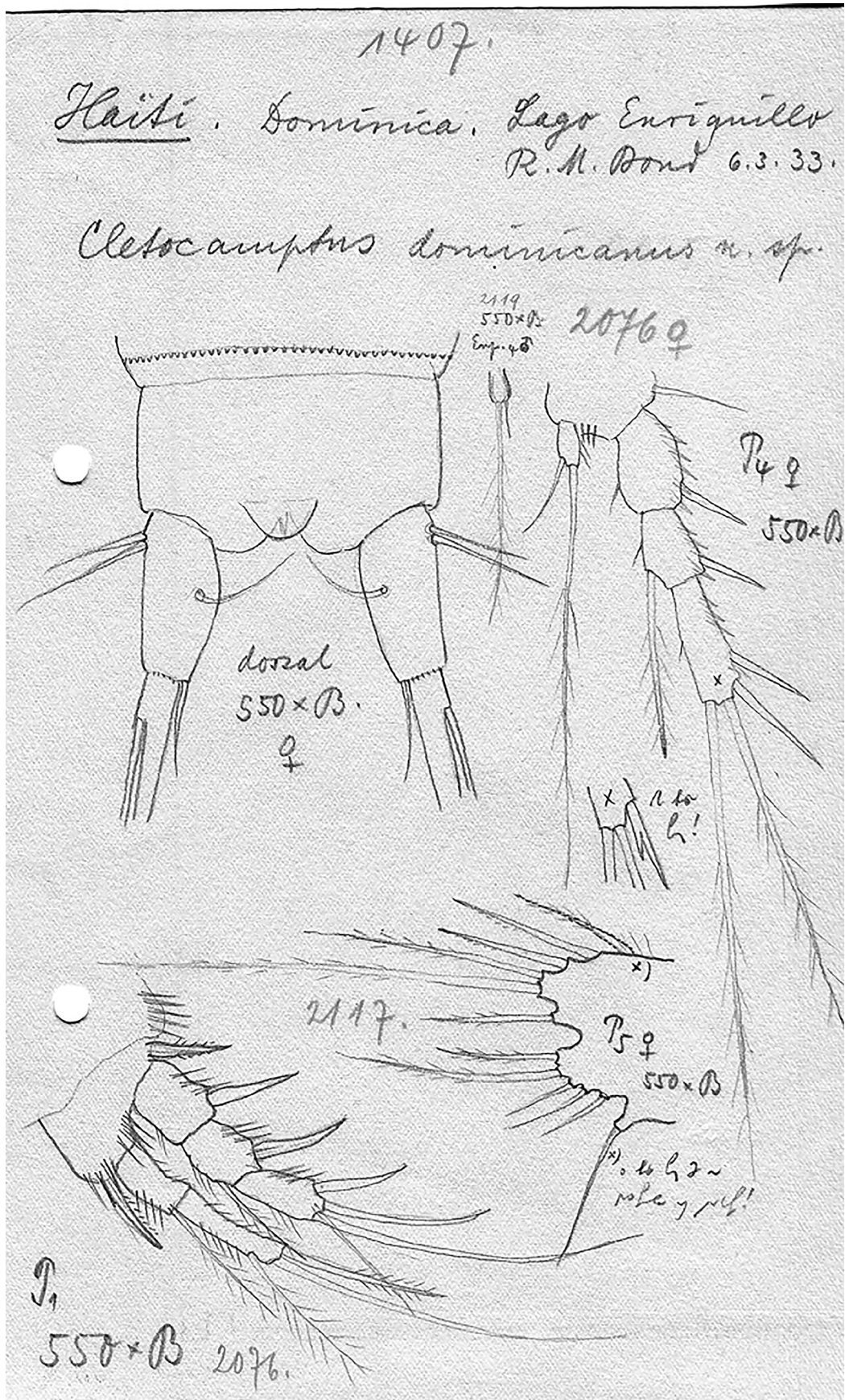


FIGURE 2. Kiefer's original drawings of *C. dominicanus* Kiefer, 1934 showing the female anal somite and caudal rami, female P1, P4, and P5, male P2ENP, and what apparently is the last exopodal segment of P2, P3 or P4. Photograph by Dr. Hubert Höfer, curator of The Kiefer Collection, State Museum of Natural History Karlsruhe (Germany).

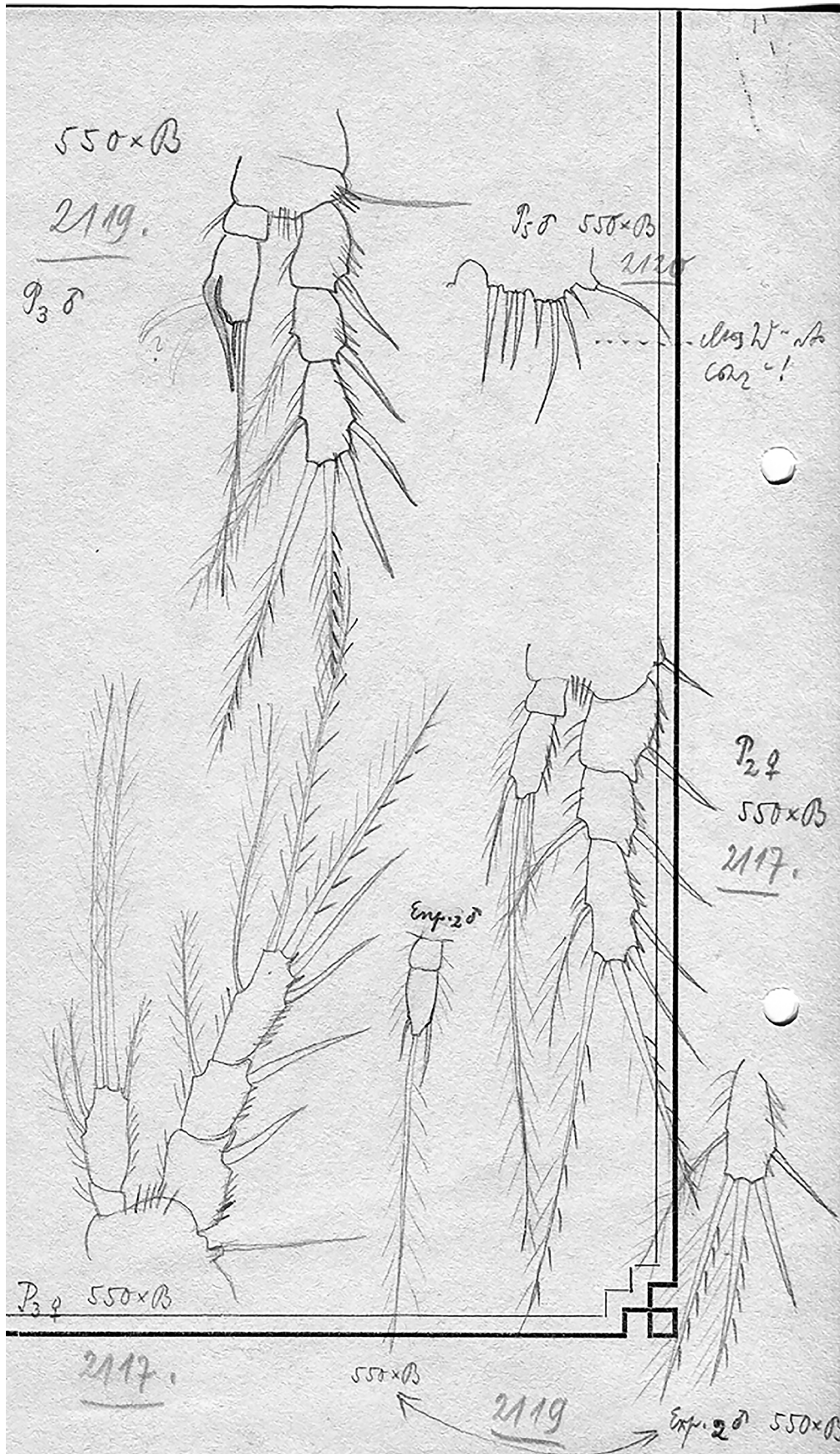


FIGURE 3. Kiefer's original drawings of *C. dominicanus* Kiefer, 1934 showing the female P2 and P3, male P2EXP3, P2ENP, P3, and P5. Courtesy of Dr. Hubert Höfer, curator of The Kiefer Collection, State Museum of Natural History Karlsruhe (Germany).

We used the terminology proposed by Huys & Boxshall (1991) for morphological descriptions. The following abbreviations are used in the text and tables: P1–P6, leg one to six; BENP, baseopod; EXP, exopod; ENP, endopod; P1(P2–P4)EXP(ENP)1(2, 3) indicates the proximal (middle, distal) exopodal (endopodal) segment of P1, P2, P3 or P4; ae, aesthetasc; Uro1–5, first to fifth urosomite; Pro1–3, first to third prosomite; Gds, genital double-somite; ICML–UAMzt, Instituto de Ciencias del Mar y Limnología at Mazatlán. The armature formulae of P1–P4 in Table 1 and Table 3 were prepared following Sewell (1949) and Huys & Boxshall (1991), where spines and setae are denoted by Roman and Arabic numerals, respectively, and the outer element or elements are given first.

The map showing the distribution of *C. albuquerqueensis* and *C. dominicanus*, and the sampling locations where the new species were found were prepared with GeoMapApp (<http://www.geomapapp.org/>) and the Global Multi-Resolution Topography (GMRT) default basemap (Ryan et al. 2009).

Taxonomy

Order HARPACTICOIDA G.O. Sars, 1903

Family CANTHOCAMPTIDAE Brady, 1880 *incertae sedis* (Por 1986)

Genus *Cletocamptus* Schmankevitch, 1875

Cletocamptus albuquerqueensis (Herrick, 1894)

(Figs. 4–14)

Synonymy. *Marshia albuquerqueensis*: Herrick 1894: 41–43, Figs. 1–11, 1895: 136–137, Plates XXXI–XXXII, Figs. 1–5; Dodds 1915: 296, Fig. 80, 1919: 73, Fig. 10, 1920: 95, Table I; Marsh 1918: 780; Weckel 1914: 201; Willey 1923: 7, 1925: 206; Young 1924: 93.

Wolterstorffia albuquerqueensis: Brehm 1913.

Cletocamptus albuquerqueensis: Lang 1936; Lang 1948 (part.); Comita 1951; Brehm 1954, 1965; Ringuet 1958; Wilson & Yeatman 1959; Pallares 1962; Fleeger 1980.

Material examined. Type material: One female neotype preserved in alcohol, USNM No. 1422182; col. Wayne Wurtsbaugh (Utah State University), April 30, 2009; id. Ray Gerber.

Additional material: The vials housed in the US National Museum (Smithsonian Institution) that were analyzed are labeled as follows. Supplementary information about the content of each vial and about the collection site is provided.

Cletocamptus albuquerqueensis, USNM No. 310388; Canada; Saskatchewan; Dead Moose Lake; collector U. T. Hammer, 14 July 1990; identification by J. W. Reid. Notes: This vial contained 13 females and 5 males. Dead Moose Lake surface area is about 10.5 km² and has an average salinity of about 30 gL⁻¹ (Last & Slezak 1986).

Cletocamptus albuquerqueensis, USNM No. 310389, Accession No. 392560; Canada; Saskatchewan; Big Quill Lake; collector U. T. Hammer, May 29, 1990; identification by J. W. Reid, 2001. Notes: This vial contained 20 females and 10 males. Big Quill Lake is about 307 km² (Schmutz 2001) and salinity ranges from 40–85 gL⁻¹ (Hammer & Hurlbert 1992).

Cletocamptus albuquerqueensis, USNM No. 119498, Accession No. 266592; Wyoming; Albany County; Twelvemile Lake; collector W. W. Rice, 1966; identification by T. E. Bowman. Notes: This vial contained 9 males and 1 copepodite. Twelvemile Lake is described as a small (0.08 km²) hypersaline pond, surrounded by salt flats, that fills with water in the spring and dries out by July (Frank Rahel (University of Wyoming) personal communication).

Cletocamptus albuquerqueensis, USNM No. 1297024; Utah, Great Salt Lake, Farmington Bay; collector Wayne Wurtsbaugh (Utah State University), June 2, 2008; salinity, 38 gL⁻¹; identification by Ray Gerber.

Cletocamptus albuquerqueensis, USNM No. 1297025; Utah, Great Salt Lake, Farmington Bay; collector Wayne Wurtsbaugh (Utah State University), June 26, 2008; salinity, 36 gL⁻¹; identification by Ray Gerber.

Cletocamptus albuquerqueensis, USNM No. 1297026; Utah, Great Salt Lake, Farmington Bay; collector Wayne Wurtsbaugh (Utah State University), April 15, 2009; salinity, 20 gL⁻¹; identification by Ray Gerber.

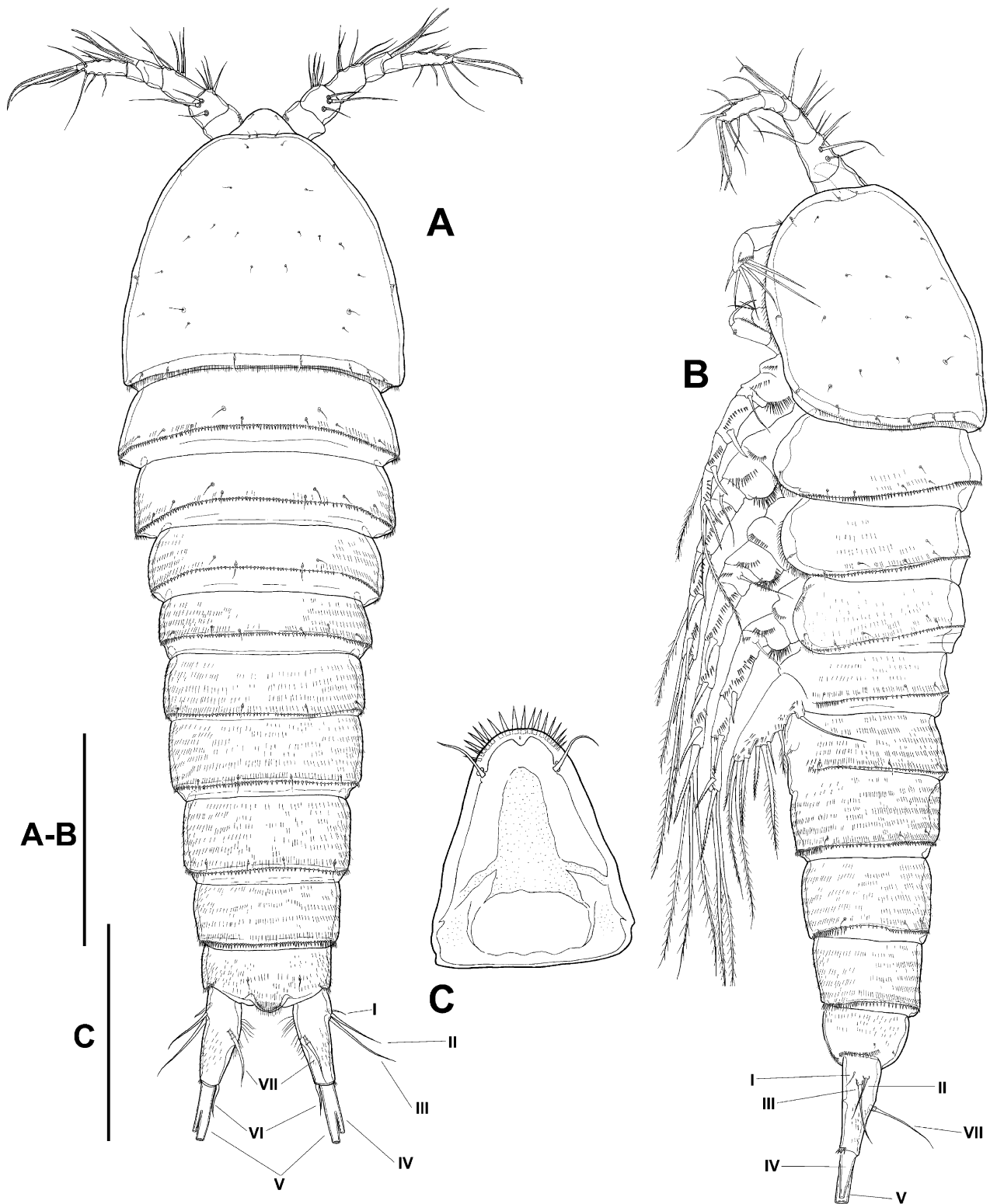


FIGURE 4. *Cletocamptus albuquerqueensis* (Herrick, 1894). Female. A, habitus, dorsal view; B, habitus, lateral view; C, rostrum. Scale bars: A–B= 200 μm ; C= 50 μm .

Cletocamptus albuquerqueensis, USNM No. 1297027; Utah, Great Salt Lake, Farmington Bay; collector Wayne Wurtsbaugh (Utah State University), April 30, 2009; salinity, 15 gL^{-1} ; identification by Ray Gerber.

Type locality. Utah, Great Salt Lake, Farmington Bay (41°3.982'N, 112°13.804'W); salinity, 15 gL^{-1} .

Distribution. Argentina: Luro lagoon (La Pampa Province) (Pallares 1962), Lucio V. Mansilla and Totoralejos

(Córdoba Province) (Brehm 1954, 1965). Canada: Dead Moose Lake and Big Quill Lake (Saskatchewan) (present study). US: Colorado (Dodds 1915, 1919, 1920), North Dakota (Devils Lake) (Willey 1923; Young 1924), Rio Grande Valley (New Mexico) (Herrick 1895), west of Mission (Texas) (Comita 1951), Salt Lake City (Utah) (Comita 1951); Farmington Bay (Great Salt Lake, Utah) (present study), Twelvemile Lake (Albany County, Wyoming) (present study).

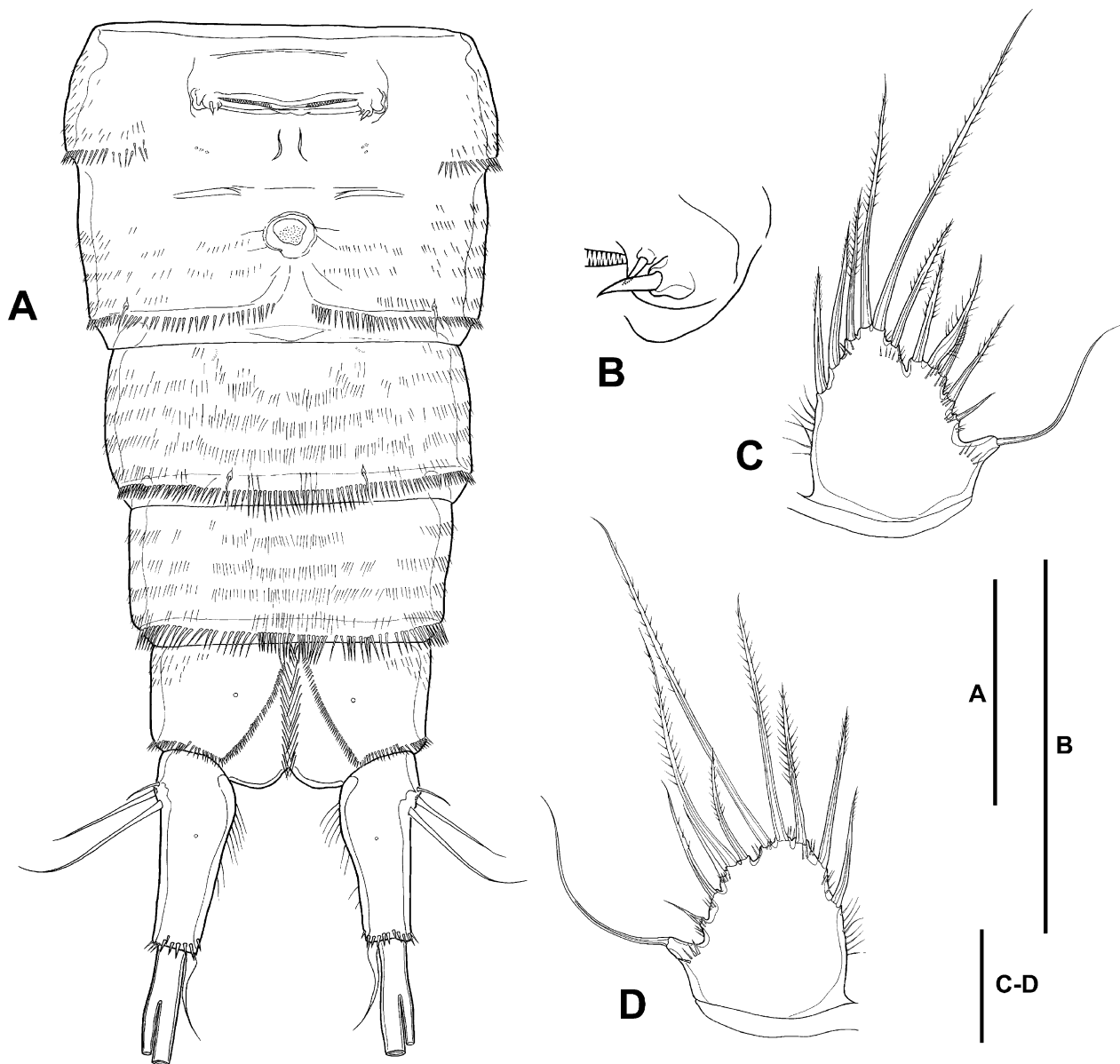


FIGURE 5. *Cletocamptus albuquerqueensis* (Herrick, 1894). Female. A, urosome ventral view (P5 bearing-somite omitted); B, P6; C, P5, anterior; D, variability on P5 showing five setae on the endopodal lobe. Scale bars: A, 100 μm ; B, 50 μm ; C–D, 50 μm .

Redescription (based on specimens from Farmington Bay). Female. Habitus (Fig. 4A, B) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 694 μm to 905 μm (mean= 836 μm ; n= 7). Rostrum set off, triangular, with pair of setules subapically and with row of spinules distally (Fig. 4C). Cephalic shield with small spinules along margin dorsolaterally (Fig. 4A, B). Dorsal and lateral surface of free thoracic somites (P2–P4 bearing-somites) with transverse rows of minute spinules, with short spinules along posterior margin (Fig. 4A, B). Dorsal and lateral surface of first urosomite (P5 bearing-somite) with transverse rows of minute spinules, with row of small spinules along posterior margin (Fig. 4A, B). Second and third urosomites distinct dorsally and laterally (Fig. 4A, B), completely fused ventrally forming genital double-

somite (Figs. 4B, 5A); dorsal and lateral surface of first and second half of genital double-somite with transverse rows of minute spinules, and row of larger spinules along posterior margin of second and third urosomites; ventrally with longer spinules (Fig. 5A); copulatory pore in the middle of genital somite. Ornamentation of fourth and fifth urosomites as in second genital somite dorsally (Fig. 4A, B); ventral surface with transverse rows of minute spinules, with larger spinules along posterior margin (Fig. 5A). Dorsal surface of anal somite (Fig. 4A) with transverse rows of minute spinules and with dorsolateral strong spinules close to joint with caudal rami; rounded anal operculum furnished with spinules (Fig. 4A). Caudal rami (Figs. 4A, B, 5A) about 2.4 times as long as wide; dorsal surface with sparse small spinules, smooth ventrally except for row of spinules close to insertion of caudal setae distally; with seven elements in all (Fig. 4A, B, 5A); seta I small, situated laterally on proximal part of ramus, close to setae II and III, the latter setae longer; setae IV and V fused basally, the former 17%, the latter 54% of total body length; seta VI situated on distal inner corner; seta VII situated dorsally midway length of ramus on inner edge (Fig. 4A, B).

Antennule (Fig. 6A): 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]).

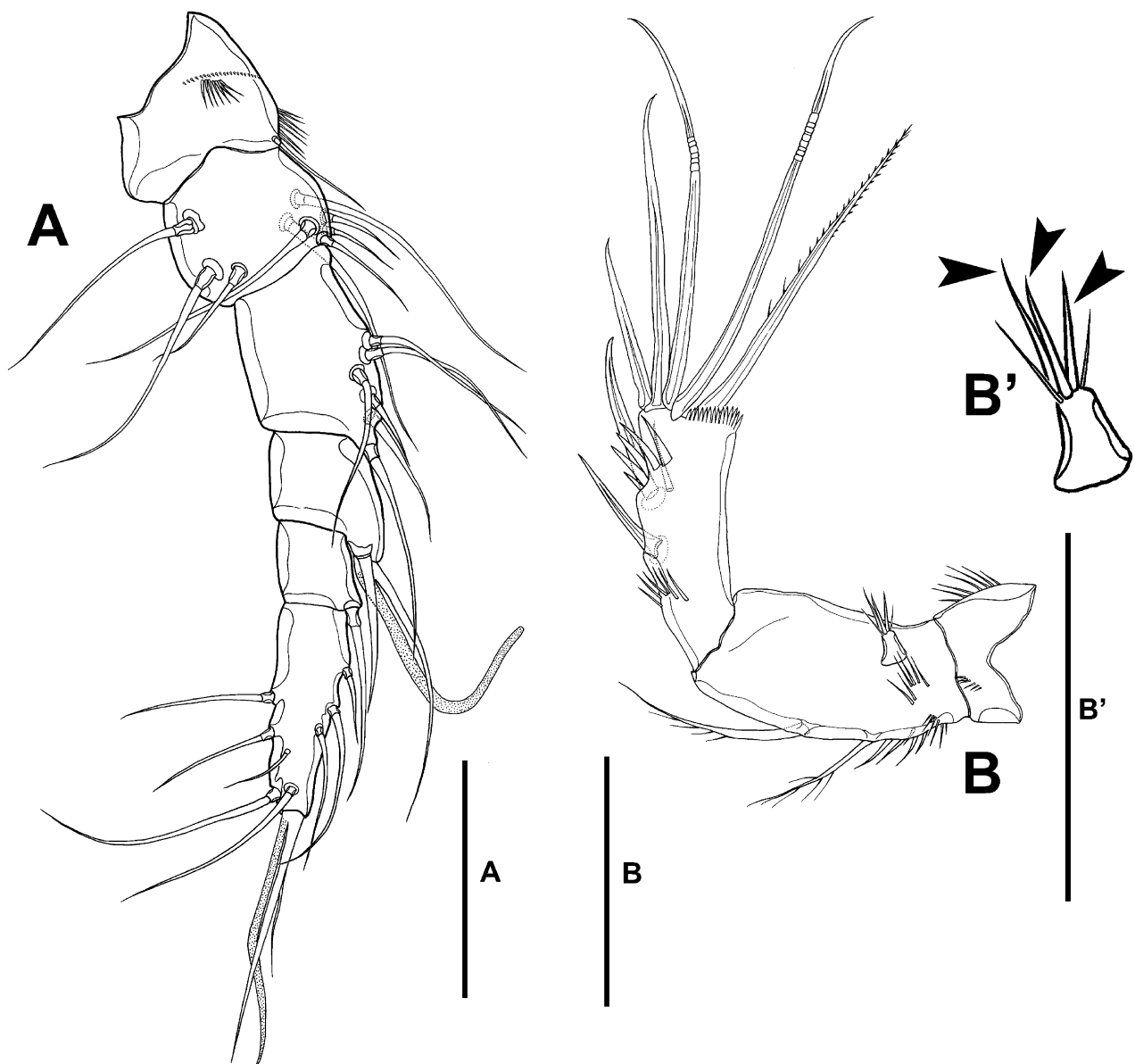


FIGURE 6. *Cletocamptus albuquerquensis* (Herrick, 1894). Female. A, antennule; B, antenna; C, close-up of exopod of antenna. Scale bars: A and B, 50 μ m; B', 25 μ m.

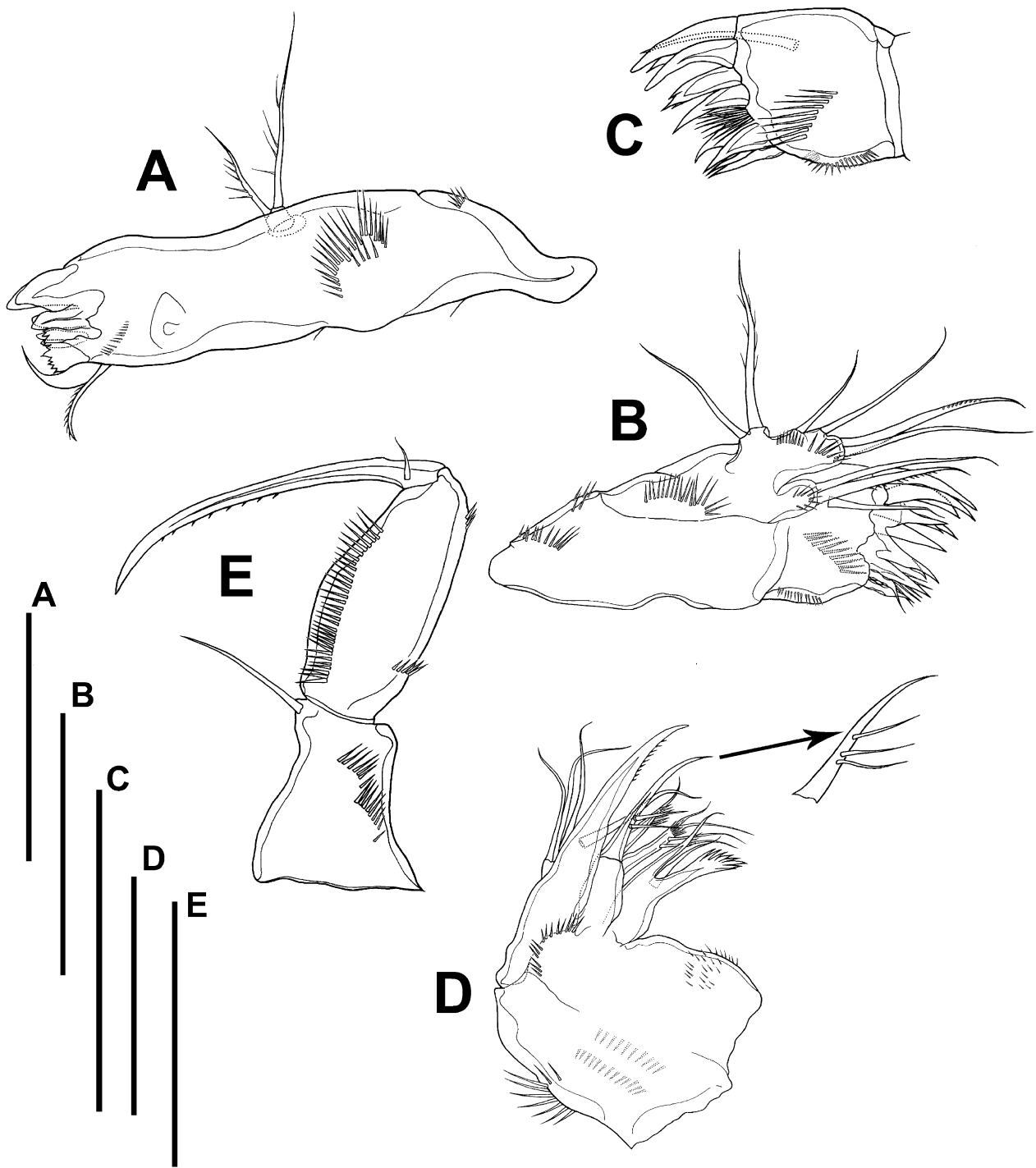


FIGURE 7. *Cletocamptus albuquerqueensis* (Herrick, 1894). Female. A, mandible; B, maxillule; C, praecoaxal arthrite of maxillule, another view; D, maxilla, arrow showing close-up of seta on distal syncoxal endite; E, maxilliped. Scale bars: A, B, C, D, and E, 50 μ m.

Antenna (Fig. 6B, B’): with small coxa ornamented with spinules as shown. Allobasis with two abexopodal setae. Free endopodal segment with inner strong spinules proximally and subdistally; with two lateral inner spines and a slender seta, and five distal elements, two of them geniculate. Exopod small, one-segmented; with few spinules and with 3 somewhat stiff and thick small setae (indicated in Fig. 6B’).

Mandible (Fig. 7A): robust, with spinules proximally; chewing edge with teeth as figured, with one pyriform element and one lateral pinnate seta. Palp one-segmented, with two long setae unequal in length.

Maxillule (Fig. 7B, C): robust; arthrite of praecoaxa with two rows of spinules and one surface seta, eight spines

and two slender setae. Coxa ornamented with some spinules, with two slender setae. Basis with spinules as figured, with two apical setae. Exopod and endopod incorporated to basis, represented by two setae each.

Maxilla (Fig. 7D): syncoxa with spinules along inner and outer margin, and close to joint with allobasis; with two endites, each bearing three setae. Allobasis drawn into strong claw with one accompanying seta. Endopod represented by three setae.

Maxilliped (Fig. 7E): subchelate. Syncoxa with row of spinules, with one seta on inner distal corner. Basis without armature, with longitudinal row of inner spinules, and with few outer spinules proximally and subdistally. Endopod drawn into long and slender claw with one accompanying small seta.

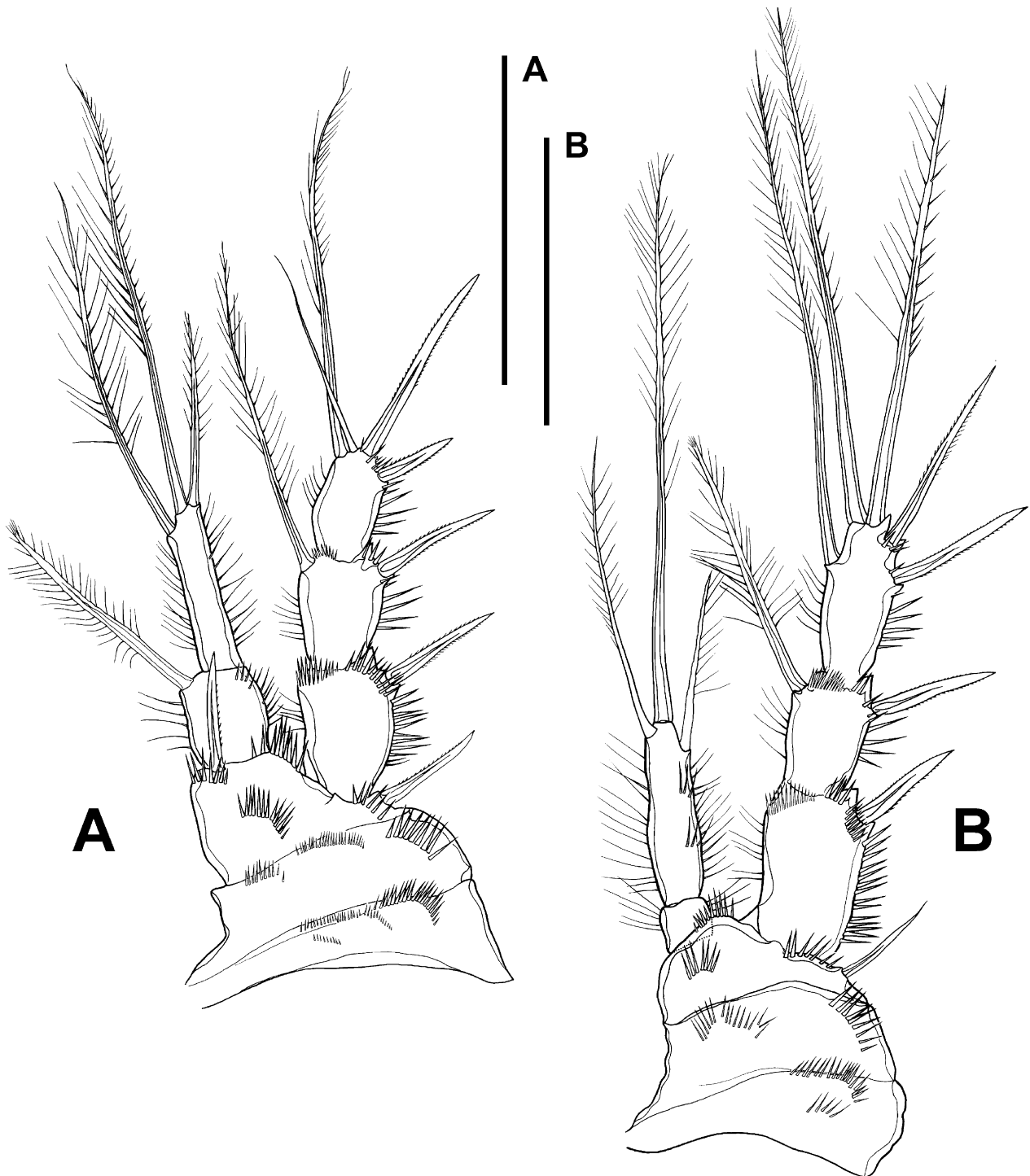


FIGURE 8. *Cletocamptus albuquerqueensis* (Herrick, 1894). Female. A, P1, anterior; B, P2, anterior. Scale bars: A and B, 50 μm .

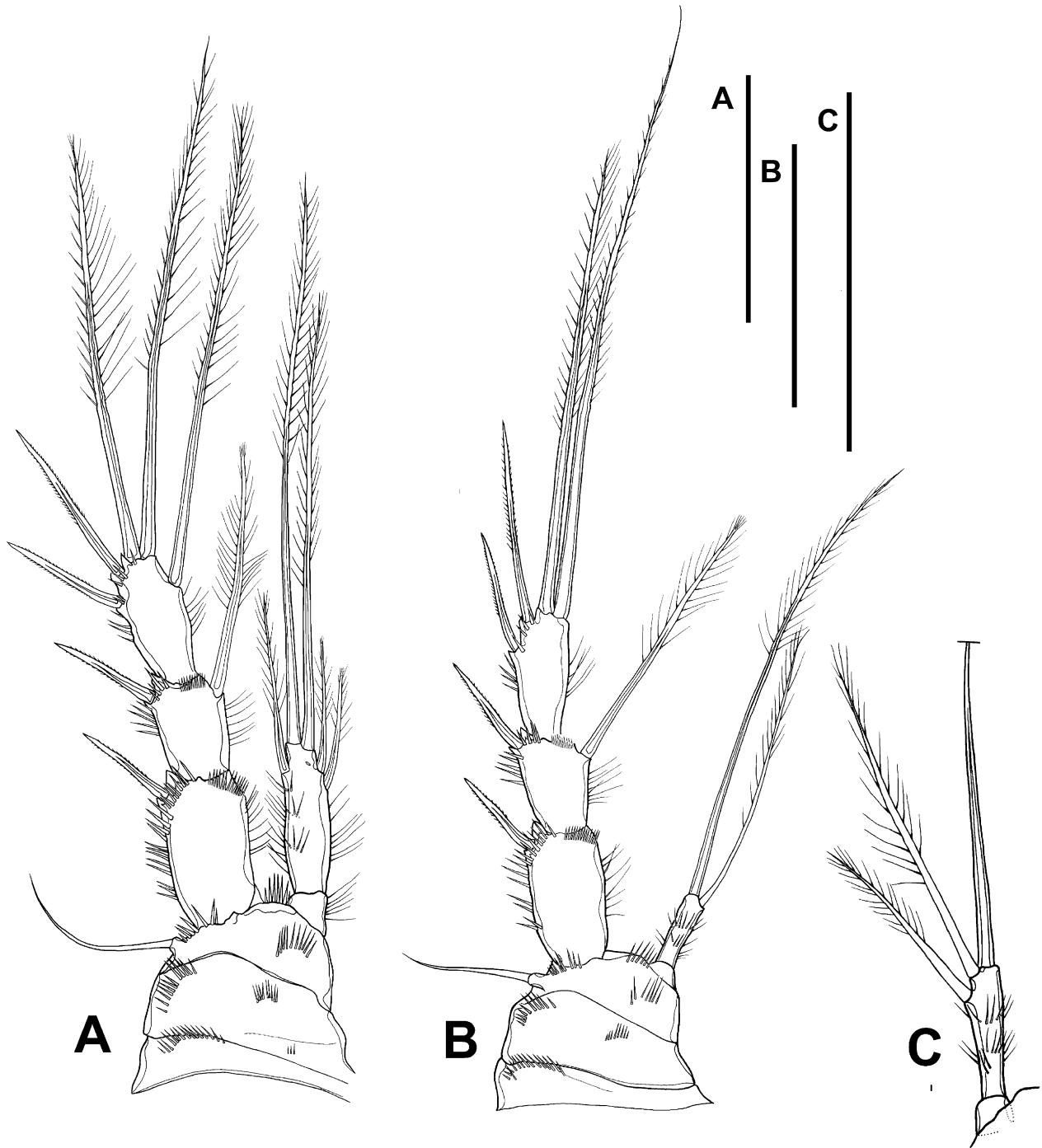


FIGURE 9. *Cletocamptus albuquerqueensis* (Herrick, 1894). Female. A, P3, anterior; B, P4, anterior; C, variability on endopod of P4 with three setae. Scale bars: A, B, and C, 100 μ m.

P1 (Fig. 8A): praecoxa with three groups of spinules close to joint with coxa. The latter with anterior transverse rows of spinules, and with stronger spinules close to outer distal corner. Basis with inner and outer spine; with median rows of spinules and with stronger spinules at base of exopod near outer spine, between exopod and endopod, and at base of inner spine. Exopod three-segmented; EXP1 without, EXP2 with inner seta; EXP3 with four elements. Endopod two-segmented, reaching proximal third of EXP3; first segment with inner seta relatively short, barely as long as both segments combined, with brush tip; second segment with one inner and two apical elements.

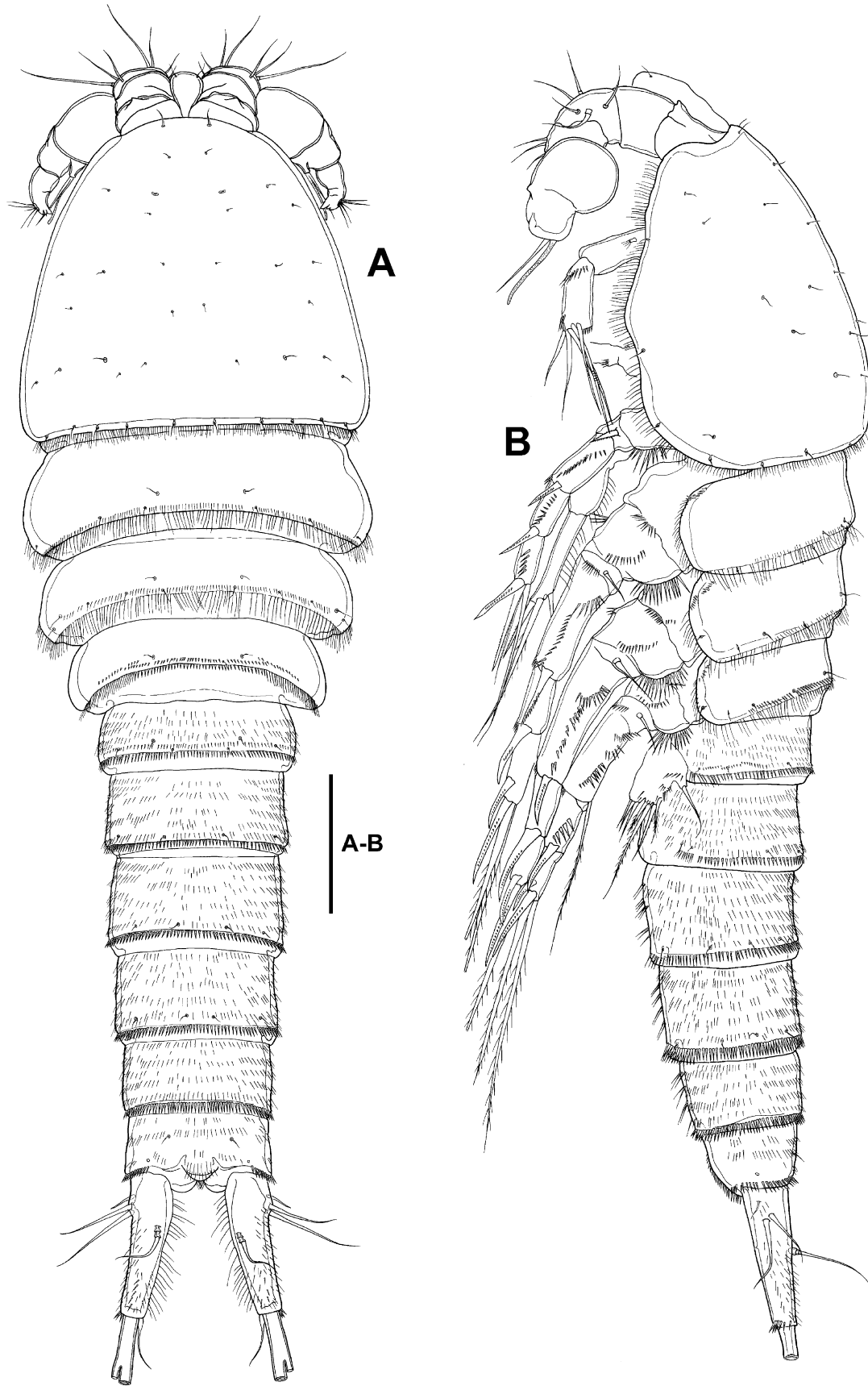


FIGURE 10. *Cletocamptus albuquerqueensis* (Herrick, 1894). Male. A, habitus, dorsal view; B, habitus, lateral view. Scale bars: A–B, 100 μ m

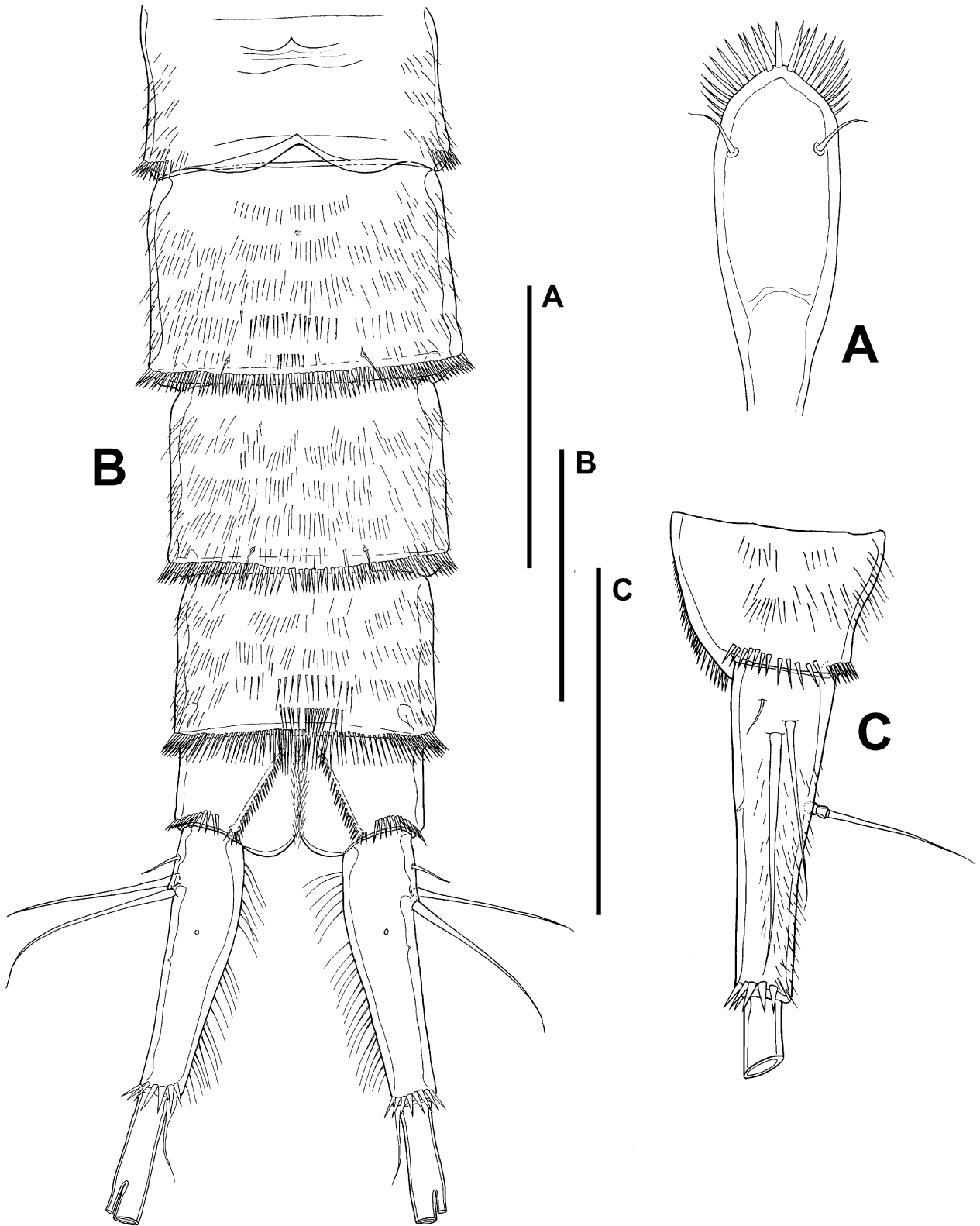


FIGURE 11. *Cletocamptus albuquerquensis* (Herrick, 1894). Male. A, rostrum, dorsal view; B, urosome, ventral view, P5 bearing-somite omitted; C, anal somite and left caudal ramus, lateral view. Scale bars: A, 50 µm; B and C, 100 µm.

P2 (Fig. 8B): praecoxa ornamented as figured; coxa with median row of small spinules and with strong spinules close to outer distal corner. Basis with medial spinules anteriorly, between rami and at base of exopod; outer element spiniform, thin, shorter than those of P3 and P4. Exopod three-segmented and ornamented as shown; EXP1 without inner seta; inner seta of EXP2 relatively short, nearly 0.6 times as long as outer apical seta of EXP3,

with brush tip; EXP3 with five elements, of which inner seta 1.1 times as long as outer apical seta, without brush tip. Endopod two segmented, reaching about the middle of EXP2; ENP1 small, slightly wider than long, with outer and inner spinules, without armature; ENP2 about 3.7 times as long as ENP1, with inner and outer long spinules, with two outer transverse rows of spinules, with one inner, one apical and one outer element, the latter shortest, apical seta longest.

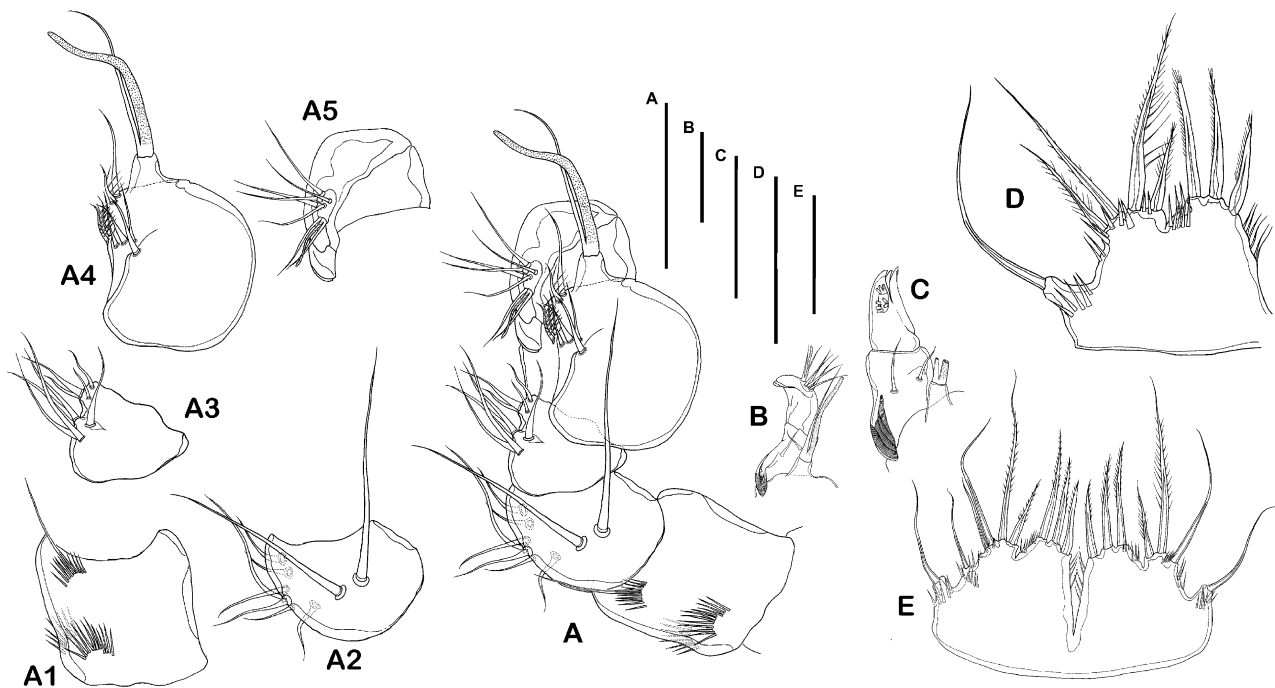


FIGURE 12. *Cletocamptus albuquerqueensis* (Herrick, 1894). Male. A, antennule (A1, segment 1; A2, segment 2; A3, segment 3; A4, segment 4; A5, segments 5 and 6); B, last antennular segment; C, another view of the same segment from another male from Dead Moose Lake, Saskatchewan, Canada; D, P5, anterior; E, variability of P5 with five and three setae on the right and left exopod. Scale bars: A, B, C, D, and E, 50 μm .

P3 (Fig. 9A): praecoxa with one row of spinules close to joint with coxa. The latter as in P2. Basis as in P2 except for setiform outer element. Exopod as in P2; inner seta on EXP2 relatively short, nearly 0.6 times as long as outer apical seta of EXP3, with brush tip; inner seta of EXP3 about 1.1 times as long as outer apical seta, without brush tip. Endopod two-segmented, reaching slightly beyond EXP1; first segment nearly as long as wide, with long inner spinules; second segment with long spinules as shown, with two inner elements, two apical setae and one outer element, the two inner setae shortest, apical setae longest.

P4 (Fig. 9B): praecoxa, coxa and basis as in P3. Exopod as in P3, except for armature formula (without inner seta in P4EXP3); inner seta on EXP2 about 0.6 times as long as outer apical seta of EXP3, with brush tip. Endopod two-segmented, barely reaching middle of EXP1; ENP1 small, slightly wider than long; ENP2 about five times as long as ENP1, with slender spinules, with two long apical setae, of which inner shorter, reaching tip of EXP3.

P5 (Fig. 5C): exopod and baseoendopod fused, barely separated by small notch. Baseoendopod with outer seta of basis; endopodal lobe longer than exopod, with outer small spinules, and long spinules along inner margin, with one outer, two apical and three inner setae, relative length of setae as shown. Exopod with outer spinules, with five setae in all.

P6 (Fig. 5A, B): represented by median plate in anterior half of first genital somite, each vestigial leg represented by two small spiniform setae.

Male. Total body length measured from tip of rostrum to posterior margin of caudal rami, ranging from 786 μm to 1033 μm (mean= 899 μm ; n= 7). Habitus as in female except for somewhat more clear distinction between prosome and urosome, and for separate second and third urosomites (Fig. 10A, B); anal somite (Figs. 10A, B, 11B, C) as in female; caudal rami (Figs. 10A, B, 11B, C) about 2.8 times as long as wide; caudal seta IV and V 20% and 61% of total body length, respectively. Ventral ornamentation of third, fourth and fifth urosomites (Fig. 11B) denser than in female.

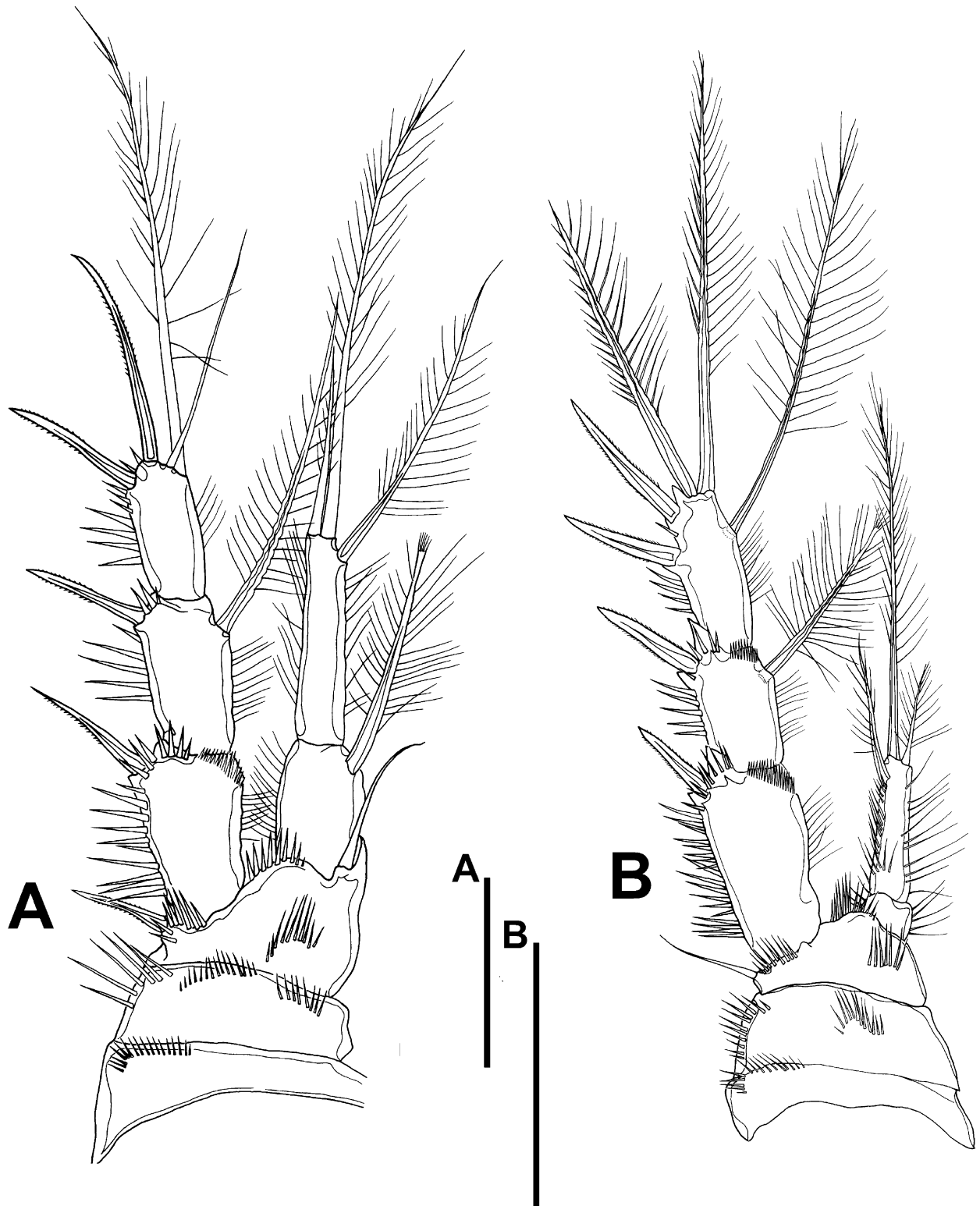


FIGURE 13. *Cletocampus albuquerqueensis* (Herrick, 1894). Male. A, P1, anterior; B, P2, anterior. Scale bars: A, 50 μm ; B, 100 μm .

Rostrum (Fig. 11A): sexually dimorphic, elongate.

Antennule (Fig. 12A–C): six-segmented; subchirocer; smooth, except for the presence of spinules on first segment (Fig. 12A1); last segment with two acute teeth (Fig. 12A, A5, B, C). Armature formula difficult to define; most probably as follows: 1-(1), 2-(9), 3-(9), 4-(8+[1+ae]), 5-(2), 6-(6+[1+ae]). The armature on the last segment

arises from a plate-like swelling, it seems not to be a true segment. The nature of this structure as well as an in-depth analysis of the segmentation of the antennule deserves further investigation.

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

P1 (Fig. 13A) as in female except for dimorphic projection on inner distal corner of basis and for relatively thinner inner spine of basis.

P2 (Fig. 13B) proportionally shorter than in female and with relatively stouter outer spines of exopod; armature of ENP2 relatively shorter than in female.

P3 (Fig. 14A, B) as in female except for relatively stouter outer spines, and for longer EXP1. Endopod clearly two-segmented; first segment slightly longer than wide, with long inner spinules, unarmed; second segment with inner distal apophysis very short and bent outwards at an angle of almost 90°, and with two apical setae relatively shorter than in female (innermost shorter); with paired asprothekes (see Discussion for definition) at base of apophysis posteriorly (Fig. 14B).

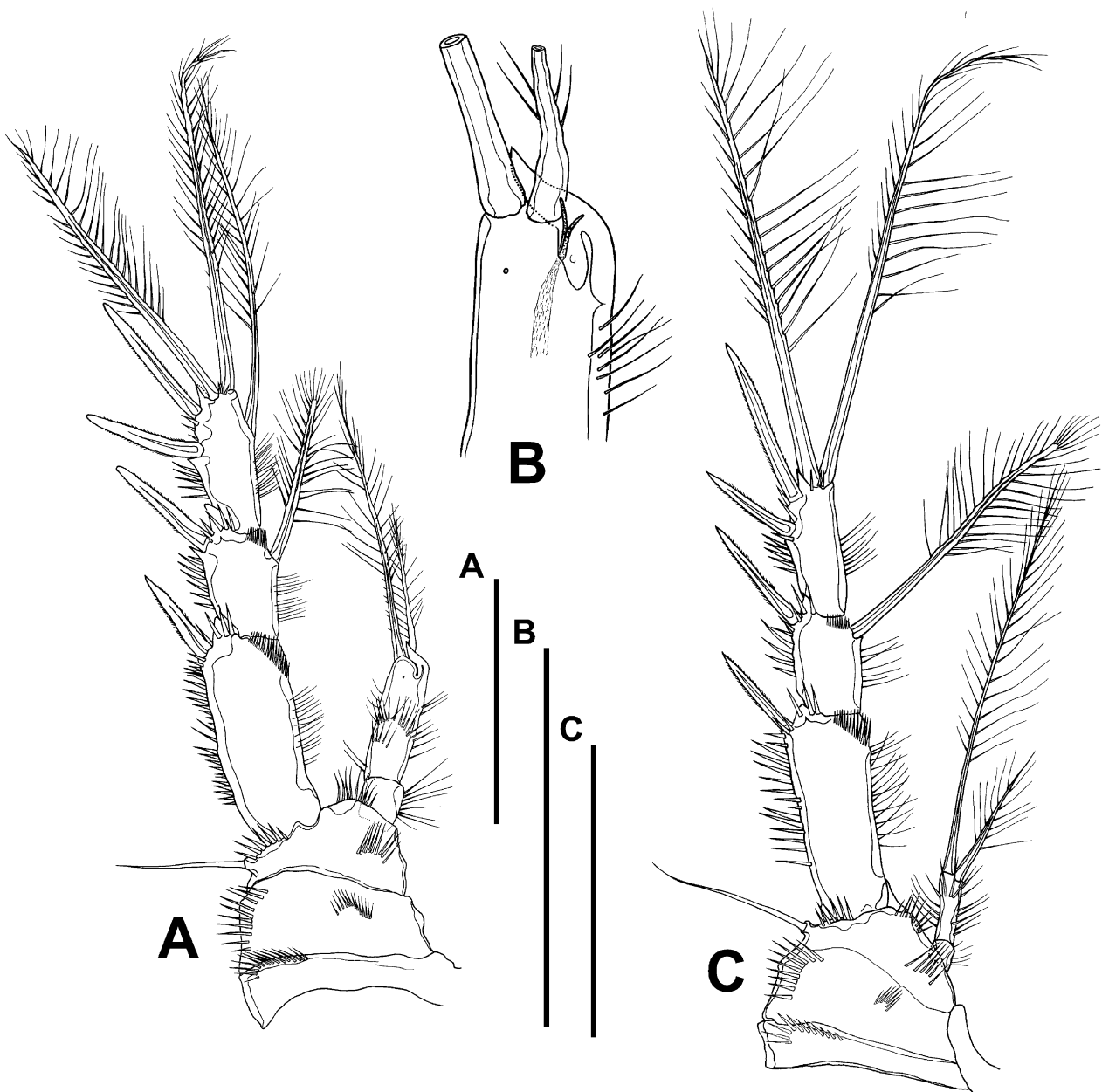


FIGURE 14. *Cletocamptus albuquerqueensis* (Herrick, 1894). Male. A, P3, anterior; B, distal part of P3ENP showing paired asprothekes; C, P4, anterior. Scale bars: A and C, 100 µm; B, 50 µm.

P4 (Fig. 14C) as in female, except for stouter outer spines of exopod, relatively longer EXP1, and relatively shorter setae of ENP2. Two-segmented endopod somewhat shorter than half the length of EXP1; first segment very small, about as long as wide; second segment elongate, about 3 times as long as wide and about 2.5 times as long as ENP1, with two elements, of which inner shorter, reduced, not reaching tip of EXP1.

Both P5 fused (Fig. 12D); exopod and baseopod fused; division between rami indicated by slight notch. Exopod with spinules at base of setae of basis; with four elements. Baseopod with outer seta of basis; endopodal lobe with outer and inner spinules as shown, with three elements in all.

P6 (Fig. 11B) represented by plate; without armature.

Armature formula in Table 1.

TABLE 1. Armature formula of *Cletocamptus albuquerqueensis* (Herrick, 1894).

Leg		P1	P2	P3	P4	P5
Female	EXP	I-0;I-1;I,II,1	I-0;I-1;II,2,1	I-0;I-1;II,2,1	I-0;I-1;II,2,0	5
	ENP	0-1;0,II,1	0-0;I,1,1	0-0;I,2,2	0-0;0,2,0	6
Male	EXP	I-0;I-1;I,II,1	I-0;I-1;II,2,1	I-0;I-1;II,2,1	I-0;I-1;II,2,0	4
	ENP	0-1;0,II,1	0-0;I,1,1	0-0;0,2,Apophysis	0-0;0,2,0	3

Variability. The variability observed between the analyzed populations is shown in Table 2. This variability was expressed in the number of setae on the second segment of the female and male antennule, on the third and sixth segment of the male antennule, in the armature complement of the endopodal lobe of the female and male P5 (see Figs. 5D, 12E), and in the number of setae on the female P4ENP (see Fig. 9C).

TABLE 2. Variability observed in the populations of *Cletocamptus albuquerqueensis* (Herrick, 1894) analyzed.

		Canada		US	
		Dead Moose Lake (Saskatchewan)	Big Quill Lake (Saskatchewan)	Farmington Bay (Great Salt Lake, Utah)	Twelvemile Lake (Albany County, Wyoming)
Total body length	Female	694 µm to 705 µm; n= 6	-	798 µm to 907 µm; n= 7	-
	Male	860 µm to 995 µm; n= 6	706 µm to 719 µm; n= 5	786 µm to 1033 µm; n= 7	876 µm to 888 µm; n= 4
Segment 2 of antennule	Female	8–9 setae	-	8–9 setae	-
	Male	8–9 setae	-	-	8–9 setae
Segment 3 of antennule	Female	-	-	-	-
	Male	9–10 setae	-	-	-
Segment 6 of antennule	Female	-	-	-	-
	Male	-	-	5–6 setae	-
P5 endopodal lobe	Female	-	-	5–6 setae (see Fig. 2D)	-
	Male	-	3–4 setae	-	-
P5 exopod	Female	-	-	-	-
	Male	3–4 setae	-	-	3–4 setae (see Fig. 9E)
P4ENP	Female	-	-	2–3 setae (see Fig. 6C)	-
	Male	-	-	-	-

***Cletocamptus dominicanus* Kiefer, 1934**

(Figs. 15–26)

Synonymy. *Cletocamptus albuquerqueensis*: Lang 1948 (part.): 1277–1278, Abb. 508-1c; Wilson & Yeatman 1959: 838.
Cletocamptus dominicanus: Kiefer 1934, 1936; Lang 1936.

Material examined. Type material. One female lectotype (slide 2076), and three paralectotypes (slides 2117, 2118, and 2119) deposited in The Kiefer Collection, State Museum of Natural History Karlsruhe (Germany).

Additional Material. The vials housed in the US National Museum (Smithsonian Institution) that were analyzed are labeled as follows (additional information about the collection site of vial USNM No. 306869 is given). The material housed in other collections is also provided.

Cletocamptus albuquerqueensis, USNM No. 128929; Trinidad; Caroni; Caroni Swamp; collector B. F. Bacon, 1966; identification by T. E. Bowman, 1969.

Cletocamptus albuquerqueensis, USNM No. 278085, Accession No. 416030; Trinidad and Tobago; Chacachacare Island; surface water of salt pond; collector A. L. Kong, May 7, 1993.

Cletocamptus albuquerqueensis, USNM No. 306869, Accession No. 2018756; British Virgin Islands; Anegada, Flaminco Pond; collected and identified by L. Jarecki, July 20, 2000.

Notes: Flaminco Pond is described as a typical Caribbean salt pond that seasonally varies widely in salinity (Jarecki, personal communication).

Cletocamptus dominicanus, USNM No. 1418187; 25 females and 9 males; Laguna Fraternidad, Cabo Rojo, Puerto Rico; Salinity, 87.6 ppt; water temperature, 31.5°C; pH, 8.56; dissolved oxygen, 8.5 mg L⁻¹; collected by Ray Gerber, January, 2010.

Cletocamptus dominicanus, USNM No. 1418188; 14 females; salt pond lagoon at Ensenada Dakity, Culebra Island, Puerto Rico; Salinity, 45.8 ppt; water temperature, 29.6°C; pH, 9.23; dissolved oxygen, >12 mg L⁻¹; collected by Ray Gerber, December, 2008.

Cletocamptus dominicanus, USNM No. 1418189; 22 females and 8 males; Laguna El Padre, Vieques Island, Puerto Rico; Salinity, 32.9 ppt; water temperature, 27.4°C; pH, 8.14; dissolved oxygen, 9.18 mg L⁻¹; collected by Ray Gerber, December, 2008.

Cletocamptus dominicanus, USNM No. 1418190; 29 females and 8 males; salt pond at Salt Pond Bay, St. John Island, US Virgin Islands; Salinity, 171.6 ppt; water temperature, 28.0°C; pH, 9.2; dissolved oxygen, 7.34 mg L⁻¹; collected by Ray Gerber, January, 2007.

Cletocamptus dominicanus, USNM No. 1418191; 15 females and 6 males; Elliot Pond, San Salvador Island, Bahamas; Salinity, 41 ppt; collected by D. Barr, January, 1994.

Cletocamptus dominicanus, six males (ICML-EMUCOP-010107-03, and -07 to -11) and one female (ICML-EMUCOP-010107-02), dissected; one undissected female mounted onto one slide (ICML-EMUCOP-010107-01); two females and one male preserved in alcohol (ICML-EMUCOP-010107-04); St. John Island (US Virgin Islands); collected by Ray Gerber, January, 2007.

Cletocamptus dominicanus, 15 females (UARC282M) and 15 males (UARC283M) preserved in alcohol; Pozos Colorado, Santa Marta, Colombia; 11° 14' 10" N, 74° 12' 6" W; found in a small temporal pond (0.3–0.6 m deep); temperature from 28 to 31°C; pH from 8.5 and 8.9; observed in both the limnetic region and in the mangrove zone, being more abundant in the latter during the rainy season when salinity was lowest (5 PSU); collected by Juan Manuel Fuentes-Reinés, August–November, 2015.

Cletocamptus dominicanus, 46 females and 33 males preserved in alcohol (ICML-EMUCOP-010815-01); Pozos Colorado, Santa Marta, Magdalena, Colombia; 1° 14' 10" N, 74° 12' 6" W. All other information as above.

Type locality. Enriquillo Lake, Dominican Republic, not far from the border with Haiti (Kiefer 1934).

Distribution. Bahama Islands: San Salvador (present study). British Virgin Islands: Flaminco Pond, Anegada (present study). Colombia: Pozos Colorados, Santa Marta (present study). Dominican Republic: Enriquillo Lake (Kiefer 1934, 1936). Trinidad and Tobago: Caroni Swamp, Caroni (present study), Chacachacare Island (present study). US: St. John Island (US Virgin Islands) (present study), Puerto Rico: Laguna Candelaria (present study), Culebra (present study) and Vieques (present study). Based on our extensive samples from the Caribbean, *C. dominicanus* is the most abundant harpacticoid copepod in the coastal saline lagoons.

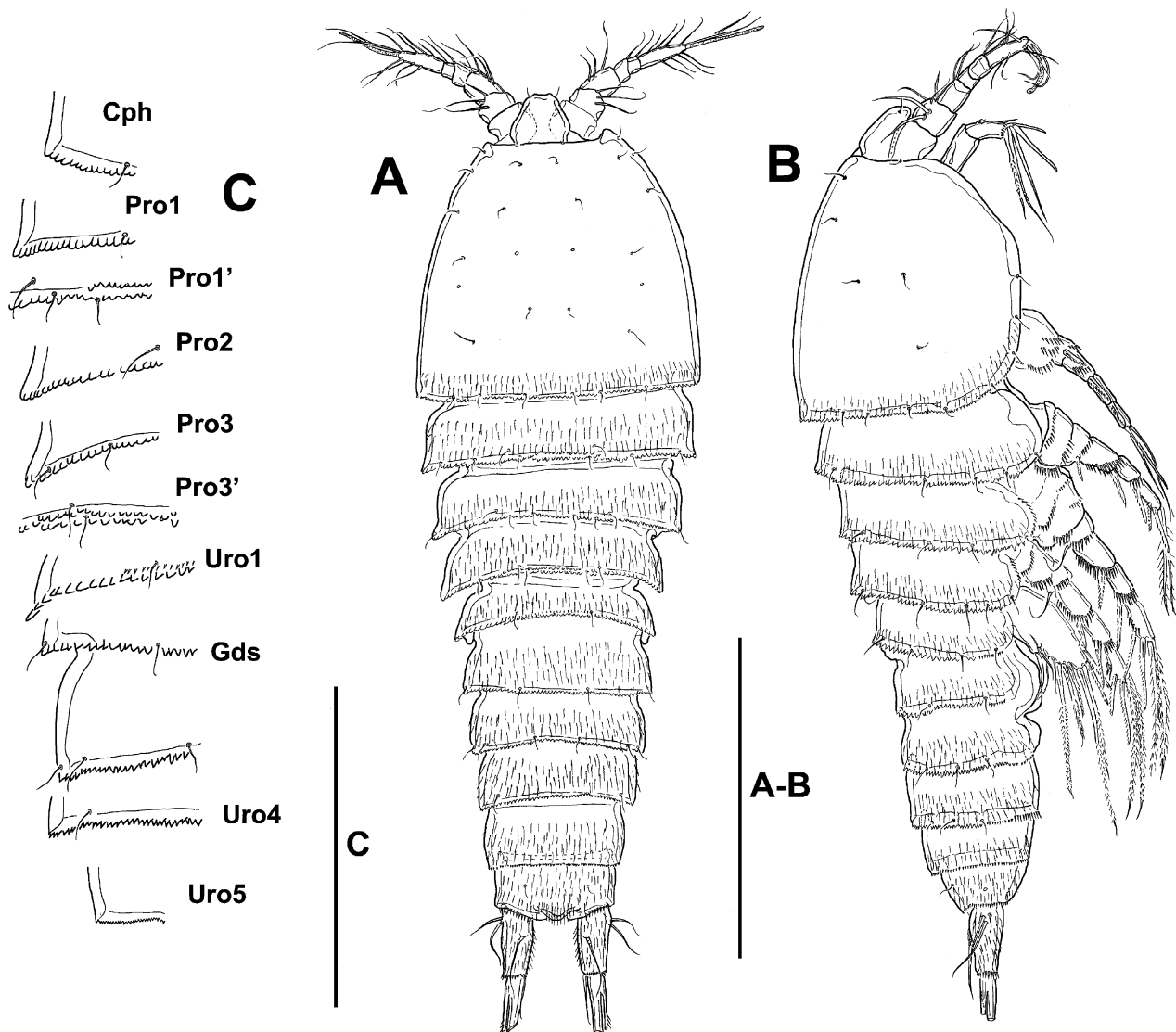


FIGURE 15. *Cletocamptus dominicanus* Kiefer, 1934. Female. A, habitus, dorsal view; B, habitus, lateral view; C, distal margin of pro- and urosomites showing distal ornamentation (Cph, cephalothorax; Pro1–3, first to third prosomite; Pro1' and 3', medial part of first and third prosomite; Uro1, 4–5, first, fourth and fifth urosomite; Gds, genital double-somite). Scale bars: A–B, 200 µm; C, 100 µm.

Redescription (based on material from the US Virgin Islands). Female. Habitus (Fig. 15A, B) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 520 µm to 644 µm (mean= 540 µm; n= 3). Rostrum set off, triangular, with pair of setules subapically and with row of spinules distally as in *C. albuquerquensis* (see Fig. 4A, B). Posterior margin of cephalothorax, pro- and urosomites ornamented with denticles conferring a serrated appearance (see Fig. 15C); denticles of P2–P5 bearing-somites coarser and blunt, those of second to fourth urosomites progressively smaller and pointed, of fifth urosomite very small; first (P2 bearing-somite) and third (P4 bearing-somite) prosomites (Pro1, 1', and Pro3, 3', in Fig. 15C) with additional row of medial denticles; P5 bearing-somite with additional row of minute spinules (see Uro1 in Fig. 15C). Second and third urosomites distinct dorsally and laterally (Fig. 15A, B), completely fused ventrally (Fig. 17A) forming genital double-somite. Anal somite (Figs. 15A, B, 16A, 17A) as shown; anal operculum crescentic medially, with spinules (Figs. 15A, 16A); ventral spinular ornamentation as shown (Fig. 17A). Caudal rami (Figs. 15A, B, 16A, B, 17A) about 2 times as long as wide; surface covered with slender spinules; with comparatively stronger ventrolateral spinules close to insertion site of setae IV and V; with seven elements in all; seta I small, situated laterally close to anterior margin of ramus, close to setae II and III, the latter setae longer; setae IV and V fused basally, the former 15%, the latter 60% of total body length; seta VI situated on distal outer corner; seta VII situated dorsally midway length of ramus on inner edge.

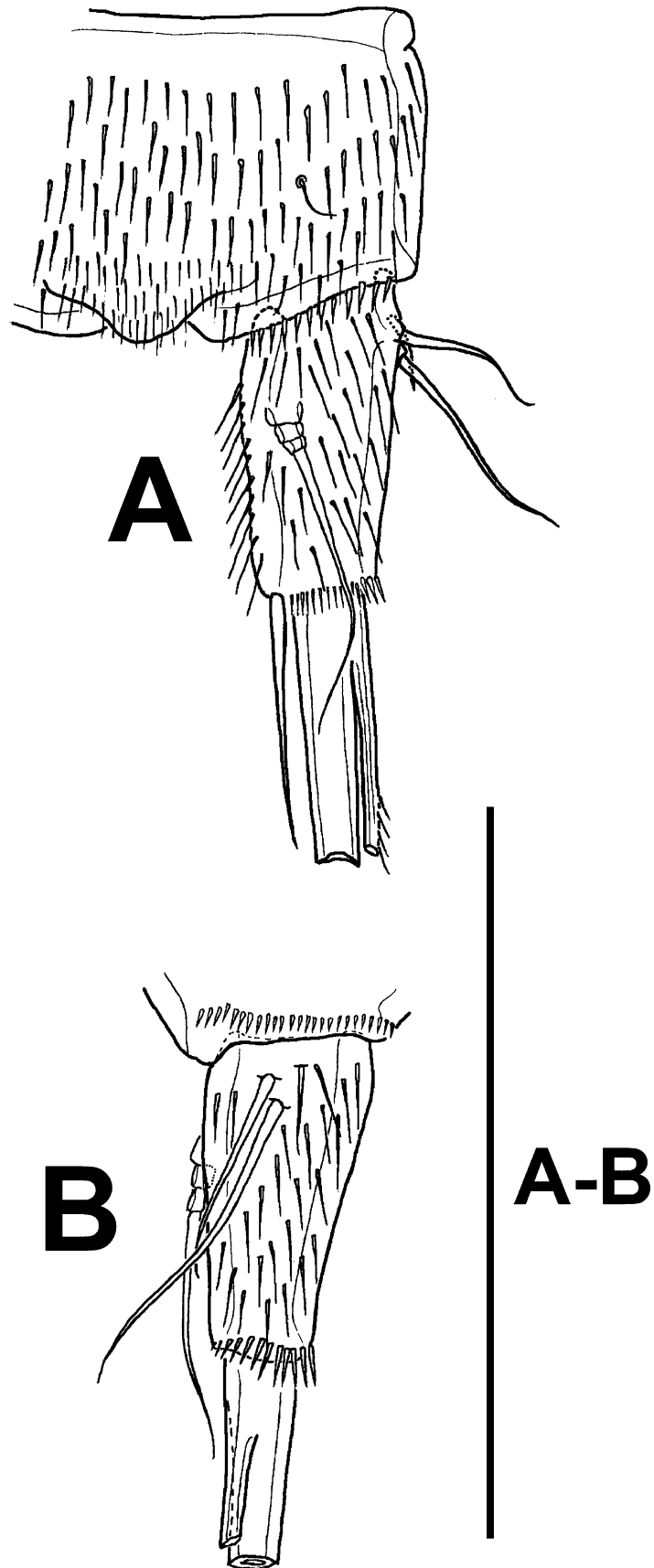


FIGURE 16. *Cletocamptus dominicanus* Kiefer, 1934. Female. A, anal somite and right caudal ramus, dorsal view; B, right caudal ramus, lateral view. Scale bars: A–B, 100 μm .

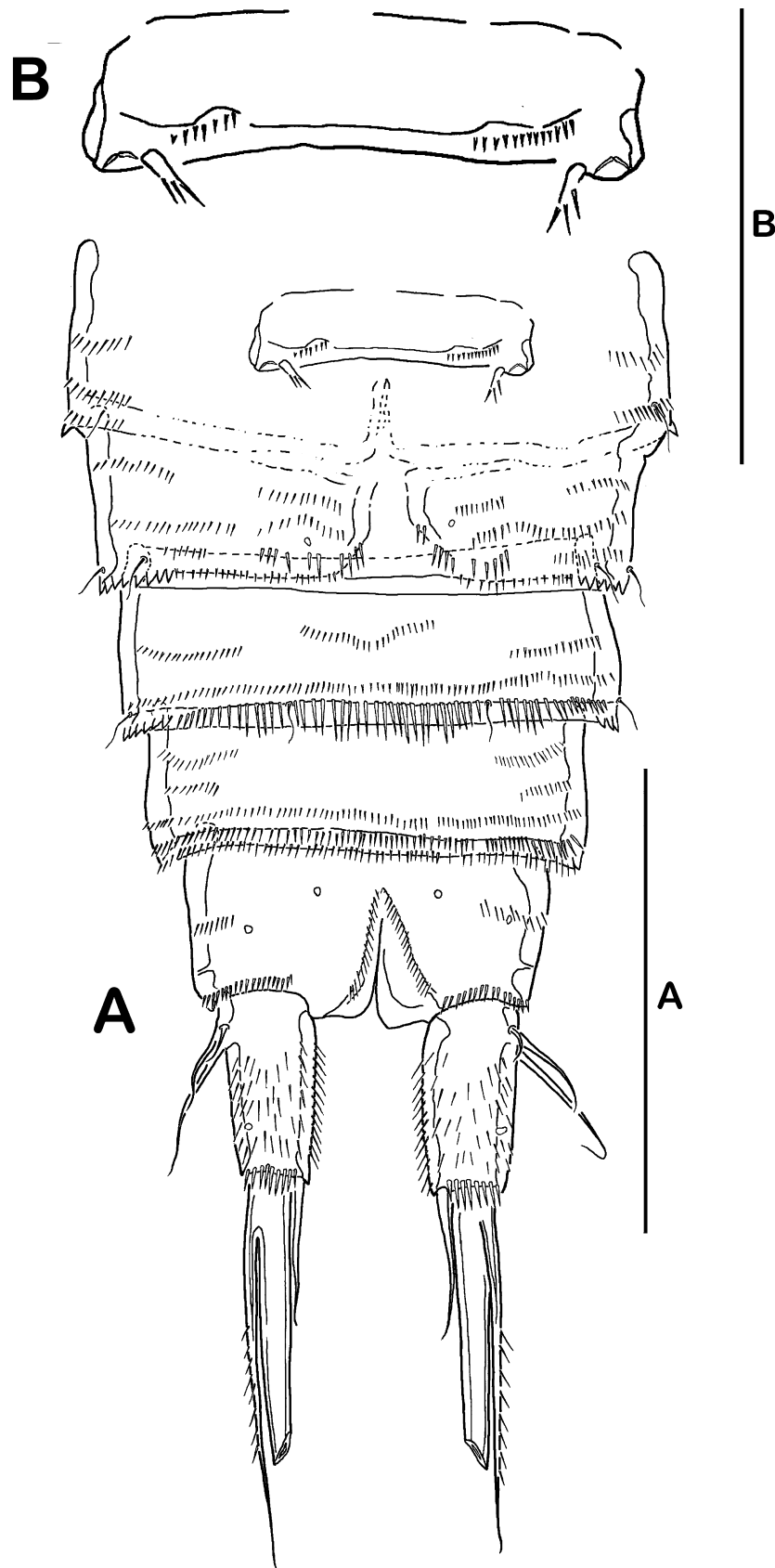


FIGURE 17. *Cletocamptus dominicanus* Kiefer, 1934. Female. A, Urosome, ventral view; B, P6. Scale bars: A, 100 μm ; B, 50 μm .

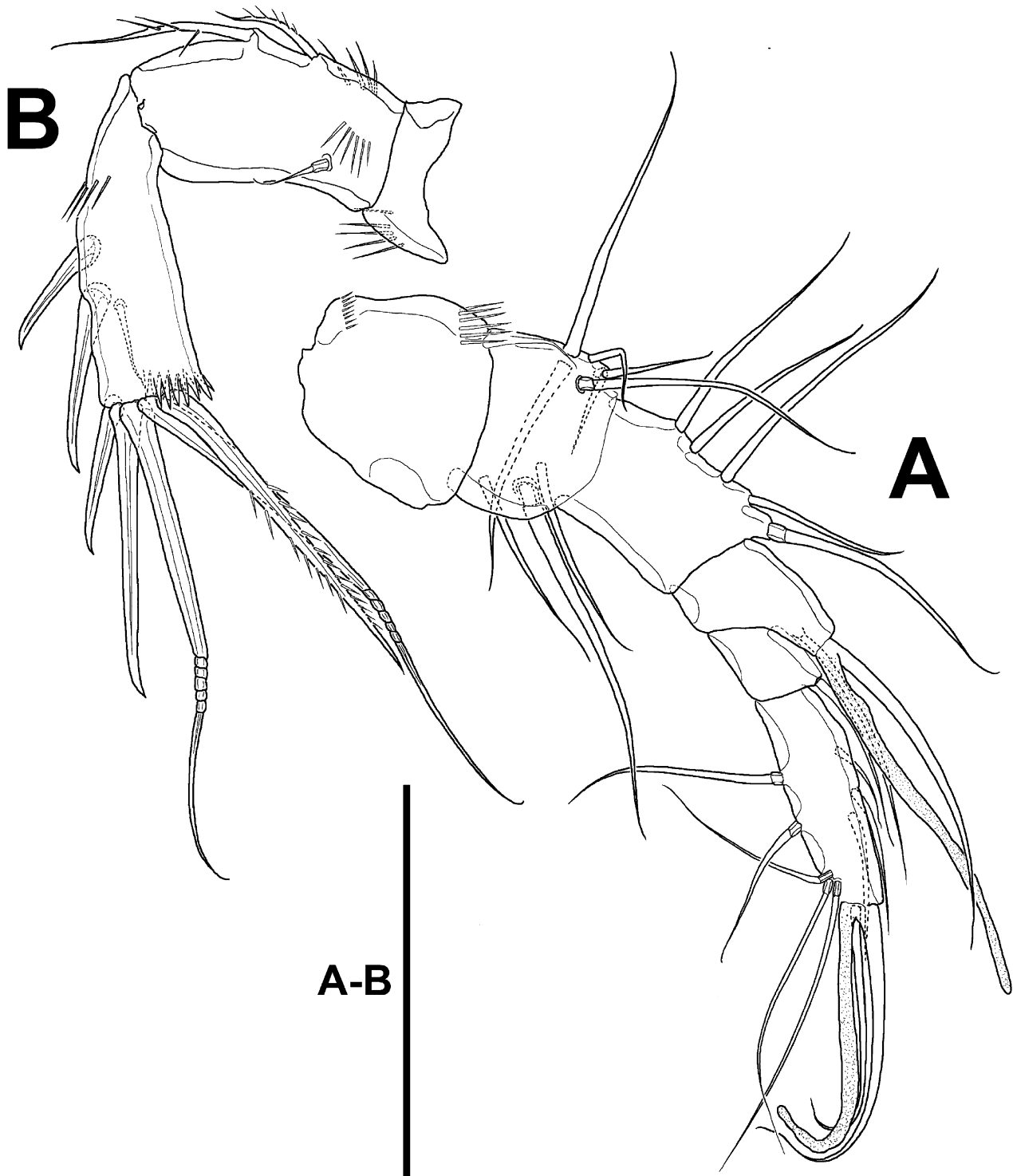


FIGURE 18. *Cletocamptus dominicanus* Kiefer, 1934. Female. A, antennule; B, antenna. Scale bar: A–B, 50 μ m.

Antennule (Fig. 18A) six-segmented; surface of segments smooth except 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 (Fig. 18B): small coxa with outer spinules. Allobasis with two abexopodal setae. Free endopodal segment with inner spinules proximally, with two lateral inner spines and a slender seta, and five distal elements, two of them geniculate. Exopod minute, one-segmented, with one seta (Figs. 18B, 26A).

Mandible (Fig. 19A): robust, with rows of spinules proximally; chewing edge with teeth as figured, with one pyriform element and one lateral pinnate seta. Palp one-segmented, with three setae unequal in length.

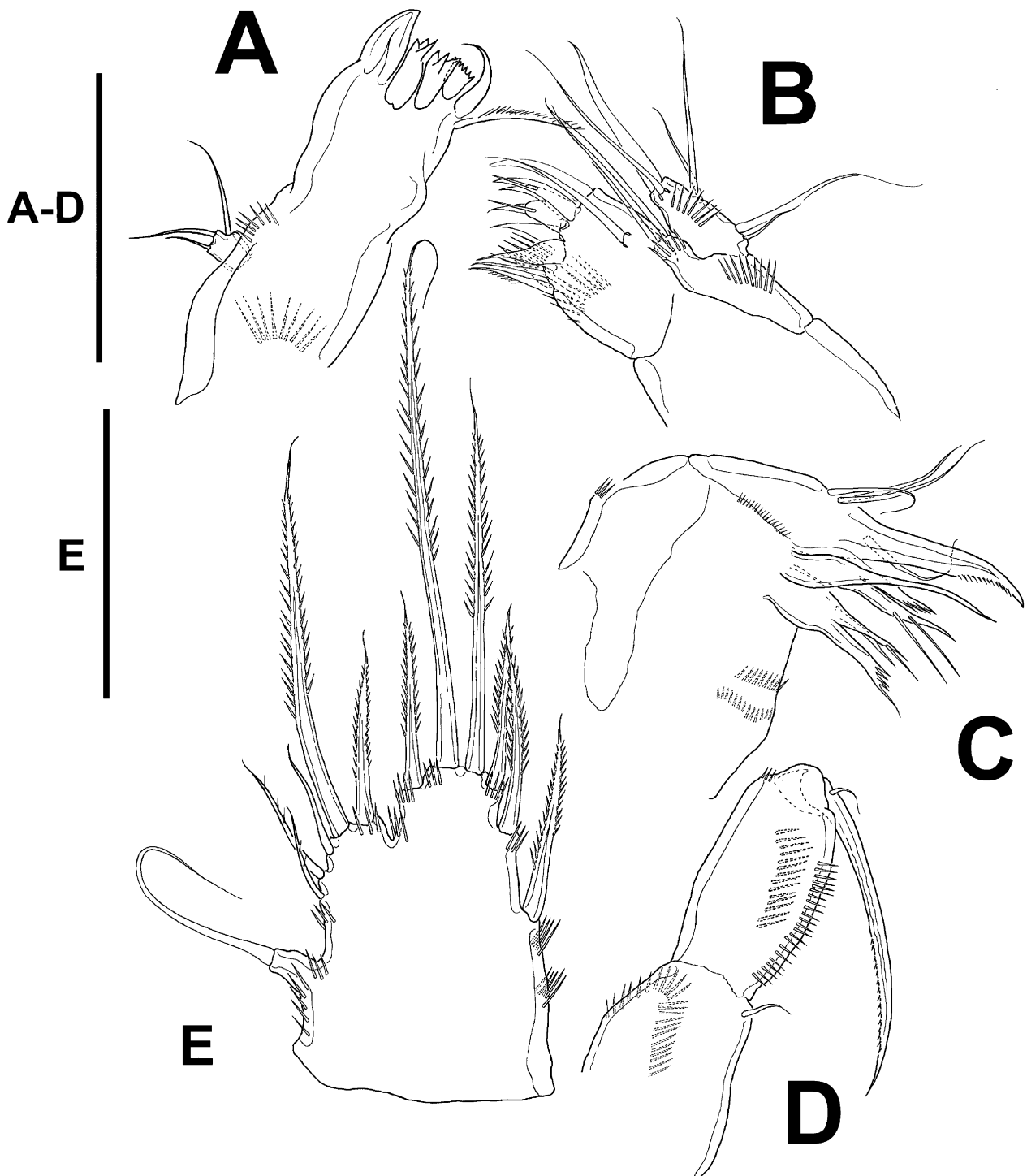


FIGURE 19. *Cletocamptus dominicanus* Kiefer, 1934. Female. A, mandible; B, maxillule; C, maxilla; D, maxilliped; E, P5. Scale bars: A–D, 35 µm; E, 50 µm.

Maxillule (Fig. 19B): robust; arthrite of praecoxa with few spinules, with one surface seta, with seven spines and two slender setae distally. Coxa with some spinules, with two setae. Basis with spinules as figured, with two apical setae. Exopod and endopod incorporated to basis, represented by two setae each.

Maxilla (Fig. 19C): syncoxa with inner and outer spinules, and close to joint with allobasis; with two endites, each bearing three setae. Allobasis drawn into strong claw with one accompanying seta. Endopod represented by three setae.

Maxilliped (Fig. 19D): subchelate. Syncoxa with row of spinules, with one tiny seta on inner distal corner.

Basis without armature, with spinules as shown. Endopod drawn into long and slender claw with one accompanying small seta.

P1 (Fig. 20A): praecoxa with spinules close to joint with coxa. The latter with anterior and posterior transverse rows of spinules as shown. Basis with inner and outer spine; with median rows of spinules, and with spinules at base of exopod, between rami and at base of inner and outer spines. Exopod three-segmented; EXP1 without, EXP2 with inner seta; EXP3 with four elements. Endopod two-segmented, slightly longer than exopod, both segments subequal; inner seta of ENP1 shorter than both endopodal segments combined, with brush tip; ENP2 with three elements.

P2 (Fig. 20B): praecoxa and coxa ornamented as figured. Basis with spinules between rami and at base of exopod; outer element spine-like. Exopod three-segmented, ornamented as shown; EXP1 without inner seta; inner seta of EXP2 relatively short, about 0.5 times as long as outer apical seta of EXP3, with brush tip; EXP3 with five elements, of which inner about 0.7 times as long as outer apical seta, without brush tip. Endopod two segmented, reaching about distal third of EXP2; ENP1 small, slightly longer than wide, with outer and inner spinules, without armature; ENP2 about 3 times as long as wide, with long spinules as shown, with one inner, one apical and one outer element; inner and outer elements subequal, apical seta longest.

P3 (Fig. 21A): praecoxa and coxa as in P2; basis as in P2 except for setiform outer element. Exopod as in P2; EXP1 without inner armature; inner seta of EXP2 about 0.4 times as long as outer apical seta of EXP3, with brush tip; EXP3 with five elements, of which inner seta about 0.8 times as long as outer apical seta, without brush tip. Endopod two-segmented, reaching distal third of EXP2; ENP1 nearly as long as wide, with long spinules as shown, without armature; ENP2 about 3 times as long as wide, ornamented as shown, with two inner and two apical setae, and one outer element; inner and outer elements subequal; apical setae longest.

P4 (Fig. 21B, 26B): praecoxa, coxa and basis as in P3. Exopod as in P3, except for armature formula of EXP3 (without inner seta); EXP1 without inner seta; inner seta of EXP2 visibly shorter than outer apical seta EXP3, with brush tip; EXP3 with four elements. Endopod one-segmented, about 1.5 times as long as wide, barely reaching middle of EXP1, with slender spinules, with two apical setae (innermost smaller).

P5 (Fig. 19E): exopod and baseoendopod fused and barely separated by small notch. Baseoendopod with outer seta of basis; endopodal lobe longer than exopod, with spinules as figured, with one outer, two apical and three inner setae, relative length of setae as shown. Exopod with outer spinules, with five setae in all.

P6 (Fig. 17A, B): represented by median plate in anterior half of first genital somite, each vestigial leg represented by one pinnate small setae. 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 345 μm to 430 μm (mean= 383 μm ; n= 5). General shape of habitus as in female except for separate second and third urosomites (Fig. 22A, B). Posterior margin of cephalothorax, pro- and urosomites not serrated (not shown); with spinules close to posterior margin of cephalothorax; P2 bearing-somite slenderer than in succeeding somites; dorsal surface covered with slender spinules. Anal somite covered with slender spinules; anal operculum and caudal rami as in female (Fig. 22A, B). Caudal seta IV and V 14% and 48% of total body length, respectively. Ventral ornamentation of third, fourth and fifth urosomites as shown (Fig. 22B).

Rostrum (Figs. 23B, 26D): sexually dimorphic, elongate.

Antennule (Fig. 23A): six-segmented; subchirocer; smooth except for the presence of spinules on first segment; last segment with two acute teeth. Armature formula difficult to define; most probably as follows: 1-(1), 2-(9), 3-(7), 4-(8+[1+ae]), 5-(3), 6-(5+[1+ae]). The armature on the last segment arises from a plate-like swelling, it seems not to be a true segment. The nature of this structure as well as an in-depth analysis of the segmentation of the antennule deserves further investigation.

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

P1 (Fig. 24A): as in female except for dimorphic projection on inner distal corner of basis.

P2 (Fig. 24B): as in female except for relatively stouter outer spines of male exopod, and for inner seta of ENP2 reduced.

P3 (Fig. 25A, 26C): as in female except for relatively stouter outer spines of exopod. Endopod clearly two-segmented; ENP1 slightly wider than long, with long inner spinules, unarmed; ENP2 with inner medial apophysis, about as long as supporting segment, with two apical setae of which outer well-developed, inner element very small, with paired elongated asprothekes (indicated in figure 26C; for definition see Discussion), without the spinular ornamentation typically found in other congeners.

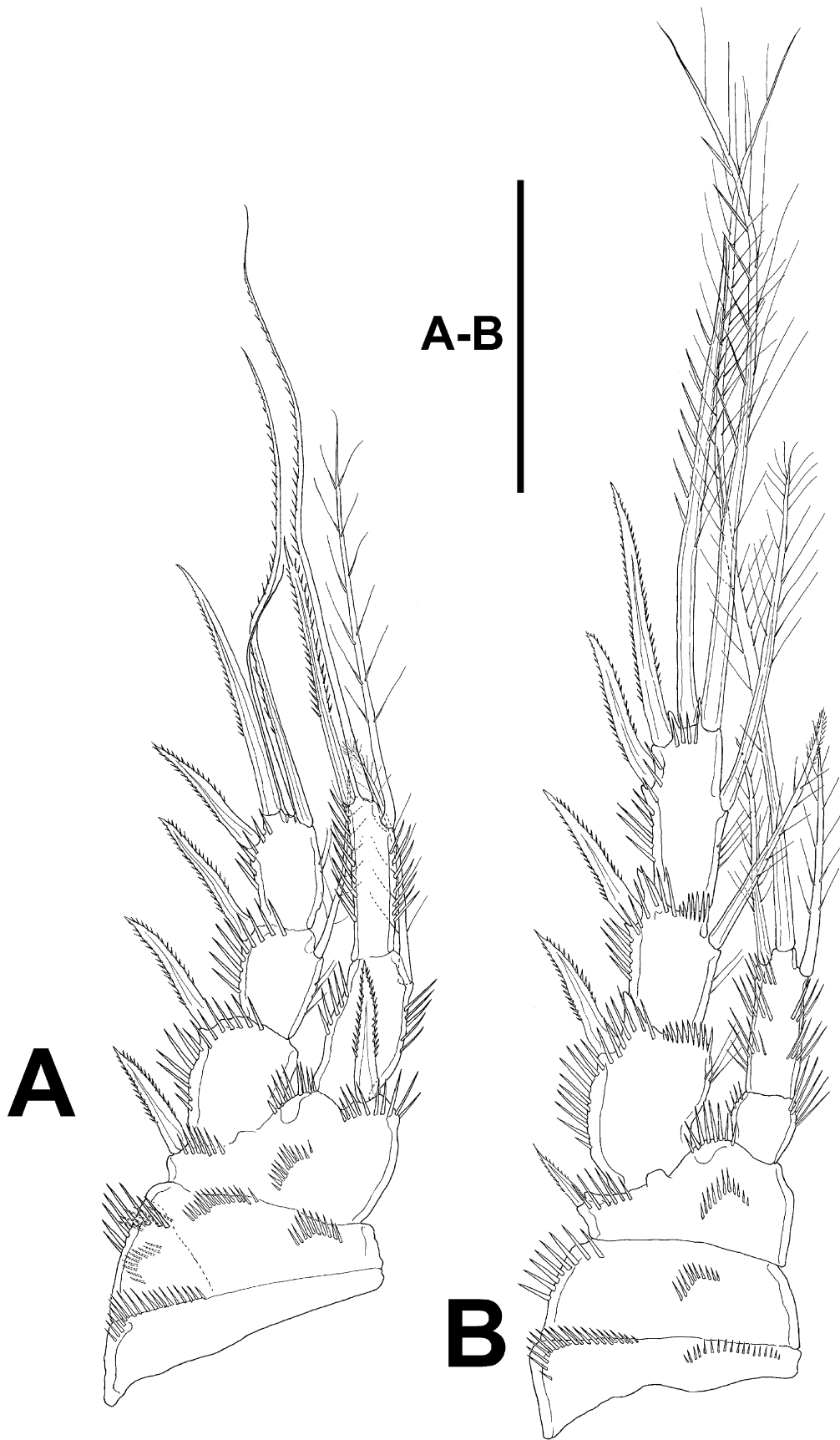


FIGURE 20. *Cletocampus dominicanus* Kiefer, 1934. Female. A, P1, anterior; B, P2, anterior. Scale bar: A–B, 50 μ m.

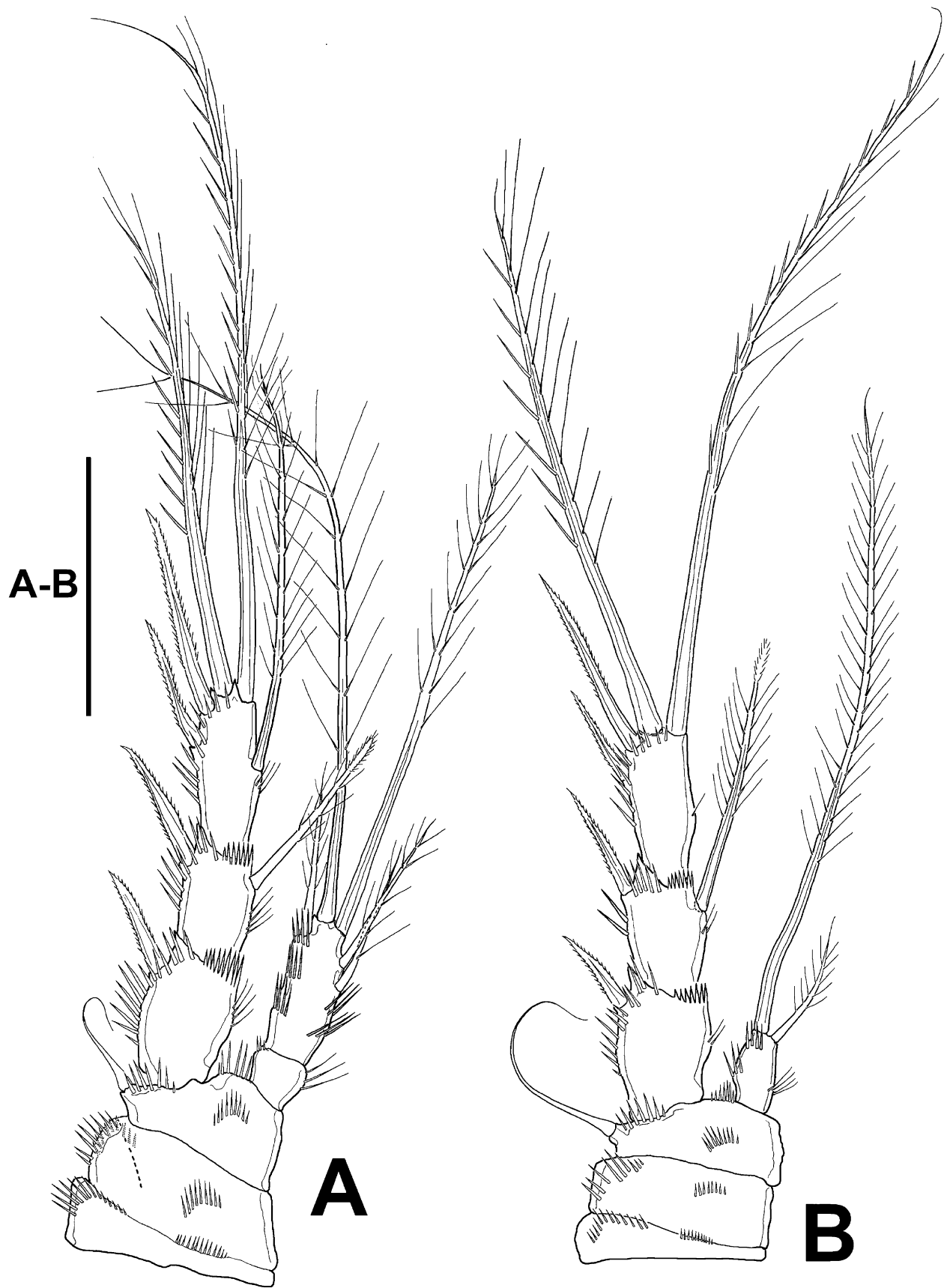


FIGURE 21. *Cletocampus dominicanus* Kiefer, 1934. Female. A, P3, anterior; B, P4, anterior. Scale bar: A–B, 50 μ m.

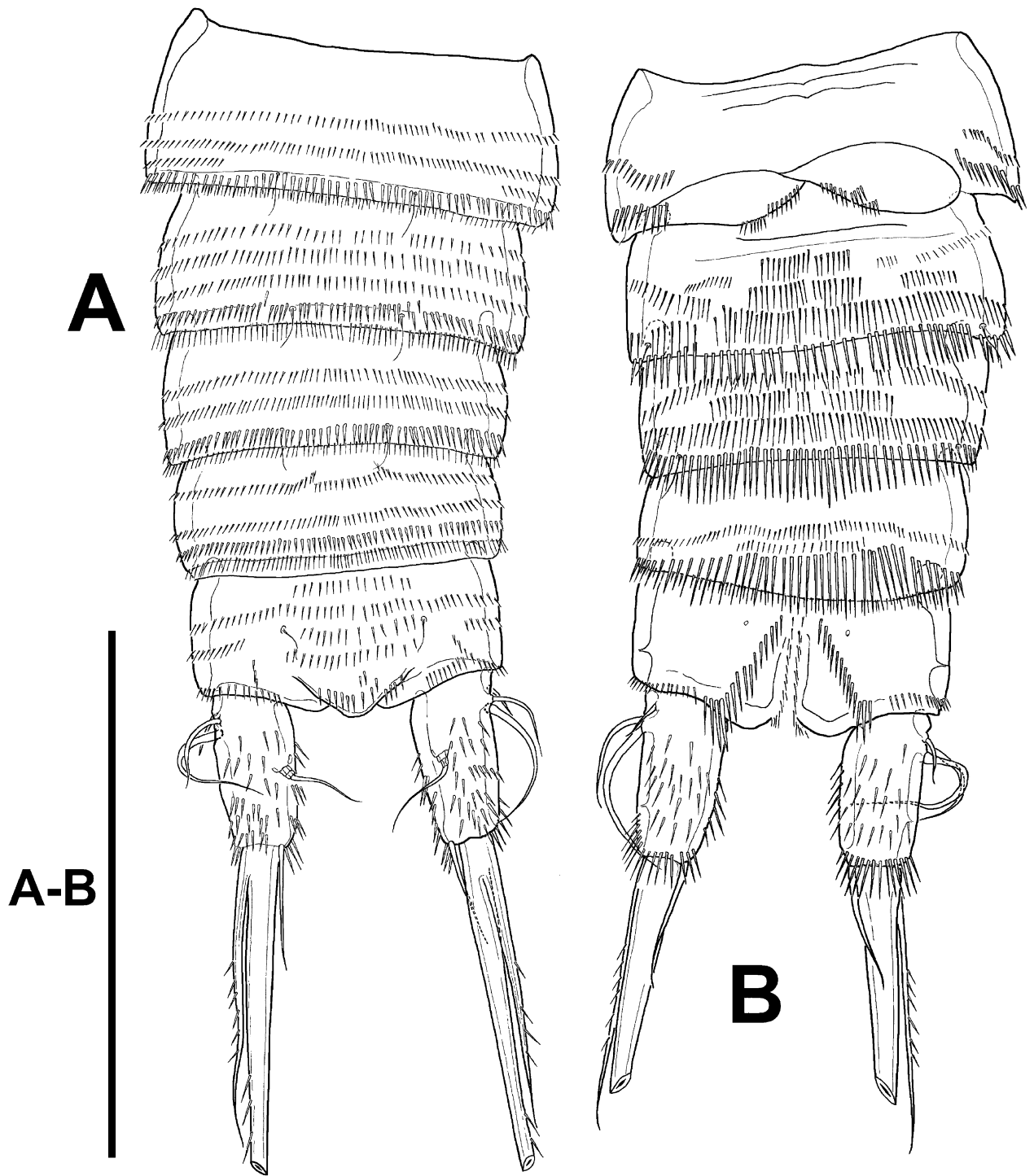


FIGURE 22. *Cletocamptus dominicanus* Kiefer, 1934. Male. A, urosome, dorsal view, P5 bearing-somite omitted; B, urosome, ventral view, P5 bearing-somite omitted. Scale bar: A–B, 100 μ m.

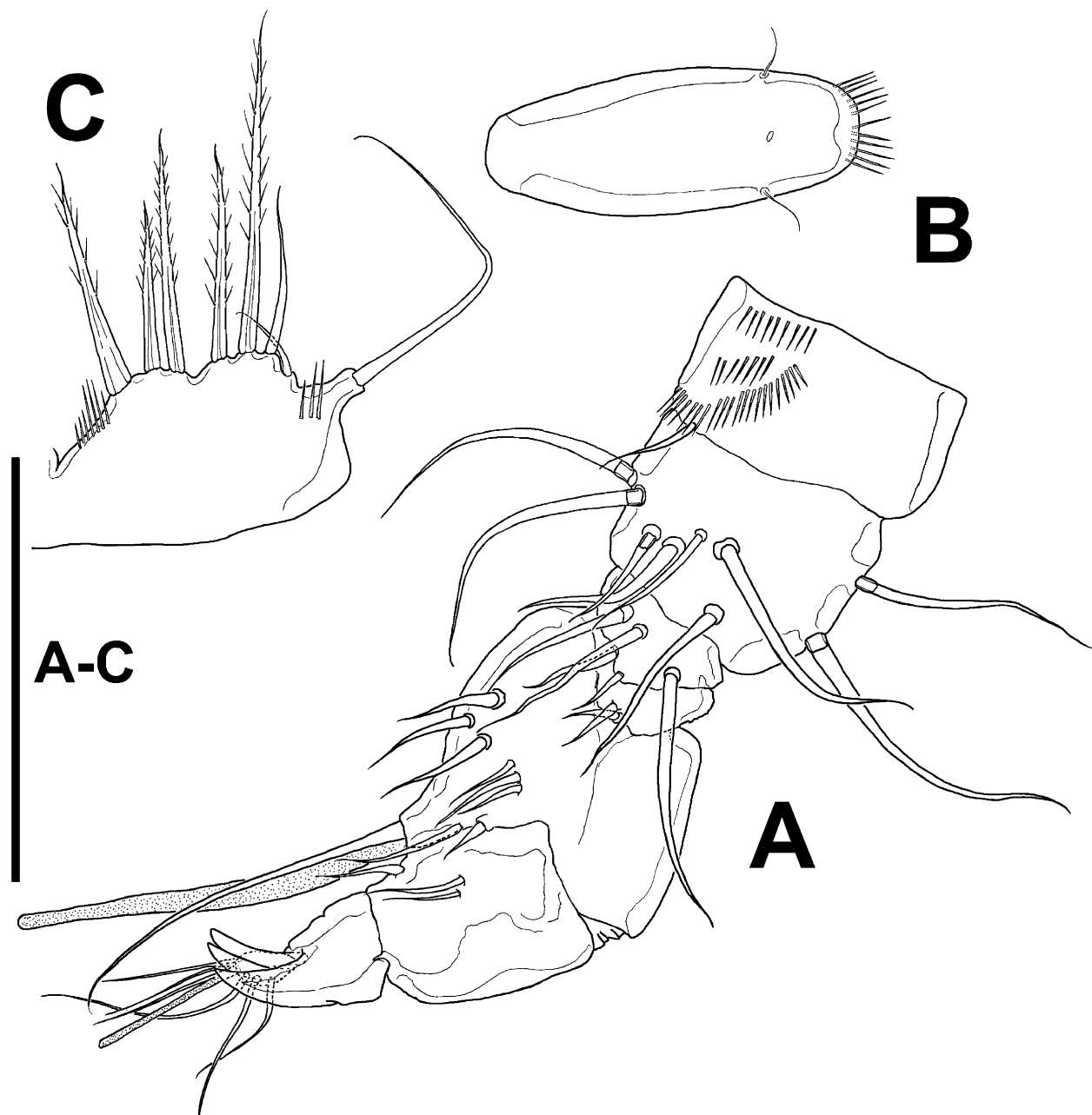


FIGURE 23. *Cletocamptus dominicanus* Kiefer, 1934. Male. A, antennule; B, rostrum, dorsal view; C, P5, anterior. Scale bar: A–C, 50 μ m.

P4 (Fig. 25B) as in female, except for stouter outer spines of all the exopodal segments, and relatively shorter setae of ENP.

P5 (Fig. 23C): both legs fused medially; exopod and baseoendopod fused; division between rami indicated by slight notch. Exopod with spinules at base of setae of basis; with four elements. Baseoendopod with outer seta of basis; endopodal lobe with inner spinules as shown, with three elements in all.

P6 (Fig. 22B) represented by plate; without armature.

Armature formula in Table 3.

Variability. US Virgin Islands: The male P4ENP may be one or two-segmented (first segment being very small; see Fig. 25C), being the one-segmented condition more common and is considered here as the normal condition. Also, as noted in Fig. 26B, the small proximal element can be an artifact due to a slight narrowing at the base of the endopodal segment.

TABLE 3. Armature formula of *Cletocamptus dominicanus* Kiefer, 1934.

Leg		P1	P2	P3	P4	P5
Female	EXP	I-0;I-1;I,II,1	I-0;I-1;II,2,1	I-0;I-1;II,2,1	I-0;I-1;II,2,0	5
	ENP	0-1;0,II,1	0-0;I,1,1	0-0;I,2,2	0,2,0	6
Male	EXP	I-0;I-1;I,II,1	I-0;I-1;II,2,1	I-0;I-1;II,2,1	I-0;I-1;II,2,0	4
	ENP	0-1;0,II,1	0-0;I,1,1	0-0;0,2,Apophysis	0,2,0	3

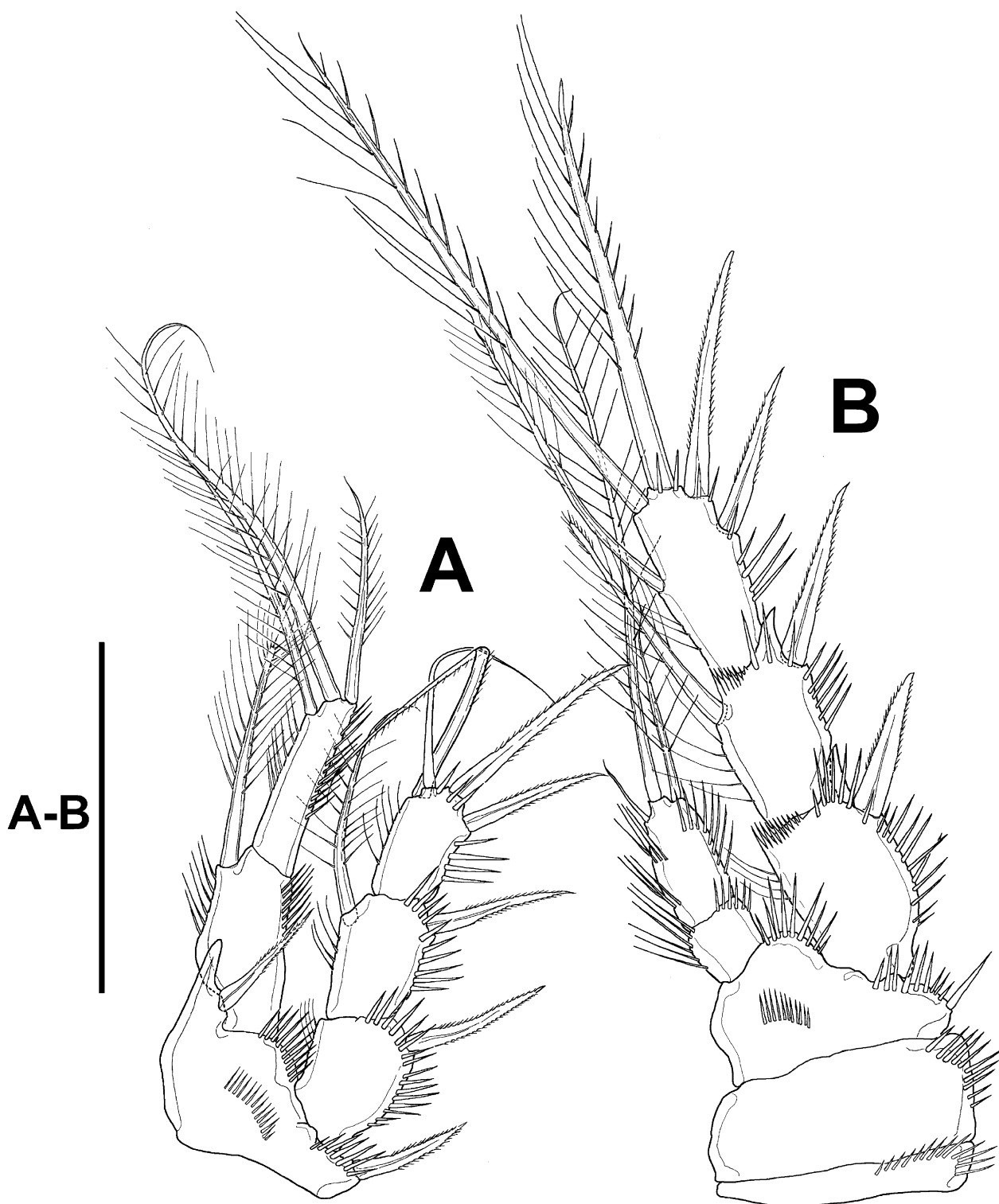


FIGURE 24. *Cletocamptus dominicanus* Kiefer, 1934. Male. A, P1, anterior; B, P2, anterior. Scale bar: A–B, 50 μ m.

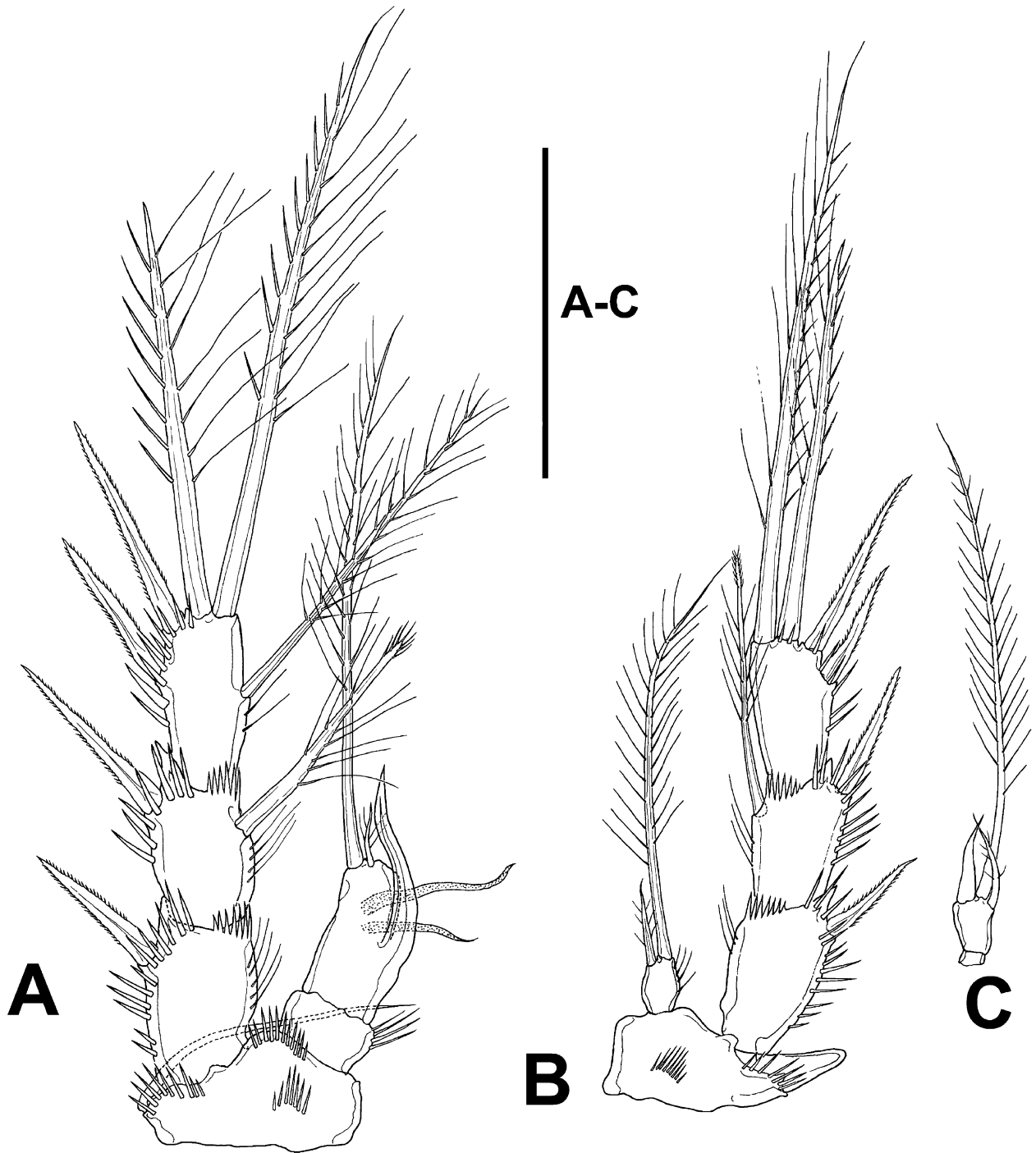


FIGURE 25. *Cletocamptus dominicanus* Kiefer, 1934. Male. A, P3, anterior; B, P4, anterior; C, variability of P4ENP with three elements. Scale bar: A–C, 50 μ m.

Santa Marta, Colombia: The right P1ENP1 of one female was observed to possess a distal spine. The left P3EXP3 of another female was observed to possess two inner distal setae instead of one lateral inner seta. The left P5 endopodal lobe of another female was observed to possess five instead of six setae.

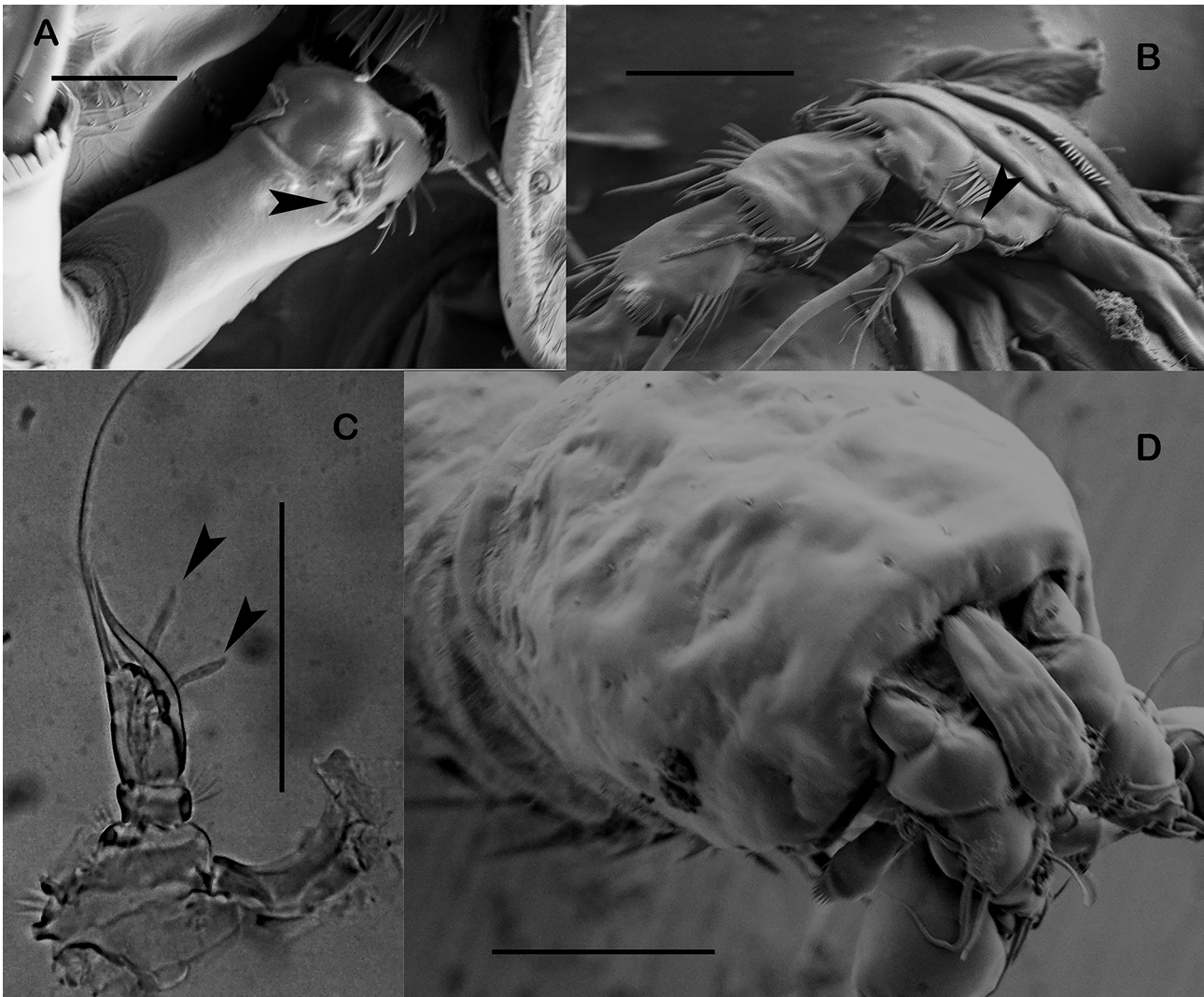


FIGURE 26. *Cletocamptus dominicanus* Kiefer, 1934. Female. SEM. Antenna, showing exopodal seta; B, P4 showing one-segmented endopod. Male. C, P3ENP showing paired asprothekes; D, male dimorphic rostrum. Scale bars: A, 10 μ m; B, 20 μ m; C, 50 μ m; D, 40 μ m.

***Cletocamptus tainoi* sp. nov.**

(Figs. 27–37)

Etymology. The species is named in honor and memory of the Taíno people who were the original inhabitants of St. John Island (as early as 880 BC) and nearby Caribbean islands (Wild 1999).

Material examined. One female holotype (USNM No. 1418184), one male allotype (USNM No. 1418185), and four female and four male paratypes (USNM No. 1418186) preserved in alcohol; 6 January, 2007; col. Ray Gerber.

Type locality. A small (0.36 ha) and shallow (less than 0.5 m depth) salt pond located near the shore of Privateer Bay, on the east end of St. John Island, US Virgin Islands (18°20'16.96" N and 64°39'58.40" W).

Distribution. US Virgin Islands: Near Privateer Bay on St. John Island (present study).

Description. Female. Habitus (Fig. 27A, B) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 526 μ m to 610 μ m (mean= 568 μ m; n= 8). Rostrum set off, triangular, with pair of setules subapically and with row of spinules distally (Fig. 27C). Cephalic shield with fine and short spinules along margin dorsolaterally (Fig. 27A, B). Dorsal and lateral surface of free thoracic somites (P2–P4 bearing-somites) with transverse rows of minute spinules as shown, with short spinules along

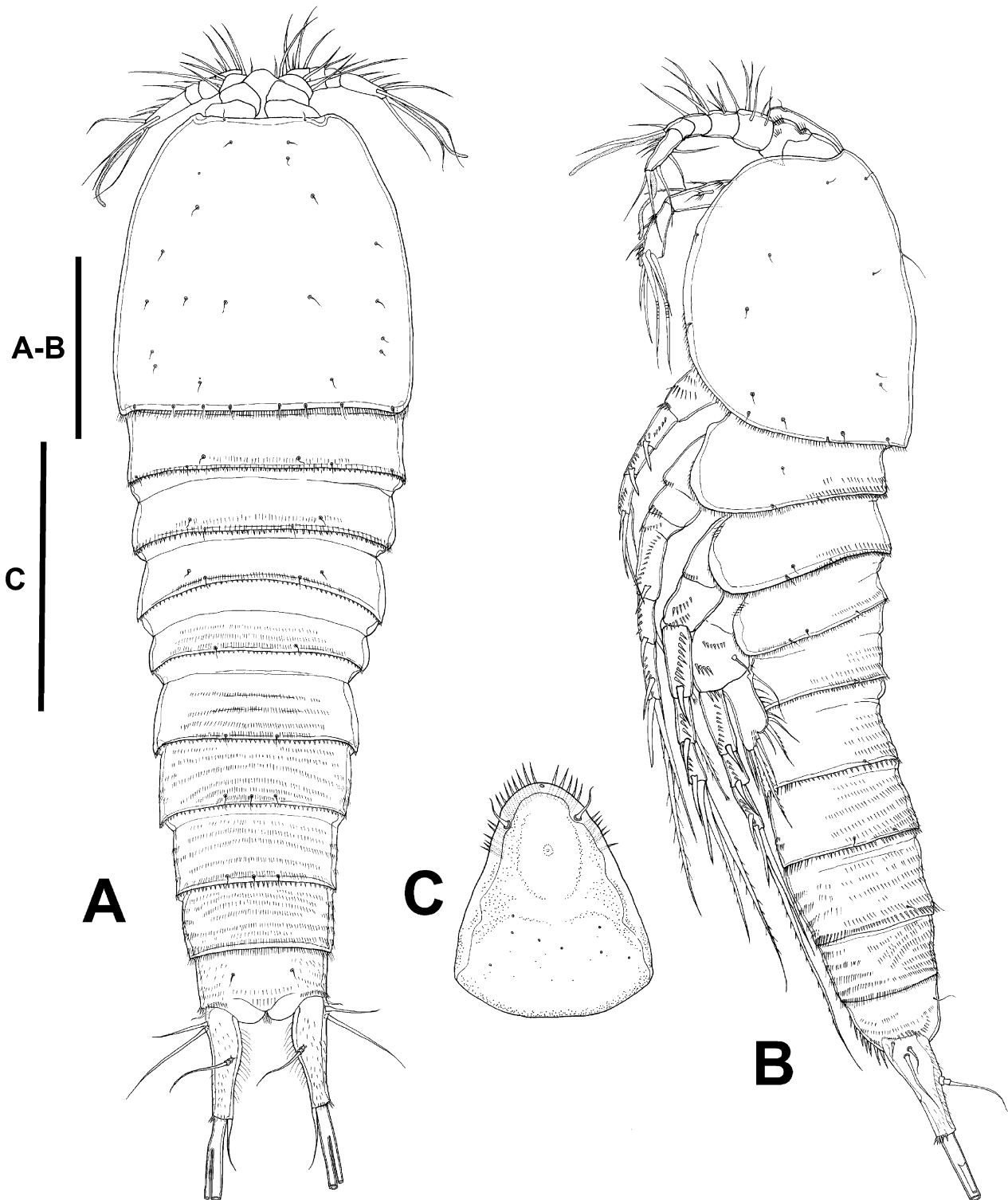


FIGURE 27. *Cletocamptus tainoi* sp. nov. Female. A, habitus, dorsal view; B, habitus, lateral view; C, rostrum. Scale bars: A–B, 100 µm; C, 50 µm.

posterior margin. Dorsal and lateral surface of first urosomite (P5 bearing-somite) (Fig. 27A, B) with transverse rows of minute spinules, with row of small spinules along posterior margin. Second and third urosomites distinct dorsally and laterally (Fig. 27A, B), completely fused ventrally forming genital double-somite (Fig. 28A); dorsal and lateral surface of first and second half of genital double-somite with transverse rows of minute spinules, with row of larger spinules along posterior margin; ventrally with longer spinules as shown (Fig. 28A). Fourth and fifth urosomites as in second half of genital double-somite dorsally (Fig. 27A), ventral surface with transverse rows of minute spinules, with larger spinules along posterior margin (Fig. 28A). Dorsal surface of anal somite (Fig. 27A)

with transverse rows of minute spinules and with dorsolateral strong spinules close to joint with caudal rami; anal operculum crescentic medially, with spinules as shown (Fig. 27A). Caudal rami (Figs. 27A, B, 28A) about 3.6 times as long as wide; dorsal surface with sparse small spinules dorsally, smooth ventrally; with ventral row of larger spinules close to insertion of caudal setae distally; with seven elements in all (Fig. 27A, B, 28A); seta I very small, situated proximally on lateral surface of ramus, close to setae II and III, the latter setae longer; setae IV and V fused basally, 16% and 49% of total body length, respectively; seta VI situated on distal inner corner; seta VII situated dorsally midway length of ramus on inner edge.

Antennule (Fig. 29A) six-segmented; surface of segments smooth except for two rows of spinules on first and third segments. Armature formula, 1-(1), 2-(9), 3-(6), 4-(1+[1+ae]), 5-(1), 6-(9+[1+ae]).

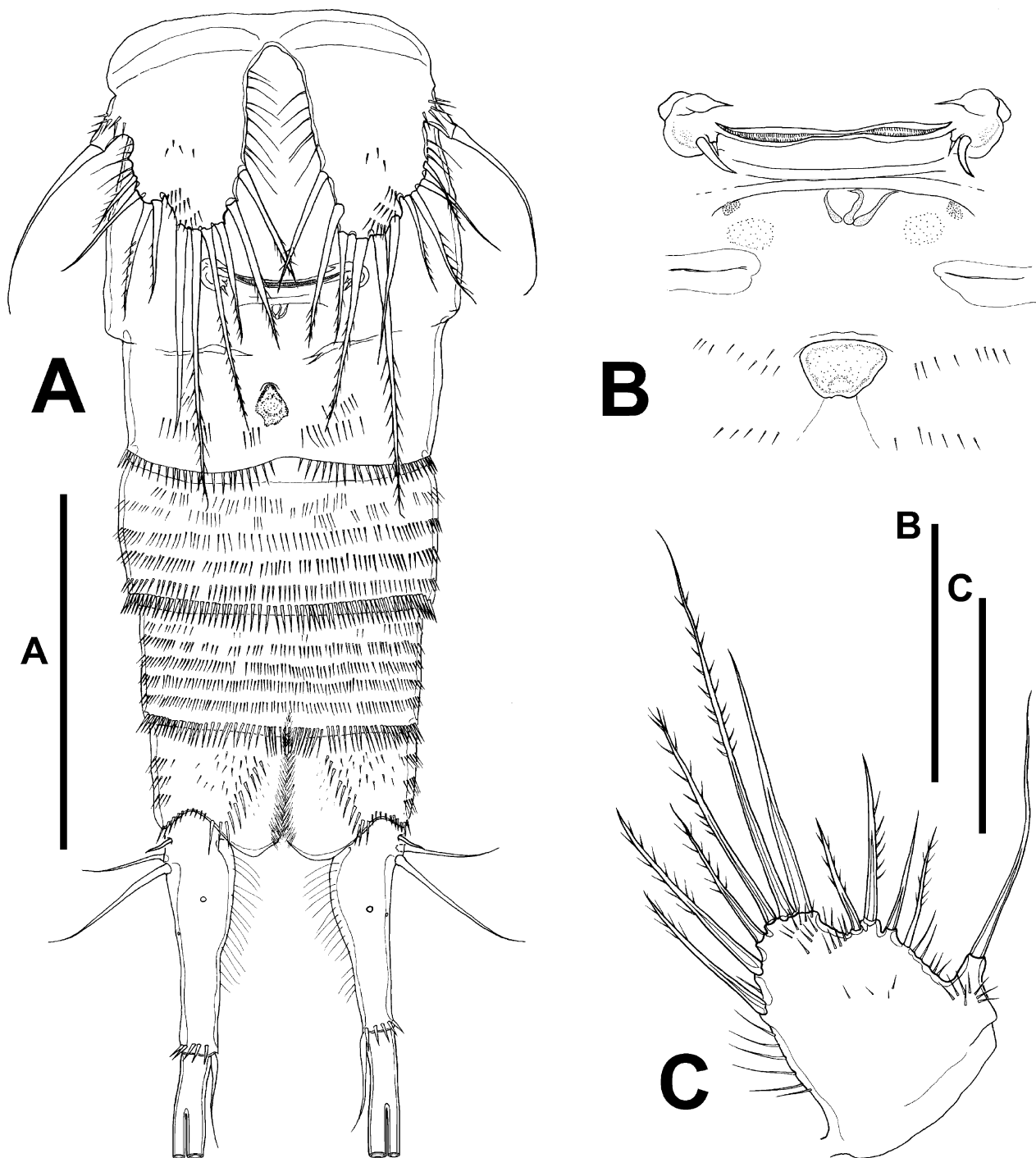


FIGURE 28. *Cletocamptus tainoi* sp. nov. Female. A, urosome, ventral view; B, genital field and P6; C, P5, anterior. Scale bars: A, 100 μ m; B and C, 50 μ m.

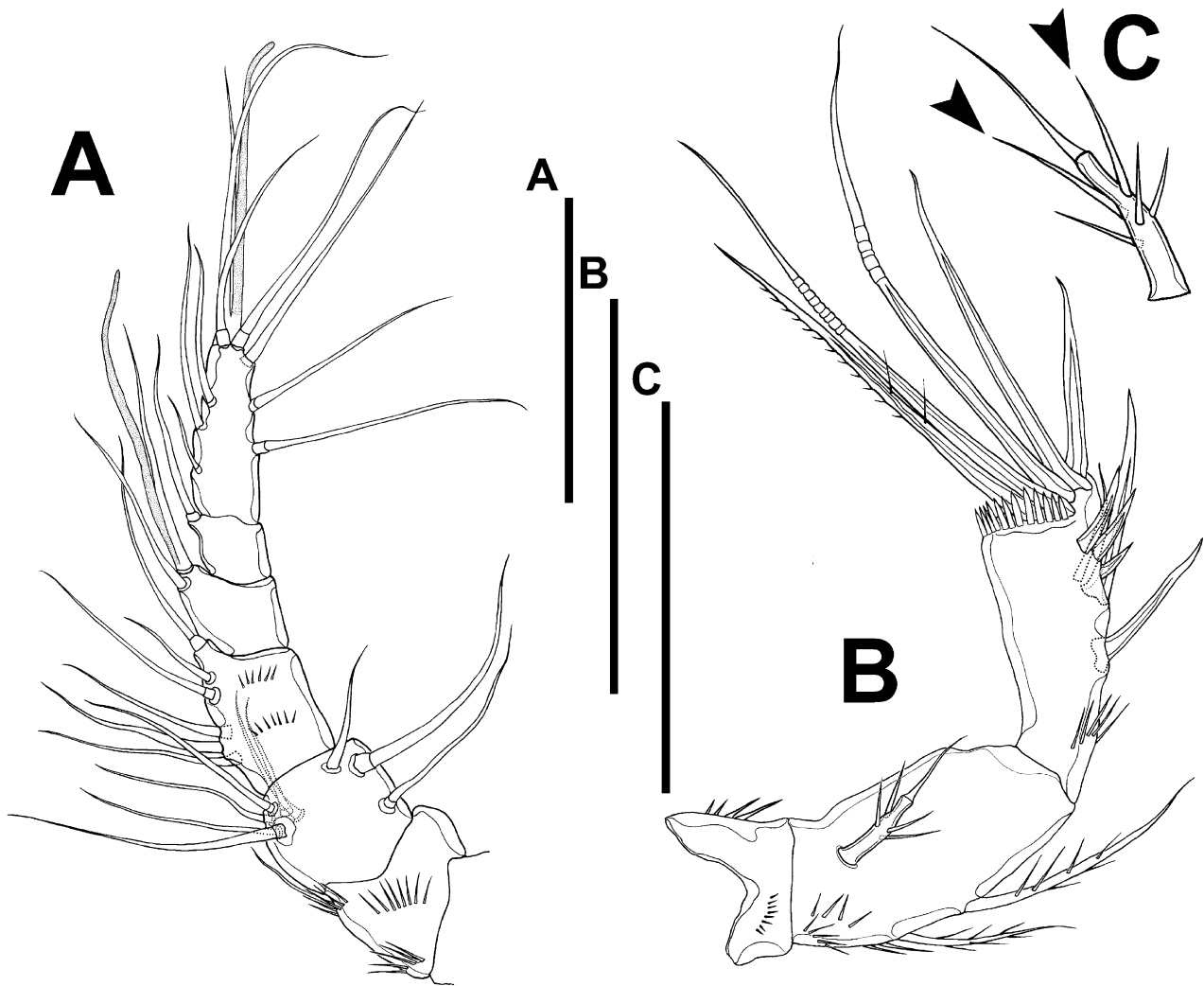


FIGURE 29. *Cletocamptus tainoi* sp. nov. Female. A, antennule; B, antenna; C, exopod of antenna, showing pair of comparatively longer, stiff setae that might actually be spinules. Scale bars: A and B, 50 µm; C, 25 µm.

Antenna (Fig. 29B, C) with small coxa. Allobasis with two abexopodal setae. Free endopodal segment with small inner spinules proximally, with stronger spinules subdistally; with two lateral inner spines and a slender seta, and five distal elements, two of them geniculate. Exopod elongate, one-segmented, with few spinules, with two lateral and one apical seta (the two lateral setae are somewhat rigid and could actually be spinules (see Fig. 29C)).

Mandible (Fig. 30A) robust, with rows of spinules proximally; chewing edge with teeth as figured, with one pyriform element and one lateral pinnate seta. Palp one-segmented, with two long setae unequal in length.

Maxillule (Fig. 30B) robust; arthrite of praecoxa with few spinules, with one surface seta, and seven spines and two slender setae distally. Coxa with some spinules, with two slender setae. Basis with spinules as figured, with two apical setae. Exopod and endopod incorporated to basis, represented by two setae each.

Maxilla (Fig. 30C): syncoxa with spinules as shown; with two endites, each bearing three setae. Allobasis drawn into strong claw with one accompanying seta. Endopod represented by three setae.

Maxilliped (Fig. 30D) subchelate. Syncoxa with row of spinules, with one seta on inner distal corner. Basis without armature, with spinules as shown. Endopod drawn into long and slender claw with one accompanying small seta.

P1 (Fig. 31A): praecoxa with spinules close to joint with coxa. The latter with anterior transverse rows of spinules and outer row of strong spinules. Basis with inner and outer spine; with median rows of spinules, with stronger spinules at base of exopod, between rami and at base of inner and outer spines. Exopod three-segmented, slightly longer than endopod; EXP1 without, EXP2 with inner seta; EXP3 with four elements. Endopod two-segmented, reaching proximal third of EXP3; ENP1 about 1.4 times as long as wide, barely reaching tip of EXP1,

inner seta shorter than both endopodal segments combined, with brush tip; ENP2 elongate, about 4.6 times as long as wide, with three elements.

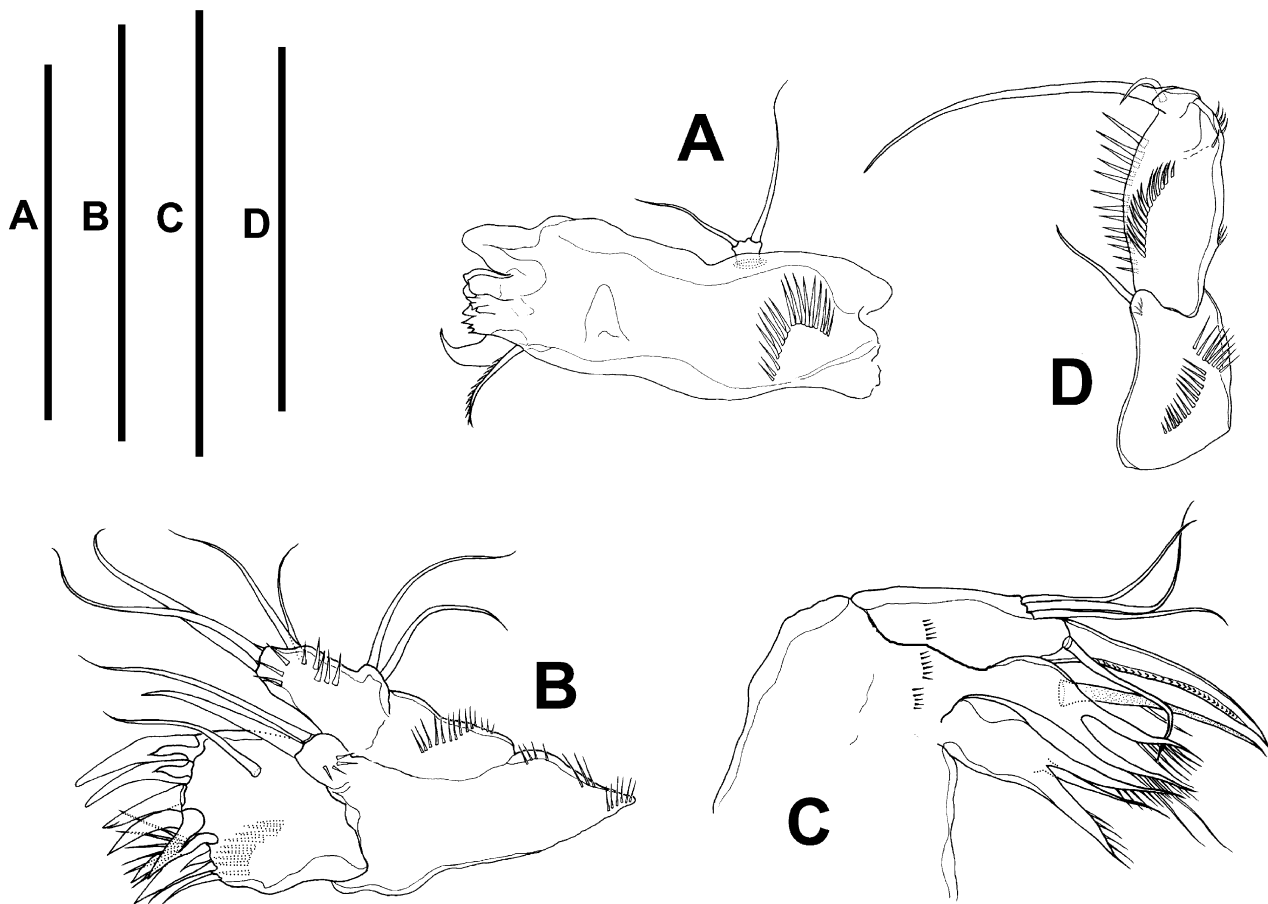


FIGURE 30. *Cletocamptus tainoi* sp. nov. Female. A, mandible; B, maxillule; C, maxilla; D, maxilliped. Scale bars: A, B, C, and D, 50 μ m.

P2 (Fig. 31B): praecoxa and coxa ornamented as figured. Basis with spinules between rami and medially close to base of endopod, and with stronger spinules at base of exopod; outer element setiform. Exopod three-segmented and ornamented as shown; EXP1 without inner seta; inner seta of EXP2 about 0.4 times as long as outer apical seta of EXP3, with brush tip; EXP3 with five elements, of which inner seta about 1.1 times as long as outer apical seta, without brush tip. Endopod two segmented, reaching distal margin of EXP1; ENP1 small, slightly wider than long, with outer and inner spinules; ENP2 elongate, about 3.5 times as long as wide, with long spinules as shown, with one outer spine-like and two apical elements; outer element shortest, apical seta longest reaching beyond EXP3.

P3 (Fig. 32A): praecoxa and coxa as in P2; basis with outer seta. Exopod as in P2; EXP1 without inner armature; inner seta of EXP2 about 0.5 times as long as outer apical seta of EXP3, with brush tip; EXP3 with five elements, of which inner seta about 1.1 times as long as outer apical seta, without brush tip. Endopod two-segmented, barely reaching tip of EXP1; ENP1 nearly as long as wide, with long spinules as shown; ENP2 elongate, about 3.3 times as long as wide, with two inner and two apical setae, and one outer spine-like element; inner setae shortest, apical setae longest (outer apical seta reaching beyond, inner apical seta barely reaching tip of EXP3).

P4 (Fig. 32B): praecoxa, coxa and basis as in P3. Exopod as in P3, except for armature formula of EXP3 (without inner seta); EXP1 without inner armature; inner seta of EXP2 slightly shorter than outer apical seta of EXP3, with brush tip; EXP3 with four elements. Endopod very small, two-segmented; ENP1 minute, about as long as wide; ENP2 elongate, about twice as long as wide, with slender spinules, with two apical setae, of which inner shorter, outer reaching middle of EXP3.

P5 (Fig. 28A, C): exopod and baseoendopod fused, barely separated by gap between rami. Baseoendopod with

outer seta of basis; endopodal lobe longer than exopod, with spinules as figured, with two inner and four apical setae; relative length of setae as shown. Exopod with outer spinules, with four setae in all.

P6 (Fig. 28B) represented by median plate, each vestigial leg represented by two small setae. Copulatory pore in the middle of genital somite.

Male. Total body length measured from tip of rostrum to posterior margin of caudal rami, ranging from 486 μm to 628 μm (mean= 556 μm ; n= 8). Habitus as in female except for clearer distinction between prosome and urosome, and for separate second and third urosomites (Fig. 33A, B); anal somite (Figs. 33A, B, 34A, C, D) as in female except for denser spinular ornamentation in the male; caudal rami as in female; caudal setae IV and V as in female, except for length relative to total body length of 17% and 61%, respectively. Ventral ornamentation of third, fourth and fifth urosomites (Fig. 34D) denser than in female.

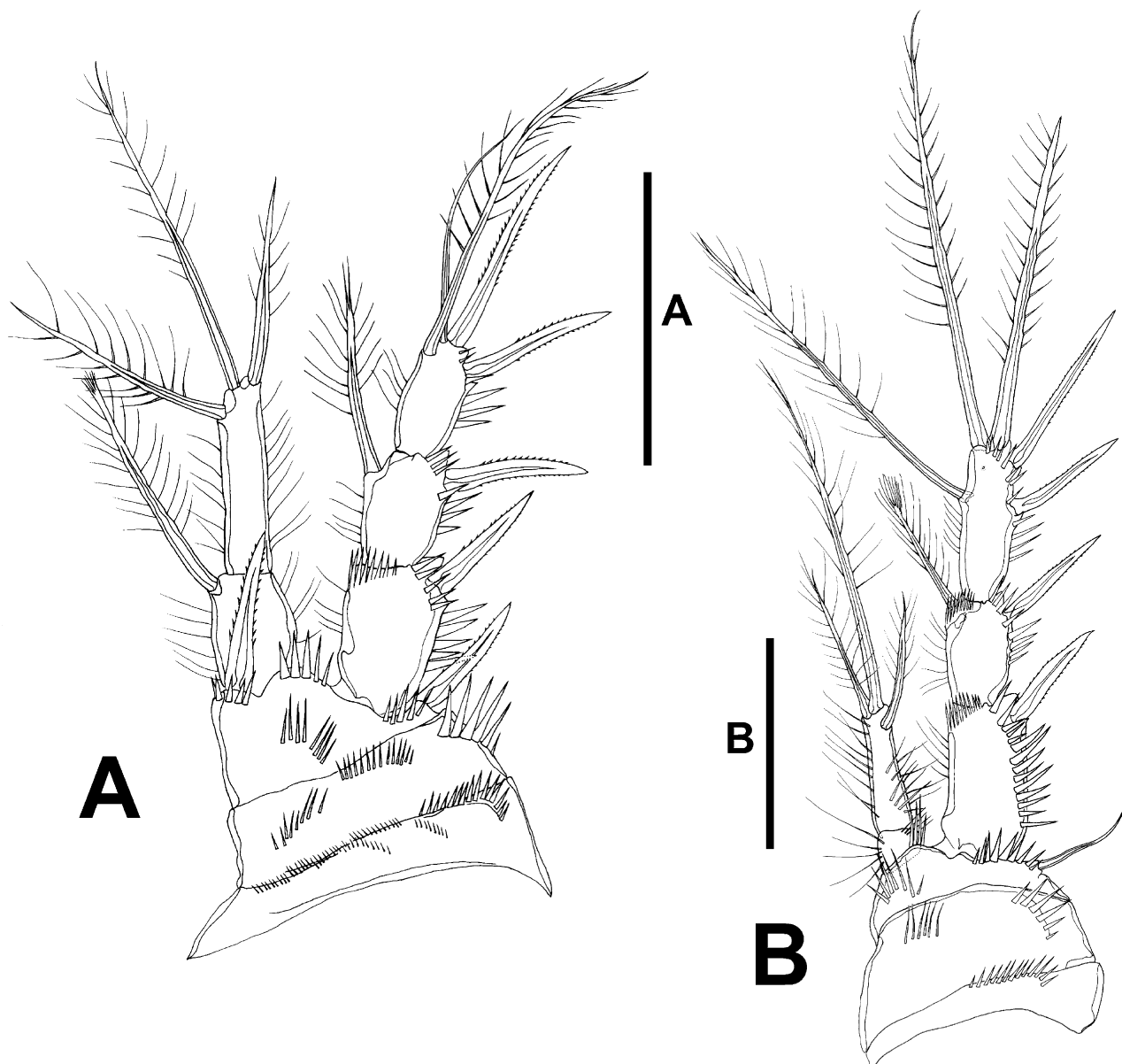


FIGURE 31. *Cletocamptus tainoi* sp. nov. Female. A, P1, anterior; B, P2, anterior. Scale bars: A and B, 50 μm .

Rostrum (Fig. 33C): sexually dimorphic, elongate.

Antennule (Fig. 35A, B): six-segmented; subchirocer; last segment with two acute teeth (Fig. 35B). Armature formula difficult to define; most probably as follows: 1-(1), 2-(9), 3-(9), 4-(8+[1+ae]), 5-(3), 6-(6+[1+ae]). The armature on the last segment arises from a plate-like swelling, it seems not to be a true segment. The nature of this structure as well as an in-depth analysis of the segmentation of the antennule deserves further investigation.

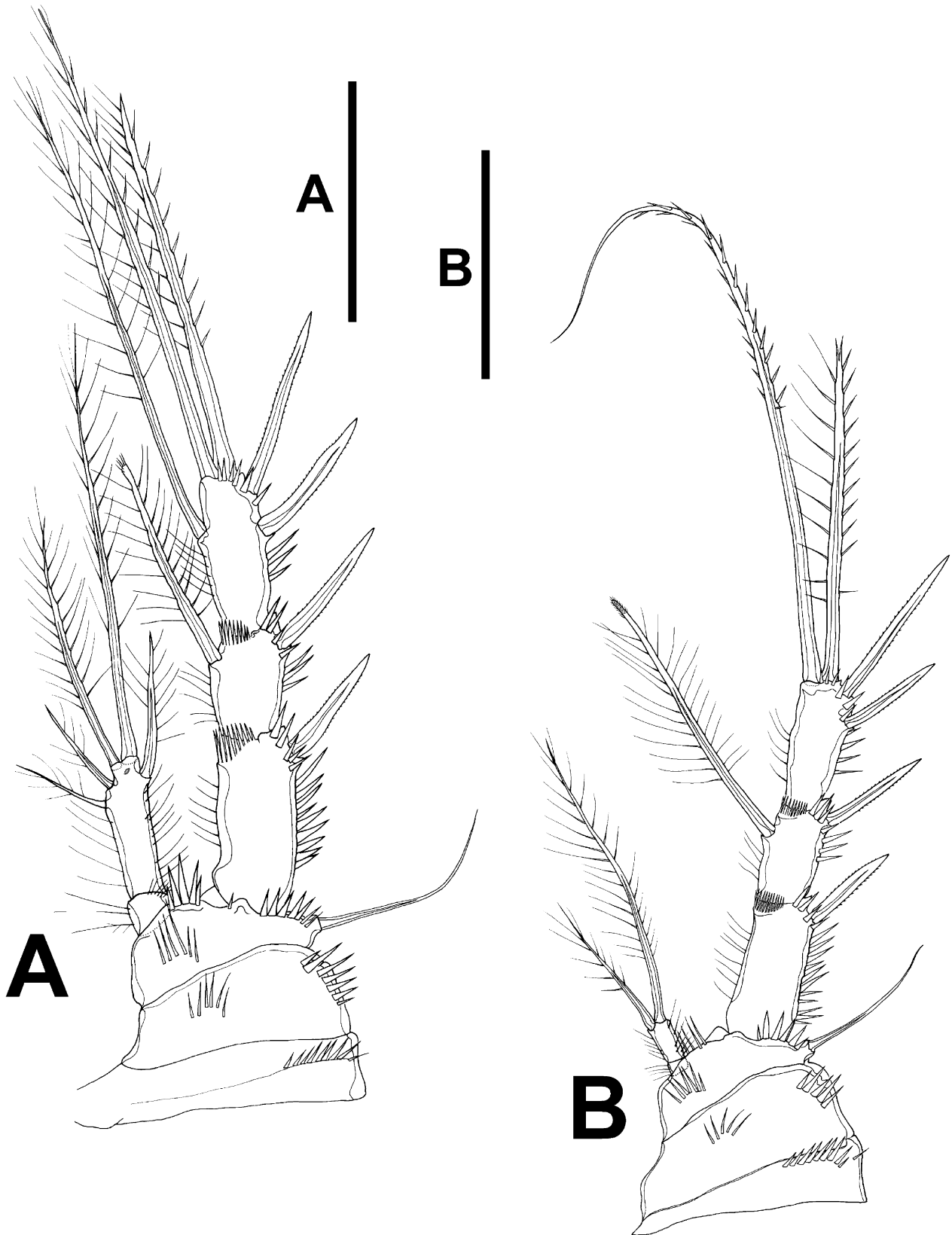


FIGURE 32. *Cletocamptus tainoi* sp. nov. Female. A, P3, anterior; B, P4, anterior. Scale bars: A and B, 50 μ m.

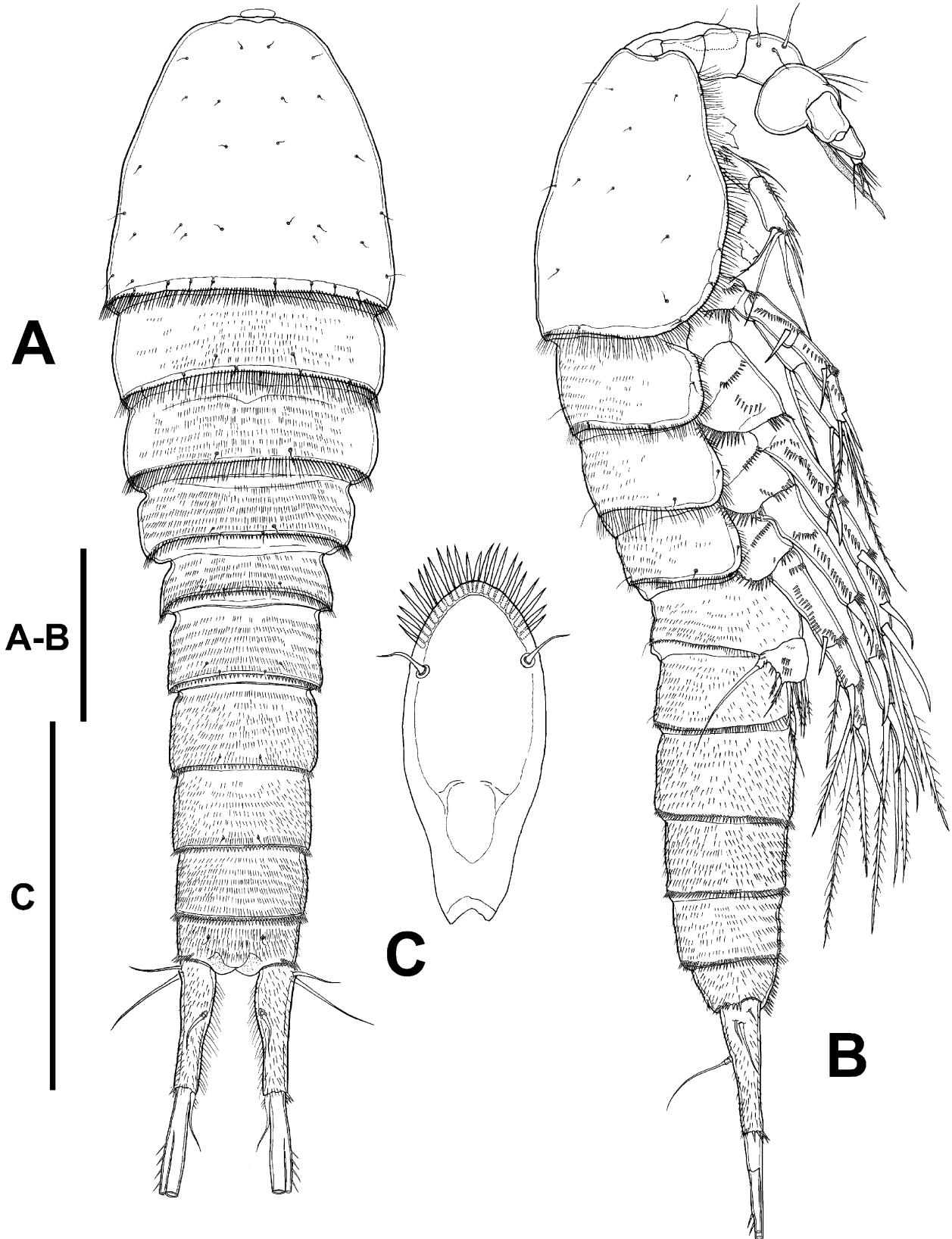


FIGURE 33. *Cletocamptus tainoi* sp. nov. Male. A, habitus, dorsal view; B, habitus, lateral view; C, rostrum. Scale bars: A–B, 100 µm; C, 50 µm.

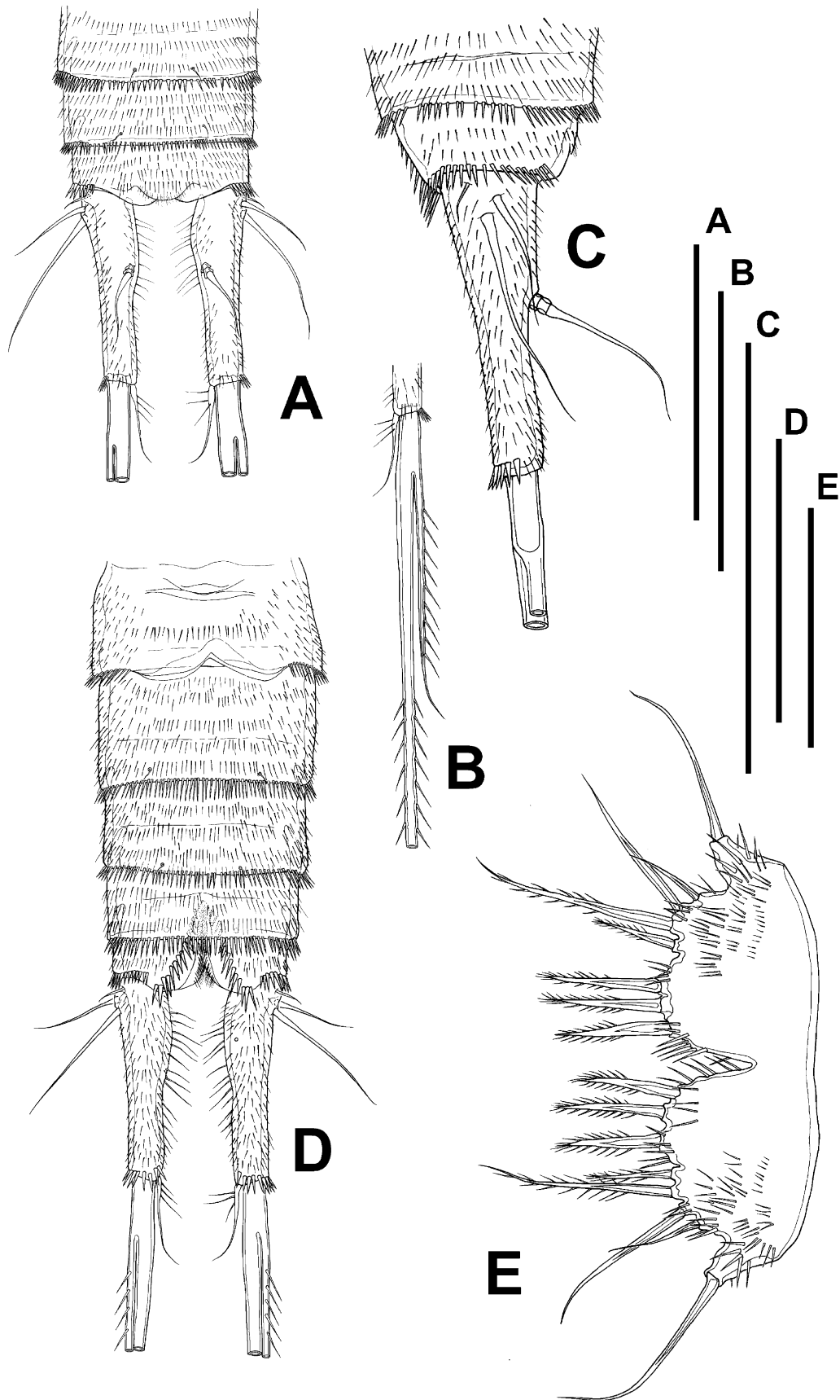


FIGURE 34. *Cletocamptus tainoi* sp. nov. Male. A, fourth, fifth and anal somite, and caudal rami, dorsal view; B, caudal setae IV, V and VI; C, fifth and anal somite, and left caudal ramus lateral view; D, urosome, ventral view, P5 bearing-somite omitted; E, P5, anterior. Scale bars: A, B, C, and D, 100 µm; E, 50 µm.

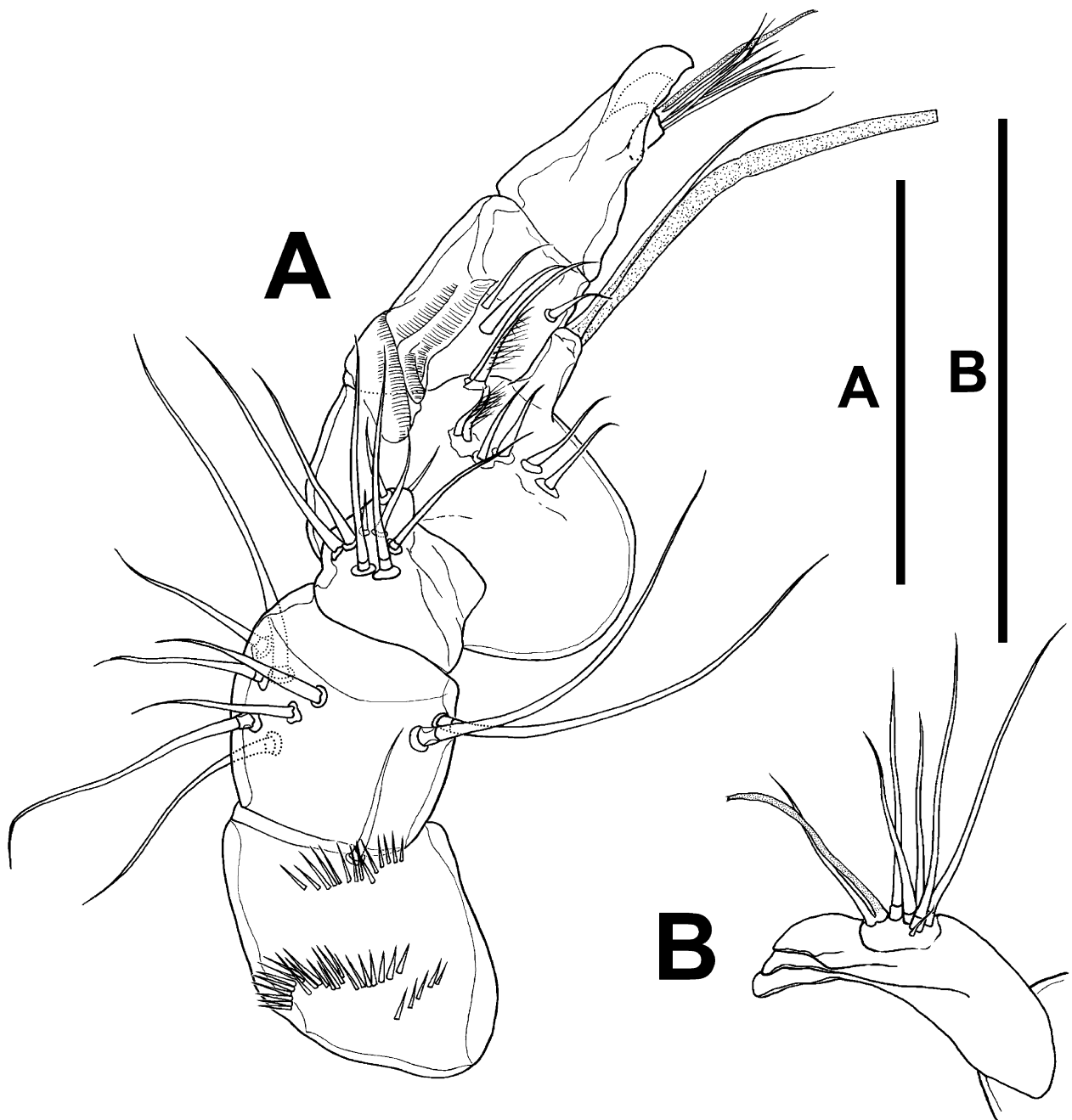


FIGURE 35. *Clotocampus tainoi* sp. nov. Male. A, antennule; B, last antennular segment. Scale bars: A and B, 50 μ m.

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

P1 (Fig. 36A): as in female except for dimorphic projection on inner distal corner of basis.

P2 (Fig. 36B) as in female except for relatively stouter outer spines of the exopod, for relatively longer EXP1, and for relatively shorter setae of ENP2 in the male, of which apical seta barely reaching tip of EXP3.

P3 (Fig. 37A, B): as in female except for relatively stouter outer spines, and for longer EXP1. Endopod clearly two-segmented; ENP1 nearly as long as wide, with long inner spinules, unarmed; ENP2 with inner distal apophysis bent outwards, very short, with two apical setae relatively shorter than in female (outer apical seta barely reaching tip of EXP3, inner apical seta barely reaching middle of EXP2); with paired asprothekes (Fig. 37B).

P4 (Fig. 37C) as in female, except for stouter outer spines of exopod, relatively longer EXP1, and relatively shorter setae of ENP2 (outer seta reaching slightly beyond EXP1).

Both P5 fused (Fig. 34E); exopod and baseoendopod fused; division between rami indicated by slight notch. Exopod with spinules as shown; with four elements. Baseoendopod with outer seta of basis; endopodal lobe with outer and inner spinules as shown; with three elements in all.

P6 (Fig. 34D) represented by plate; without armature.
 Armature formula in Table 4.

TABLE 4. Armature formula of *Cletocamptus tainoi* sp. nov.

Leg		P1	P2	P3	P4	P5
Female	EXP	I-0;I-1;I,II,1	I-0;I-1;II,2,1	I-0;I-1;II,2,1	I-0;I-1;II,2,0	4
	ENP	0-1;0,II,1	0-0;I,2,0	0-0;I,2,2	0,0;0,2,0	6
Male	EXP	I-0;I-1;I,II,1	I-0;I-1;II,2,1	I-0;I-1;II,2,1	I-0;I-1;II,2,0	4
	ENP	0-1;0,II,1	0-0;I,2,0	0-0;0,2,Apophysis	0,0;0,2,0	3

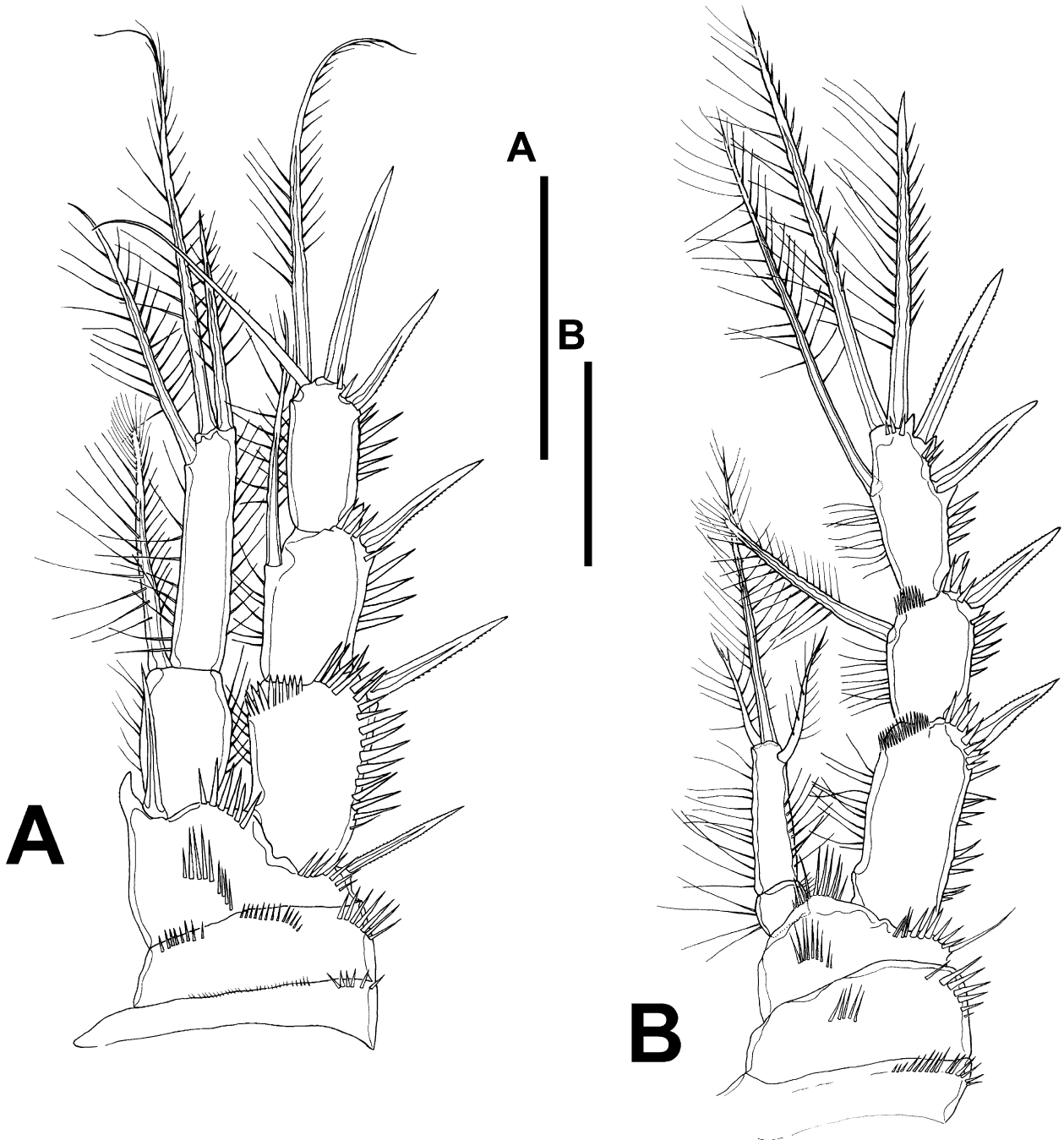


FIGURE 36. *Cletocamptus tainoi* sp. nov. Male. A, P1, anterior; B, P2, anterior. Scale bars: A and B, 50 μ m.

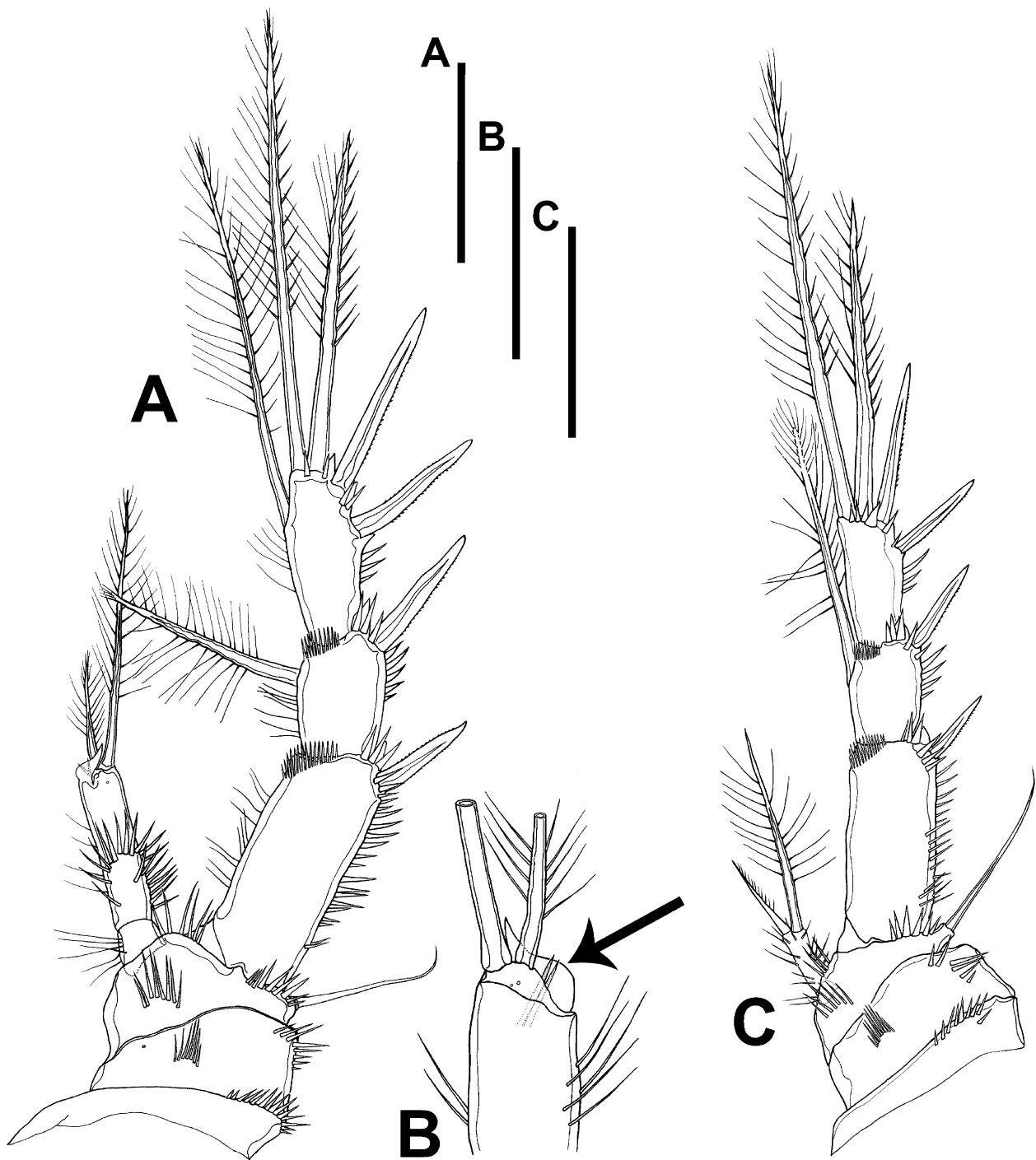


FIGURE 37. *Cletocamptus tainoi* sp. nov. Male. A, P3, anterior; B, distal part of P3ENP showing asprothekes; C, P4, anterior. Scale bars: A and B, 50 μ m; C, 25 μ m.

Variability. The number of spinules/setae on the antennary exopod can vary from four to five in females and males. The number of seta on the second and last antennular segment of the female can vary from 8 to 9. The number of setae on the fourth antennular segment of the male can vary from 7 to 8.

***Cletocamptus chappuisi* sp. nov.**

Synonymy. *Cletocamptus albuquerqueensis* sensu Chappuis (1933: 399–400, Figs. 9–11).

Etymology. The species has been named after Pierre-Alfred Chappuis (1891–1960).

Type material. The male described by Chappuis (1933) is herein designated as the lectotype and only name-bearing type of the species (Art. 74.4, International Commission on Zoological Nomenclature 1999).

Type locality. Pos Shiki, Bonaire; muddy pond; temperature, 31°C; polyhaline.

Distribution. Bonaire: Pos Shiki (Chappuis 1933: 392).

Redescription (based on the original description in Chappuis 1933). Male. Total body length measured from tip of rostrum to posterior margin of caudal rami, 660 µm. General shape as in *C. retrogressus*. Posterior margin of somites smooth; posterior margin of abdominal somites with continuous row of setules dorsally, ventrally with parallel rows of slender setules (spinules?). Anal operculum rounded, bare. Caudal rami slightly divergent, slightly more than 3 times as long as wide; dorsal seta VII inserted medially on first half of ramus, articulated at its base; setae II and III inserted proximally on outer margin; setae IV, V and VI inserted distally; setae IV and V fused basally; seta VI short.

Antennule short, strong, similar to that of *C. retrogressus*.

Exopod of the antenna a single seta.

P1 as in the female of *C. albuquerquensis*; endopod two-segmented, first segment as long as EXP1, with one inner seta; second segment with three setae.

P2 with three-segmented exopod; EXP3 with one inner and two apical setae, and two outer spines: Endopod two-segmented; first segment small, squarish; second segment elongate, reaching tip of EXP1, with one inner and one outer small seta, and one apical long element.

P3 with three-segmented exopod; EXP1 about 3 times as long as wide, and about 0.8 times as long as EXP2 and EXP3 combined, without inner armature; EXP2 with inner seta; EXP3 with one inner seta, two apical elements, and two outer spines. Endopod dimorphic, two-segmented; first segment slightly longer than wide; second segment elongate, about 2.8 times as long as wide, reaching slightly beyond EXP1; with short inner apophysis bent outwards at an angle of 90°; with two apical setae.

P4 with three segmented exopod; first segment elongate, about 3 times as long as wide and about 0.75 times as long as EXP2 and EXP3 combined, without inner armature; EXP2 with inner seta; EXP3 without inner seta, with two apical setae and two outer spines. Endopod two-segmented; first segment very small, wider than long, without armature; second segment about four times as long as wide, barely reaching proximal seventh of EXP1, with two setae.

P5 with fused rami separated only by small notch; both legs fused medially. Baseoendopod with outer seta of basis, endopodal lobe with three subequal setae. Exopod with four setae, of which outermost shortest, apical outer seta longest.

P6 a plate without armature.

Female. Unknown.

Discussion

Historical background. Herrick (1894) created the genus *Marshia* Herrick, 1894 to accommodate *M. albuquerquensis* Herrick, 1894 and *M. brevicaudata*, found in temporary ponds in the Rio Grande valley, New Mexico. He also gave a brief diagnosis for the genus in which he stressed the one-segmented endopod of P4 and the antenna “without obvious palpus” (erroneously referred by Herrick (1894) as the “outer ramus” of P4 and “palpus” of the antennule, respectively). Some other errors in Herrick’s (1894) diagnosis of the genus include the transposition of the endopods and exopods of all the swimming legs, as well as the transposition of the antennule and the antenna. The same errors appear in the original description of *M. albuquerquensis* and *M. brevicaudata*. One year later, Herrick (1895) presented again the diagnosis of the genus *Marshia* and the description of both *M. albuquerquensis* and *M. brevicaudata* to which he added some slight changes and some new figures, but kept the same errors. This was noted also by Marsh (1918) and Wilson (1932). Also, in his description of *M. albuquerquensis*, Herrick (1894, 1895) made no additional comments about the exopod of the antenna, suggesting that the condition of this appendage was as in the generic diagnosis. He also omitted any comment about the mandibular palp. Herrick (1894, 1895) described the female P4 endopod as one-segmented, and noted that the female P5 exopod and baseoendopod are separated only by a “simple rounded incision” (Herrick 1894) and that the

caudal setae IV and V are fused basally. He also noted that the caudal rami were about 2.5 times as long as wide in the female, but over 4 times as long as wide in the male; this criterion was used by Weckel (1914) in his key to separate *M. albuquerquensis* and *M. brevicaudata*. The male of *M. albuquerquensis* did not receive too much attention and only some lines were given about the general shape of the antennule, the P5, and the caudal rami, and nothing is said about the general shape of the P3 endopod and rostrum. In the description of *M. brevicaudata*, Herrick (1894) pointed out that this species was similar to *M. albuquerquensis* in most respects, but that they can be distinguished by the general shape and length of the proximal aesthetasc of the male antennule (shorter and clavate in *M. brevicaudata*), length:width ratio of the caudal rami (more elongated in the male than in the female in *M. albuquerquensis*, but twice as long as wide in the female and male in *M. brevicaudata*), in the shape of the caudal setae IV and V (fused basally in *M. albuquerquensis*, separated in *M. brevicaudata*), and in the relative length of some setae of the female P5, but did not mention the deep incision between the exopod and baseoendopod of the female and male P5. Also, it would have been useful if Herrick (1894, 1895) had described the endopod of the male P3. Concluding the description, Herrick (1894: 44; 1895: 138) wrote that "it must remain for larger experience to determine the value of these distinctions which rest upon —on— comparatively few individuals in the case of *M. brevicaudata*."

Some years later, Wilson (1932) presented an amended diagnosis of the genus *Marshia* in which he noted the lack of an exopod on the antenna, that the endopods of P1 to P4 are two-segmented but that the two segments of the endopod of P4 are sometimes fused, and that the caudal ramus is much longer than wide. Based on five females and one male, he gave a complementary redescription of *M. brevicaudata* from Ashumet Pond and Penikese Island, Massachusetts. Here, Wilson (1932) noted that the female endopod of P4 can be two- or one-segmented with no trace of division, that the caudal rami are 1.5 times as long as wide in the female but twice as long as wide in the male, that the caudal setae IV and V are separated, that the female P5 exopod and baseoendopod are distinctly indicated by a deep incision, and that the proximal aesthetasc of the male antennule is short and club-shaped. Most noteworthy, Wilson (1932) did not observe any sexual dimorphism in the endopod of the male P3. This and the deep incision between the P5EXP and baseoendopod of both the male and female (similar to Herrick's (1894, 1895) figure of the female P5 of *M. brevicaudata*), are probably the most outstanding features of his material.

At Bonaire Chappuis (1933) found two male specimens of *Marshia* that had P4 with two-segmented endopods. Though *M. albuquerquensis* was originally described as having P4 with one-segmented endopods, Chappuis (1933) identified the specimens from Bonaire with *M. albuquerquensis* and suggested there was no need to re-diagnose the genus *Marshia*. Chappuis (1933) synonymised *Marshia* and *Cletocamptus*, and described his material from Bonaire as "identical" with Herrick's (1894) *C. albuquerquensis*, with the caudal setae IV and V fused, antennal exopod represented by a single seta, and male endopod of P3 and P4 two-segmented. Noteworthy, Chappuis (1933) described the inner apophysis of the second endopodal segment of the male P3 situated subdistally, very short and bent outwards at an angle of nearly 90°. He also suggested that the identity of Herrick's *C. brevicaudatus* (note that Chappuis 1933: 400 changed the specific epithet *brevicaudata* for *brevicaudatus*) could not be assessed given the brief original description and decided not to include the species in his key to the species of *Cletocamptus*. Chappuis (1933) further considered Wilson's (1932) record of *C. brevicaudatus* doubtful mainly because of the lack of sexual dimorphism in the male legs, arguing that, if correct, Wilson's (1932) material of *M. brevicaudata* could not be attributed to the genus *Cletocamptus*.

Soon after, Kiefer (1934) presented the description of *C. dominicanus*, from Enriquillo Lake (Dominican Republic) (Kiefer 1934, 1936). He described his new species with the caudal setae IV and V fused, female and male endopod of P4 one-segmented, male endopod of P3 two-segmented, and noted that his material resembles closely *C. albuquerquensis*. Slightly later, Lang (1936) recognized *C. albuquerquensis* and *C. dominicanus* as distinct species, and given the fragmentary knowledge of *C. brevicaudatus* decided not to include this species in his key to the species of *Cletocamptus*.

In Lang's (1948) monograph there is an amended diagnosis of *C. albuquerquensis* with a one- or two-segmented female and male endopod of P4 (in his table XXIII: 1249 he shows a one-segmented endopod of P4, but in his figure 508: 1277 he shows Chappuis' (1933) figure of the male P4 with a two-segmented endopod), a two-segmented male endopod of P3, and caudal setae IV and V fused, being the antennal exopod and the mandibular palp unknown. Most significantly, he now synonymised *C. albuquerquensis* and *C. dominicanus*, and, following Chappuis' (1933) view, considered *M. brevicaudata* as *species incertae* and probably conspecific with *C. deitersi* (Richard, 1897). He also noted that *C. albuquerquensis* was distributed in Colorado (Dodds 1915, 1919, 1920),

North Dakota (Willey 1923; Young 1924) and Haiti (Kiefer 1934, 1936), and considered Chappuis' (1933) record from Bonaire, as doubtful.

However, Chappuis' (1933) scheme regarding the synonymy of *Marshia* and *Cletocamptus*, and Lang's (1948) view regarding the *species incertae* status of *M. brevicaudata* were not followed by Jakobi (1956). He reported two males of *M. brevicaudata* from brackish systems in Cananéia (Brazil), arguing that the general body shape, general shape and relative size of the exopod and baseoendopod of the P5 of his material from Brazil is identical to *M. brevicaudata* as described by Herrick (1894, 1895). Jakobi (1956) considered *C. albuquerqueensis* and *M. brevicaudata* as distinct species, and questioned Lang's (1948) view about the possible synonymy of *M. brevicaudata* and *C. deitersi*. Additionally, Jakobi (1956) considered that *M. brevicaudata* is distributed in Massachusetts (US) (Wilson's (1932) record), New Mexico (Herrick's (1894, 1895) records) and in the coast of São Paulo–Paraná (Brazil) based on his own record.

Interestingly, Pallares (1962) presented an additional redescription of *C. albuquerqueensis* based on several females and males from the temporary Luro lagoon near the city of Santa Rosa in La Pampa Province (Argentina). She described her material with a one-segmented antennal exopod armed with three apical setae, rudimentary mandibular palp with two setae, a two-segmented endopod of P4 (though the division is weak), caudal setae IV and V fused, male endopod of P3 two-segmented with inner apophysis short and bent outwards at an angle of nearly 90°, male and female exopod and baseoendopod of P5 separated by small notch, and caudal rami 3 times as long as wide in the female but up to 5 times as long as wide in the male.

Chappuis' (1933) scheme on the synonymy of *Marshia* and *Cletocamptus*, and Lang's (1948) on the synonymy of *C. albuquerqueensis* and *C. dominicanus* (and *species incertae* status of *M. brevicaudata*), have been traditionally adopted by later researchers who identified material of *Cletocamptus* from North and South America and the Caribbean, with *C. albuquerqueensis* (see references cited above). As a result, the identity of *C. albuquerqueensis* and *C. dominicanus* has become unclear.

Recently, Gómez (2005) suggested that *C. albuquerqueensis* as presently known, might be a complex of species, and after examination of the taxonomical history of the species, Gómez & Gee (2009) suggested to relegate *C. albuquerqueensis* to *species inquirenda*.

Cletocamptus albuquerqueensis. Before this study, other researchers have identified *Cletocamptus* specimens from southern Canada (Saskatchewan) and central US (Wyoming) with *C. albuquerqueensis* (see USNM No. 310388, 310389, 119498 in "Additional material" above for the redescription of *C. albuquerqueensis*). In the present study, additional field samplings were carried out in a variety of ponds in southern New Mexico, southern Texas and the Rio Grande Valley to re-collect *C. albuquerqueensis* or *M. brevicaudata* near Albuquerque, New Mexico. Unfortunately, these attempts were unsuccessful. Clearly, this region near the Rio Grande River has undergone major environmental changes over the past 100 plus years with urban expansion and agricultural development and climate change, particularly long term drought (Ralf L. Price, Los Alamos National Laboratory, New Mexico, and Wiebke J. Boeing, New Mexico State University, pers. com. to RG). However, four samples containing *C. albuquerqueensis* were obtained from Farmington Bay (Great Salt Lake, Utah) by Wayne Wurtsbaugh (Utah State University). Careful inspection of all this material revealed the presence of a one-segmented antennal exopod armed with three setae and ornamented with few spinules, that the P4ENP is two-segmented, that the caudal setae IV and V are fused basally, that the male caudal rami are longer than in the female, and that the exopod and baseoendopod of the female and male P5 are separated by a small notch only. This analysis revealed also that the only variability observed within and between the populations analyzed is the number of armature elements of the male and female antennule, female and male P5, and female P4ENP, i.e., the general shape of the antennal exopod (small and one-segmented with three setae), and the male and female P5 (exopod and baseoendopod separated by a small notch or incision) remain constant.

Further, the identity of *C. albuquerqueensis* as suggested here is supported by Pallares' (1962) record and redescription of the species from Argentina. In fact, Pallares' (1962) material of *C. albuquerqueensis* was very similar to the material examined here, particularly the armature formula of swimming legs, shape of female and male P5, caudal setae IV and V fused, and above all, the two-segmented male P3ENP and the shape of the subdistal apophysis on the second segment, being very short and strongly bent outwards at an angle of nearly 90°. The differences observed in the length:width ratio of the female and male caudal rami (2.4 and 2.8 in the female and male of the material examined here, respectively, but 3 and 5 in Pallares' (1962) females and males, respectively) are considered here as geographical variability.

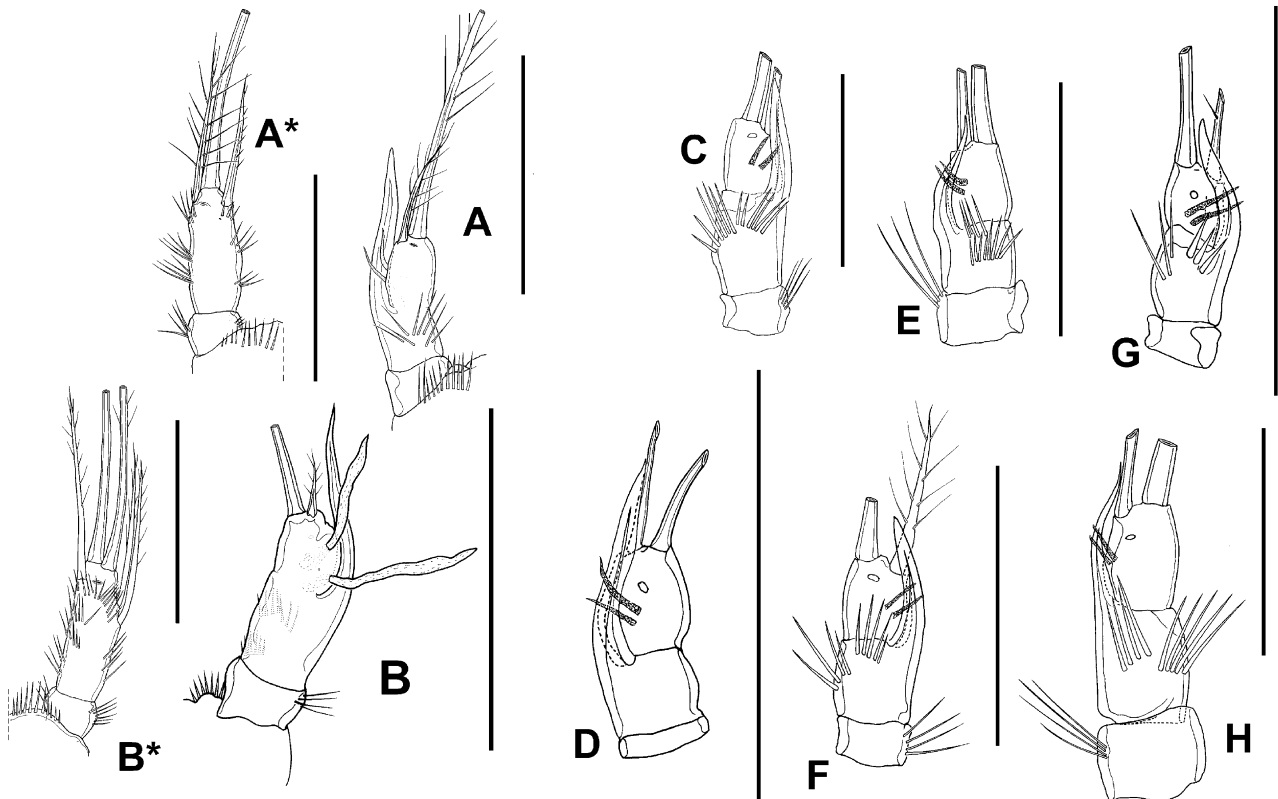


FIGURE 38. Asprothekes in different species of *Cletocamptus*. A and A*, male and female P3ENP, respectively, of *Cletocamptus* sp. from Fraternidad Lagoon (Puerto Rico); B and B*, male and female P3ENP, respectively, of *Cletocamptus dominicanus* Kiefer, 1934 from Laguna Candelaria (Puerto Rico); C, male P3ENP of *Cletocamptus axi* Mielke, 2000b; D, male P3ENP of *Cletocamptus goenchim* Gómez, Ingole, Sawant & Singh, 2013; E, male P3ENP of *Cletocamptus cesurirensis* Gómez, Scheihing & Labarca, 2007; F, male P3ENP of *Cletocamptus sinaloensis* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004; G, male P3ENP of *Cletocamptus stimpsoni* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004; H, male P3ENP of *Cletocamptus spinulosus* Gómez & Gee, 2009. Scale bars: A–H, 50 μ m.

***Cletocamptus dominicanus*.** As mentioned above, other researchers have identified *Cletocamptus* specimens from Trinidad and Tobago and from the British Virgin Islands with *C. albuquerquensis*. Probably, these identifications were made based on Lang's (1948) view about the synonymy of *C. albuquerquensis* and *C. dominicanus*. Careful inspection of the material collected from the US Virgin Islands, Puerto Rico, Bahamas and Colombia for this study revealed, in both genders, (1) the presence of denticles along the posterior margin of the cephalothorax, pro- and urosomites conferring a serrated appearance, (2) the antennal exopod one-segmented, minute, with one seta, (3) the one-segmented condition of P4ENP, (4) that the caudal setae IV and V are fused basally, (5) that the length:width ratio of the female and the male caudal rami are about 2 times as long as wide, (6) that the mandibular palp possesses three setae; (7) that the exopod and baseopod of the female and male P5 are separated by a small incision, and (8) that the male P3ENP is two-segmented, with inner apophysis sigmoid and as long as entire segment. The key characters that may have justified the synonymy of *C. albuquerquensis* and *C. dominicanus* by Lang (1948) was the variable number of segments (one or two) of the P4ENP in *C. dominicanus* (though the small proximal segment can be an artifact due to a small fold or narrowing at the base of the single segment of the P4ENP; see Fig. 26B), the general shape of the female and male P5 and the two-segmented male P3ENP. Since Herrick (1894, 1895) did not show the male P3ENP in the original description of *C. albuquerquensis*, no comparison of the shape of the apophysis could be made at that time. Of particular interest in *C. dominicanus*, as redescribed here, is the combination of (1) the tiny one-segmented exopod of the antenna with one seta, (2) the mandibular palp with three elements, (3) the female P3ENP3 with five setae, (4) the caudal rami of about 2 times as long as wide, (5) the shape of the female and male P5, but above all, (6) the presence of exceedingly long paired tube-pore-like structures called here asprothekes, from the Greek $\acute{\alpha}\sigma\pi\rho\varsigma$, $\acute{\alpha}\sigma\pi\rho\varsigma$, white, and $\theta\acute{\eta}\kappa\eta$, $\theta\acute{\eta}\kappa\eta$, sheath, white sheath, referring to its tube-pore-like appearance (see below).

***Cletocamptus tainoi* sp. nov.** A close relationship between *Cletocamptus trichotus* Kiefer, 1929, *C. confluens* (Schmeil, 1894), *C. albuquerqueensis*, *C. dominicanus*, *C. helobius* Fleeger, 1980, *C. chappuisi* and *C. tainoi* is assumed as all share the male and female P5EXP and baseoendopod separated only by a small notch (see below). The antennal exopod of *C. trichotus* and *C. chappuisi* is unknown. It is relatively well developed and one-segmented in *C. tainoi* and *C. albuquerqueensis*, very small with one seta only in *C. confluens* and *C. dominicanus*, and is represented by a single seta in *C. helobius*.

The mandible of *C. trichotus* and *C. chappuisi* remain unknown. On the other hand, *C. confluens*, *C. helobius* and *C. dominicanus* share the one-segmented mandibular palp with three setae. The mandibular palp of *C. confluens* and *C. helobius* is well developed, but the palp of *C. dominicanus* seems to have undergone some reduction. The setae on the mandibular palp are also well developed in *C. confluens* but are relatively shorter in *C. helobius* and *C. dominicanus*. On the other hand, *C. albuquerqueensis* and *C. tainoi* share the minute one-segmented palp with two setae only.

The maxillule of *C. trichotus* and *C. chappuisi* are unknown, but the maxillule of *C. helobius* exhibit a very strong lateral seta on the praecoxal arthrite. A similar seta has been observed, for example, in *C. levis* Gómez, 2005, *C. assimilis* Gómez & Gee, 2009, *C. axi* Mielke, 2000b, *C. cecsurirensis* Gómez, Scheihing & Labarca, 2007, among other species. *Cletocamptus confluens*, *C. albuquerqueensis*, *C. dominicanus*, and *C. tainoi* share the slender lateral seta on the praecoxal arthrite of the maxillule. A similar seta has been observed, for example, in *C. goenchim* Gómez, Ingole, Sawant & Singh, 2013, *C. gomezi* Suárez-Morales, Barrera-Moreno & Ciro-Pérez, 2013, *C. koreanus* Chang, 2013, *C. merbokensis* Gee, 1999, *C. pilosus* Gómez & Gee, 2009, *C. spinulosus* Gómez & Gee, 2009, and *C. stimpsoni* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004.

The Old World *C. trichotus* and *C. confluens*, and the American *C. albuquerqueensis* share the dimorphic caudal rami (the female of the Neotropical *C. chappuisi* remains unknown). In contrast, the American species from the Caribbean, *C. helobius*, *C. dominicanus*, and *C. tainoi* share the non-dimorphic caudal rami and seem to be closely related.

By using the material in this study plus published figures of other species (Gómez *et al.* 2004, 2007, 2013; Gómez, 2005 and Gómez & Gee, 2009) and upon re-inspection of type material and of material of *C. helobius*, *C. confluens* and *C. axi* deposited in the Copepoda collection of ICML–UAMzt, two situations occur with respect to the inner seta(e) of P1ENP1, P2EXP2–3, P3EXP2–3, and/or the P4EXP2–3. Specifically, they can be either relatively short (usually less than 0.7 times as long as the outer apical seta of the respective EXP3 for P2, P3 and P4) and with a brush tip, or long (usually 0.8 or more times as long as outer apical seta of the respective EXP3 for P2, P3 and P4), whip-like without brush-tip. Unfortunately, their condition is known only for eighteen species shown in Table 5, which can be grouped into six groups. The biggest group is composed of those species lacking an inner seta on P4EXP3, but with a relatively short inner seta with brush tip on P1ENP1, P2EXP2–3; P3EXP2–3, and P4EXP2. These species are *C. axi*, *C. deborahdexterae* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004, *C. sinaloensis* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004, *C. fourchensis* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004, *C. spinulosus*, *C. cecsurirensis*, *C. assimilis*, *C. tertius* Gómez & Gee, 2009, and *C. levis*. Among the species in table 5, *C. goenchim*, *C. stimpsoni*, *C. nudus* Gómez, 2005, and *C. pilosus* are the only four species with two inner setae on P3EXP3 and one inner seta on P4EXP3. These four species share the relatively short inner seta with brush tip of P1ENP1, P2EXP2–3, P3EXP2, the proximal seta with brush tip on P3EXP3, and on P4EXP2. However, these four species can be grouped into two different groups based on the shape of the distal inner seta of P3EXP3 and the inner seta of P4EXP3. The Indian *C. goenchim* and the American *C. stimpsoni* share the relatively long inner distal seta without brush tip on P3EXP3 and on P4EXP3. The same setae are relatively short and with brush tip in *C. nudus* and *C. pilosus*.

Of interest, is the condition of the inner seta on P1ENP1, P2EXP2–3, P3EXP2–3, and P4EXP2 of *C. albuquerqueensis*, *C. dominicanus*, *C. tainoi*, *C. helobius*, and *C. confluens* (the condition of these setae is unknown for *C. chappuisi* and *C. trichotus*), which also lack the inner seta on P4EXP3. Among these species, *C. confluens* occupies an isolated position due to the possession of the plesiomorphic condition of the inner setae on P1ENP1, P2EXP2–3, P3EXP2–3, and P4EXP2, i.e. a long whip-like seta without brush tip. *Cletocamptus albuquerqueensis*, *C. dominicanus*, *C. tainoi*, and *C. helobius* share the plesiomorphic setae on P2–P3EXP3, as well as the derived relatively short seta with brush tip on P2–P4EXP2, but *C. helobius* occupies an isolated position among these species due to the lack of inner seta on P1ENP1.

From all the above it seem reasonable to hypothesize that the condition of the inner seta(e) of P1ENP1,

P2EXP2–3, P3EXP2–3, and/or the P4EXP2–3, is of taxonomic importance, and could shed some light on the relationship among the species of *Cletocamptus*.

TABLE 5. Shape of the inner seta(e) on endo- and exopodal segments of P1–P4 of some species of *Cletocamptus*: W, seta relatively short, with brush tip; W/O, seta relatively long, whip-like, without brush tip; W-W, W-W/O, indicates the presence of two inner setae; N/A, without inner seta.

Leg and ramus	P1ENP	P2EXP		P3EXP		P4EXP	
Segment	1	2	3	2	3	2	3
<i>C. albuquerqueensis</i> (Herrick, 1894)	W	W	W/O	W	W/O	W	N/A
<i>C. dominicanus</i> Kiefer, 1934	W	W	W/O	W	W/O	W	N/A
<i>C. tainoi</i> sp. nov.	W	W	W/O	W	W/O	W	N/A
<i>C. helobius</i> Fleeger, 1980	N/A	W	W/O	W	W/O	W	N/A
<i>C. confluens</i> (Schmeil, 1894)	W/O	W/O	W/O	W/O	W/O	W/O	N/A
<i>C. nudus</i> Gómez, 2005	W	W	W	W	W-W	W	W
<i>C. pilosus</i> Gómez & Gee, 2009	W	W	W	W	W-W	W	W
<i>C. stimpsoni</i> Gómez, Fleeger, Rocha-Olivares & Foltz, 2004	W	W	W	W	W-W/O	W	W/O
<i>C. goenchim</i> Gómez, Ingole, Sawant & Singh, 2013	W	W	W	W	W-W/O	W	W/O
<i>C. deborahdexterae</i> Gómez, Fleeger, Rocha-Olivares & Foltz, 2004	W	W	W	W	W	W	N/A
<i>C. sinaloensis</i> Gómez, Fleeger, Rocha-Olivares & Foltz, 2004	W	W	W	W	W	W	N/A
<i>C. fourchensis</i> Gómez, Fleeger, Rocha-Olivares & Foltz, 2004	W	W	W	W	W	W	N/A
<i>C. spinulosus</i> Gómez & Gee, 2009	W	W	W	W	W	W	N/A
<i>C. ceccurirensis</i> Gómez, Scheihing & Labarca, 2007	W	W	W	W	W	W	N/A
<i>C. assimilis</i> Gómez & Gee, 2009	W	W	W	W	W	W	N/A
<i>C. tertius</i> Gómez & Gee, 2009	W	W	W	W	W	W	N/A
<i>C. levis</i> Gómez, 2005	W	W	W	W	W	W	N/A
<i>C. axi</i> Mielke, 2000b	W	W	W	W	W	W	N/A

***Cletocamptus chappuisi*.** The identity of Chappuis' (1933) material (two males only) found in a polyhaline pond in Pos Shiki (Bonaire) is intriguing. Chappuis' (1933) description appears to be accurate and the material from Bonaire fits the description of *C. albuquerqueensis* as defined here in, at least, for the most important traits that define the species, especially the male P3ENP (two-segmented, with subdistal apophysis on second segment short and bent outwards at an angle of nearly 90°), armature formula of swimming legs, shape of the male P5, and fused caudal setae IV and V. The only difference we could detect is that the antennal exopod is represented by one single seta in Chappuis' (1933) material, while in *C. albuquerqueensis* it is one-segmented and armed with three setae in the redescription presented herein. Also, considering the distribution of *C. albuquerqueensis* as proposed here, it seems possible that Chappuis' (1933) material from coastal Bonaire represents a species closely related to the inland *C. albuquerqueensis*.

Based on this analysis, we propose that Chappuis' (1933) specimens from Bonaire represent a new species, *Cletocamptus chappuisi*. The description of this new species is given above based on the description and illustrations by Chappuis (1933).

***Marshia brevicaudata*.** The identity of *M. brevicaudata* is rather puzzling. The original description contains numerous errors and it is unclear how many individuals were analyzed by Herrick (1894, 1895) from New Mexico. Therefore, there is no information on morphological variability. Wilson's (1932) record of the species from Massachusetts further complicates the situation given the lack of sexual dimorphism in the swimming legs of the male (especially the P3ENP) in his description. This was considered by Chappuis (1933) who suggested that, if

Wilson's (1932) observations are correct on the lack of sexual dimorphism in the male P3ENP, then Wilson's (1932) material of *M. brevicaudata* could not be attributed to the genus *Cletocamptus*. Let us assume that Wilson's (1932) observation on the lack of sexual dimorphism in the male P3ENP is incorrect, that the identification by Jakobi (1956) is correct, and that, the shape of the P5 of *M. brevicaudata* does not correspond to the range of variation of P5 in *C. albuquerquensis* (i.e., the presence of an unvarying small notch separating the exopod and baseopod of P5 of *C. albuquerquensis*). In this case, *M. brevicaudata* could represent a different species defined by the lack of antennal exopod, and exopod and baseopod of the female and male P5 separated by a deep incision as shown by Herrick (1894, 1895) and Wilson (1932). However, pending a more complete redescription and comparison of *M. brevicaudata* as originally described by Herrick (1894, 1895), and until the identity of Wilson's (1932) and Jakobi's (1956) material is assessed, we follow Lang's (1948) view here, and relegate *M. brevicaudata* to *species incertae*. One of us (SG) had the opportunity to check Wilson's material of *M. brevicaudata* housed in the US National Museum (Smithsonian Institution) (USNM60421, USNM60320). There were two vials. One of the vials contained three labels as follows: *Cletocamptus brevicaudatus* / 60421 / *Marshia brevicaudata* Herrick, South Pond, Aug 7 1925, Penikese Island. The other vial also contained three labels: *Cletocamptus brevicaudatus* / 60320 / *Marshia brevicaudata* Herrick, Lily Pond south of Ashumet Pond, Falmouth, Mass., July 15, 1926. Unfortunately, there were no copepods in these two vials, and this material is presumably lost.

Asprothekes. To better understand the occurrence and morphology of asprothekes observations were extended to other male *Cletocamptus* species not directly part of this study. Further inspection of *Cletocamptus* material kept in the Copepoda collection of ICML–UAMzt revealed the presence of asprothekes on the male P3ENP3 of *C. axi*, *C. goenchim*, *C. ceccurirensis*, *C. sinaloensis*, *C. stimpsoni*, and *C. spinulosus* (see Fig. 38). These asprothekes occur in pairs except for one rare exception where they occurred singly on a male of *C. albuquerquensis* from Big Quill Lake, Saskatchewan. Typically, the asprothekes are located midway along the inner margin of the primitive P3ENP3 or the derived P3ENP2 (ENP2 and 3 fused), except for *C. albuquerquensis* and *C. tainoi* (with two-segmented P3ENP), where they seem to have undergone subdistal displacement along with the apophysis (see below). The asprothekes are tubular, simple, translucent, tapering distally and flexible. In most species, they are small and difficult to see except in *C. dominicanus* where they are exceedingly long (see Figs. 25A, 26C). Sometimes, they can be obscured by the apophysis and/or the distal P3 endopodal segment, or can be broken off during dissection. The base of each asprotheke emerges from a granular, dense region within the distal endopodal segment of P3 that at times appears sac-like. They are much larger and morphologically different from typical pore tubes, no pore opening has been observed at the tip of asprothekes, and their nature and function is still obscure. It should be noted that Kiefer too observed paired asprothekes for *C. dominicanus* (see the male P3 in Fig. 3), but no comment was made on these structures. Such new inner structures other than setae have been observed on the male P3ENP3 of other canthocamptids, e.g., *Mesochra pseudoparva* Gómez Noguera & Fiers, 1997 (Gómez Noguera & Fiers 1997), and *M. wolskii* Jakubisiak, 1933 (Fiers & Rutledge 1990). Because of the difficulty in observing the asprothekes they have probably often been overlooked or misinterpreted as in several species of *Cletocamptus*. The homology of these structures in some species, e.g., *Mesochra inconspicua* (Scott T., 1899) or *M. lilljeborgi* Boeck, 1865, is uncertain, but these structures are probably not homologous in some species given their subdistal position, e.g., *M. flava* Lang, 1933, and *M. pallaresae* Soyer, 1977 as shown in Soyer (1977) and Pallares (1968), respectively. Also, as a general rule, the inner seta(e) (when present) on the female P3ENP2 of canthocamptid species, is(are) missing in the distal segment of the male P3ENP (Gómez Noguera & Fiers 1997). This is also true for *Cletocamptus* species as can be seen in Fig. 38B, B*, in which the female P3ENP2 possesses two inner setae (armature formula of ENP2 1,2,2), and for all those species whose male and female have been described (*C. affinis* Kiefer, 1957, *C. albuquerquensis*, *C. confluens*, *C. dominicanus*, *C. goenchim*, *C. gomezi*, *C. gravhiatus* (Shen & Sung, 1963), *C. koreanus*, *C. pilosus*, *C. stimpsoni*, *C. tainoi*, and *C. trichotus*) with the same complement formula on the female P3ENP2. Whether the asprothekes on the distal endopodal segment of the male P3ENP are homologous to the inner setae on the female P3ENP2 is difficult to ascertain at this point, since the paired asprothekes are also present in those species in which the armature formula of the female P3ENP2 is 1,1,1 (see for example Fig. 38A, A*, and Figs 38C, E, F and H, for *C. axi*, *C. ceccurirensis*, *C. sinaloensis*, and *C. spinulosus*), suggesting that the asprothekes, as in other canthocamptids, might be novel in origin (Gómez Noguera & Fiers 1997) or that the female may have lost one or more setae. Interestingly, Fiers (in Gómez Noguera & Fiers 1997) noted that the two inner setae on the distal endopodal segment of P3 of *Canthocamptus staphylinus* (Jurine, 1820)

appear in the CIII of both the male and female. In the female these setae continue to develop through successive stages while in the male their development is arrested. This suggests that the inner spinule/setule-like elements on the inner margin of the male P3ENP3 and the two inner setae on the female P3ENP3 of *C. staphylinus*, as well as the inner structures observed in the male P3ENP3 and the inner setae of the female P3ENP2 of *M. pseudoparva* and *M. wolskii* are homologous.

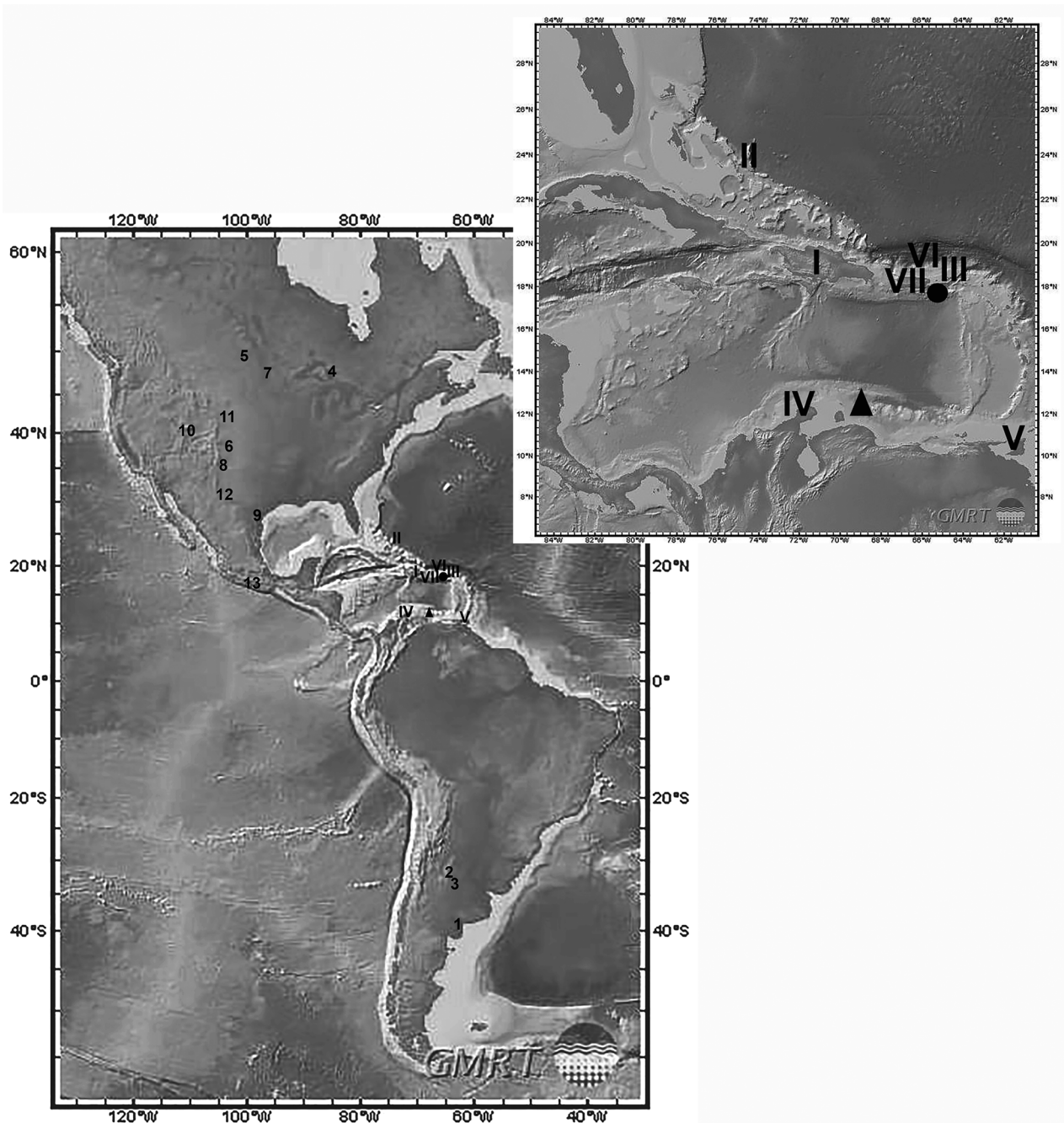


FIGURE 39. Distribution of *Cletocamptus albuquerquensis* (Herrick, 1894) (Arabic numerals), *C. dominicanus* Kiefer, 1934 (Roman numerals), *C. tainoi* sp. nov. (circle), and *C. chappuisi* sp. nov. (triangle). 1, Luro lagoon (La Pampa Province, Argentina); 2, Lucio V. Mansilla (Córdoba Province, Argentina); 3, Totoralejos (Córdoba Province, Argentina); 4, Dead Moose Lake (Canada); 5, Big Quill Lake (Canada); 6, Colorado (US); 7, Devils Lake (North Dakota, US); 8, Rio Grande Valley near Albuquerque (New Mexico, US); 9, west of Mission (Texas, US); 10, Salt Lake City and Farmington Bay (Great Salt Lake, Utah, US); 11, Twelvemile Lake (Albany County, Wyoming, US); 12, Coahuila State (Mexico), doubtful record; 13, Guerrero State (Mexico), doubtful record; I, Enriquillo Lake (Dominican Republic); II, San Salvador (Bahama Islands); III, Anegada (British Virgin Islands); IV, Pozos Colorados (Santa Marta, Colombia); V, Caroni Swamp and Chacachacare Island (Trinidad and Tobago); VI, St. John Island (US Virgin Islands, US); VII, Laguna Candelaria, Culebra and Vieques (Puerto Rico).

Phylogenetic considerations. The present study supports the hypothesis that *C. albuquerqueensis* and *C. dominicanus* are two distinct species, each with a more restricted distribution (see Fig. 39). *Cletocamptus albuquerqueensis* seems to be an inland species distributed in southern Canada (Saskatchewan), northern, central and southern US (North Dakota, Wyoming, Colorado, Utah, Texas, and New Mexico), and in the Chacoan and Pampean provinces sensu Morrone (2014) (La Pampa and Córdoba Provinces, central Argentina). This species has been reported also from springs, lakes, pools and reservoirs of low salinity in Coahuila State (central Mexico) in a graduate thesis by Zamudio-Valdéz (1991). Unfortunately, this record was not published and remains unverifiable. This record was subsequently mentioned in Suárez-Morales & Reid (1998) who mentioned its presence also in Guerrero (southwestern Mexico), and in Gómez & Morales-Serna (2014) and Reid (1990, 2015). Gómez & Morales-Serna (2014) referred to Wilson's (1936) record of *C. albuquerqueensis* from Ciruak Cenote, Yucatan. This record is erroneous. Gómez & Morales-Serna (2014) mixed up Wilson's (1936) record of *Mastigodiptomus* (= *Diaptomus*) *albuquerqueensis* (Herrick, 1894) with *C. albuquerqueensis*. In contrast, *C. dominicanus* seems to be a Caribbean species distributed in the Antillean subregion and in the Venezuelan province (see Morrone 2014).

Cletocamptus trichotus and *C. confluens* are the only two species outside the New World whose male and female P5 exopod and baseoendopod have been described as barely discernible and separated by a small incision, and with sexual dimorphism expressed also in the caudal rami, being about twice as long as wide in the female but about 2.5 times as long as wide in the male of *C. trichotus*, and about 3 times as long as wide in the female but 4 times as long as wide in the male of *C. confluens* (see Lang 1948 and references cited therein, and Mielke 2000a). So far, *Cletocamptus trichotus* is known only from South Africa (Kiefer 1929; but see also Lang 1948, and references cited therein). It is distinguished by a one-segmented antennary exopod armed with three setae, P1ENP1 reaching the middle of EXP2, armature formula of the female P3ENP2 2,2,1, two-segmented P4ENP with two apical setae on ENP2, male P3ENP three-segmented with a long inner apophysis on ENP2 and two apical setae on ENP3, and caudal setae IV and V separated. *Cletocamptus confluens*, on the other hand, was originally described from Kolberger Heide (Germany) and has been reported from several other places in that country as well as from France, Italy, Romania, Bulgaria, Poland, Russia, Caspian Sea, India, Libia, Egypt, East Africa, Australia and Namibia (see also Lang 1948, for a more complete list and references, and Mielke 2000a: 139, for a map showing the distribution of the species), and South Africa (pers. obs. SG from material sent by Dr. Nicola Carrasco, School of Life Sciences, University of KwaZulu-Natal, South Africa). In his redescription of *C. confluens* from Namibia, Mielke (2000a) described the antennary exopod of this species as very small, one-segmented and armed with one seta, mandibular palp one-segmented armed with three well-developed setae, P1ENP1 reaching the distal margin of EXP1, armature formula of the female P3ENP2 2,2,1, two-segmented P4ENP with two apical setae on ENP2, male P3ENP two-segmented with two dentiform projections (outer one shorter and slightly bent upwards, inner one as long as ENP1 and ENP2 combined and straight) framing two setae (inner seta shorter), and caudal setae IV and V fused basally. Re-inspection of material of *C. confluens* from South Africa deposited in the Copepoda collection of ICML-UAMzt revealed also the plesiomorphic condition of the inner setae of P1ENP1, P2-P4EXP2, and P2-P3EXP3. *Cletocamptus confluens* seems to be almost cosmopolitan in distribution. However, though records of this species occur in numerous lists and ecological papers, information on its morphology was not included. Since, morphological differences are to be expected in the widespread populations so far recorded, they may represent "an assemblage of barely discernible species" (Mielke 2000a). Interestingly, Mielke (2000a) implicitly suggested that *C. confluens* and *C. albuquerqueensis* might be related, the latter being the American counterpart of the former. In fact, based on several shared characteristics shown above, there appears to be a close relationship between *C. trichotus*, *C. confluens*, *C. albuquerqueensis*, *C. dominicanus*, *C. helobius*, *C. chappuisi* and *C. tainoi*.

From an evolutionary view an ancestral *Cletocamptus* species, would exhibit the most primitive condition of the appendages. This is particularly evident in *C. trichotus*, as well as in *C. confluens*, *C. albuquerqueensis*, *C. dominicanus*, *C. helobius*, *C. chappuisi* and *C. tainoi*. Specifically, this would include: three setae on the one-segmented and elongate antennary exopod; three long setae on the mandibular palp; long whip-like setae without brush tip on P1ENP1 and P2-P4EXP2-3; armature formula of P1EXP/ENP 0,1,022/0,111, of P2EXP/ENP 0,1,122/0,121, of female P3EXP/ENP 0,1,122/0,221, of female and male P4EXP/ENP 0,1,022/0,020, of female P5EXP/BENP 6/6, of male P5EXP/BENP 4/3; male P3ENP three-segmented without armature on ENP1, ENP2 with long inner apophysis, ENP3 with two apical setae; caudal rami sexually dimorphic and caudal seta IV and V separated. The original population of this hypothetical ancestral *Cletocamptus* species may have diversified into two main lineages sometime during the Triassic or Jurassic. One lineage led to the trichotus-dominicanus-

albuquerqueensis lineage (assumed here to be composed of *C. trichotus*, *C. dominicanus*, *C. albuquerqueensis*, *C. helobius*, *C. tainoi*, and *C. chappuisi*), and another one led to the confluens-lineage (assumed here to be composed of *C. confluens* and all its different forms). Note that at present, *C. confluens* is known from the west and east coast of Africa, from South Africa, the Persian Gulf and India, and from the Mediterranean, the Cantabric, the Caspian, the Baltic, and the Black Seas, and that *C. trichotus* is known only from South Africa. The confluens-lineage may have diversified along the south coast of Laurasia and the north coast of Gondwana, and in the Tethys Sea. A similar scenario was proposed by Boxshall & Jaume (1999) and Corgosinho et al. (2016) to explain the present distribution of some misophrioid and novocriniid copepods. This scenario also seems congruent with the known distribution of the species of the two lineages above and with the dimorphic caudal rami observed in all the populations of *C. confluens* along with its unique plesiomorphic long inner setae on P1ENP1, P2–P4EXP2 and P2–P3EXP3, and the two-segmented male P3ENP with ENP1 broadened and ENP2 with two dentiform apophyses framing two setae. The outer small apophysis is considered here a novel structure for *C. confluens*, while the inner long apophysis is homologous to the inner apophysis observed in the other species. Interestingly, Gurney (1927: 565, Fig. 165B) showed the male P3ENP of his material of *C. confluens* from the Suez Canal with the inner apophysis strongly bent outwards at an angle of nearly 90° like in *C. albuquerqueensis*, *C. tainoi*, and *C. chappuisi*. The three long setae on the one-segmented mandibular palp in *C. confluens*, as well as the plesiomorphic condition of the inner setae of P1ENP1, P2–P4EXP2 and P2–P3EXP3, seem to be indicative of this ancient lineage. *Cletocamptus confluens* also exhibits secondary fusion of the caudal setae IV and V, as well as secondary loss of armature elements of the female P5EXP (four setae instead of five setae as in the other species) and male P5EXP (three setae instead of four elements as in other species), and a reduction of the antennary exopod to a small segment with only one seta.

The common ancestor of the trichotus-dominicanus-albuquerqueensis-lineage may have been characterized by: an elongated antennary exopod with three setae; mandibular palp one-segmented with three setae; male P3ENP three-segmented with inner long apophysis on ENP2 and two setae on ENP3; armature formula of female P1EXP/ENP 0,1,022/1,111, of P2EXP/ENP 0,1,122/0,111, of P3EXP/ENP 0,1,122/0,221, of P4EXP/ENP 0,1,022/0,020; relatively short inner setae with brush tip on P1ENP1 and P2–P4EXP2; relatively long whip-like inner setae without brush tip on P2–P3EXP3; female P5EXP and baseopod with five and six setae respectively; male P5EXP and baseopod with four and three setae, respectively; dimorphic caudal rami; caudal setae IV and V separated. On one hand, *C. trichotus* underwent secondary loss of one apical seta of the P1EXP3, and one seta of the female P5EXP. Yet, gained an additional seta on the P2ENP2 that is considered here a novel element for this species. Also, *C. trichotus* kept the plesiomorphic three-segmented male P3ENP with a long inner apophysis on ENP2 and two setae on ENP3, and the elongated antennary exopod with three setae. The condition of the inner setae on P1ENP1, P2–P4EXP2 and P2–P3EXP3 of *C. trichotus* remains unknown. On the other hand, another group of species, *C. dominicanus*, *C. albuquerqueensis*, *C. helobius*, *C. tainoi*, and *C. chappuisi*, may have diversified in the Caribbean, and is hypothesized to have a sister-group relationship with *C. trichotus*. *Cletocamptus dominicanus*, considered here as an early offshoot, kept the plesiomorphic long inner apophysis of the male P3ENP and the one-segmented mandibular palp with three setae, but underwent reduction of the P4ENP from a two-segmented to a one-segmented ramus with two setae, developed non-dimorphic caudal rami, and caudal setae IV and V became fused. Also, *C. dominicanus* underwent fusion of the second and third endopodal segments of the male P3ENP. The inner apophysis kept its plesiomorphic position midway along the inner margin of the second endopodal segment indicating the place of the original division between second and third segments. In fact, there is a hint of this former division as seen by a slight groove along the outer margin on the P3ENP2 (see Figs. 25A and 38B). The exceedingly long asprothekes observed in *C. dominicanus* are unique and are considered here autapomorphic for the species. The other group of related species, *C. helobius* known from Louisiana and South Carolina (Fleeger 1980), and from Navío Quebrado lagoon in the Caribbean coast of Colombia (Fuentes-Reinés & Suárez-Morales 2014), *C. albuquerqueensis*, *C. tainoi*, and *C. chappuisi*, underwent further fusion of the second and third segment of the male P3ENP. The medial spinules of the second (distal) endopodal segment of the male P3 of *C. dominicanus* (see also Fig. 38B), *C. chappuisi*, *C. albuquerqueensis* and *C. tainoi* (these spinules were not illustrated for *C. helobius* in Fleeger (1980) nor in Fuentes-Reinés & Suárez-Morales (2014)) are homologous to the spinules observed on the medial endopodal segment of other species with a three-segmented male P3ENP thereby indicating the site of the original division between the second and third segments. Also, the presence of a small subdistal pore on the second endopodal segment of the male P3 of *C. chappuisi*, *C. albuquerqueensis* and *C.*

tainoi, indicates the former third segment, suggesting fusion of the second and third segments, and secondary displacement and reduction of the inner apophysis and asprothekes. Interestingly, the apophysis of *C. chappuisi*, *C. albuquerqueensis*, *C. tainoi* and the Colombian population of *C. helobius* is strongly bent outwards at an angle of nearly 90°, but it seems to be straight in the North American population of *C. helobius*. Both the North American and the Colombian population of *C. helobius* are provisionally assumed to belong to the same species, but see below.

Cletocamptus helobius and *C. chappuisi* share the reduced antennary exopod represented by one seta only, and probably the one-segmented mandibular palp with three setae (this remains unknown for *C. chappuisi*). *Cletocamptus helobius* underwent loss of the inner seta on P1ENP1, two setae on the P3ENP2 (with three instead of five setae), two setae on the female P5EXP (with three instead of five setae), and extreme reduction of the P4ENP (from a two-segmented ramus to one single seta representing the endopod). The caudal setae IV and V are separated in *C. helobius*, but fused in *C. chappuisi*. *Cletocamptus helobius* is unique among the species of this lineage in the long lateral seta of the maxillule. A similar, but shorter seta has been observed in some other species (see above). *Cletocamptus albuquerqueensis* and *C. tainoi* share the plesiomorphic, rather elongated (2 or more times as long as wide), one-segmented antennary exopod. This ramus bears three setae in *C. albuquerqueensis*, but the number of setae in *C. tainoi* is not clear, since two lateral rather stiff setae might actually be spinules (see Fig. 29C). These two species share also the apomorphic condition of the one-segmented mandibular palp with two setae only. *Cletocamptus tainoi* underwent loss of one seta on the female P5EXP (with four instead of five elements). These two species share the caudal setae IV and V fused, but are different in the caudal rami, being dimorphic in *C. albuquerqueensis*, but non-dimorphic in *C. tainoi*.

Palmer (1960) described a fossil *Cletocamptus* from the Barstow formation of middle and late Miocene age in the Mojave Desert, California, and suggested a close relationship of her material with *C. albuquerqueensis* based on the fused caudal setae IV and V, which is the condition also for *C. dominicanus* as redescribed here, and for *C. tainoi*. The length:width ratio of the caudal rami of Palmer's (1960) material points also to a closer relationship with *C. albuquerqueensis* and *C. tainoi*, than with *C. dominicanus*. All the above suggests that *C. albuquerqueensis* or its ancestor could have reached inland situations in southern Canada, central US, central Mexico and probably central Argentina sometime during the Cretaceous or Late Tertiary (Late Paleogene–Early Neogene) when oceans inundated the central portion of North America. Successive regression/transgression events could have caused the isolation of several populations of *C. albuquerqueensis* or its ancestor leading to the present distribution of *C. albuquerqueensis*. Interestingly, Huys et al. (2016) reported on some *Cletocamptus* specimens and some other mangrove-associated harpacticoids found as inclusions in Early Miocene amber from Campo La Granja mines in the northern section of Chiapas State, southeast Mexico, indicating that this area was located on the coast of the Gulf of Mexico during Early Miocene times. Also, Rocha-Olivares et al. (2001) and Gómez et al. (2004) found that four species of *Cletocamptus* from four localities in North America diverged in the Miocene. This scenario of sea level fluctuations and isolation could apply also for *M. brevicaudata* suggesting that this could be a distinct species with relatives in Brazil, New Mexico and Massachusetts.

Fuentes-Reinés & Suárez-Morales (2014) found *C. helobius* in plankton samples from Navío Quebrado lagoon, in the Caribbean coast of Colombia. They noted some differences between the Colombian and the North American population: (1) the P2ENP is shorter in the North American population, barely reaching the distal margin of the P2EXP1, but reaching well beyond the distal margin of EXP2 in the Colombian population, (2) a short seta is present at the insertion site of the P4 endopodal seta in the Colombian population, this seta is absent in the North American population, (3) the caudal rami are slightly longer in the Colombian population (1.5 times as long as wide), (4) the caudal rami bear six setae in the Colombian specimens, but only four in the North American population. These differences might indicate the presence of a new species in the Caribbean coast of Colombia, closely related to *C. helobius*. Further analysis of these two species is required. Note that Fleeger (1980) described the maxilliped without inner seta on the syncoxa nor with the typical accompanying small seta on the endopodal claw, and the endopod of the maxilla represented by two setae only. However, after examination of some females of *C. helobius* kindly sent by Dr. Fleeger to one of us (SG), the presence of one inner distal seta on the syncoxa as well as a small accessory seta on the endopodal claw of the maxilliped, and three instead of two setae on the maxillary endopod, was clearly seen.

Acknowledgements

Funding for RG was provided by a Saint Joseph's College of Maine Professorship Award; with special thanks to Daniel P. Sheridan (former Vice President for Academic Affairs and Dean of the College). The Biology Department is acknowledged for its constant support; thank you Elizabeth Auger (Chairperson). A sincere appreciation is given to Mary Gerber, who assisted with field sampling and provided encouragement. Juan G. Gonzáles (University of Puerto Rico, Mayagüez) assisted with field sampling and guiding to sampling sites in Puerto Rico and Vieques. Rafe Boulon (Resource Manager) permitted sampling in the St. John Island US National Park, US Virgin Islands. The US National Museum, Division of Invertebrate Zoology, is acknowledged for the loan of specimens. Dr. David Fields (Bigelow Laboratory of Ocean Sciences, East Boothbay Harbor, Maine, US) generously allowed one of us (RG) to use the SEM. The following colleagues are recognized for collecting samples in the southwest US and/or providing field information: Wiebke J. Boeing (New Mexico State University), Ayesha Burdett (University of New Mexico, Albuquerque), Donald Hockaday (The University of Texas-Pan American Coastal Studies Laboratory), Lianna Jarecki (H. Lavity Stoutt Community College, Tortola, British Virgin Islands), Robert Knowlton and Douglas Barr (George Washington University, Washington, D. C.), Ralf L. Price (Los Alamos National Laboratory, NM), Frank Rahel (University of Wyoming, Laramie) and Wayne Wurtsbaugh (Utah State University, Logan, Utah). Scot O'Donnell (B.A., Saint Joseph's College of Maine) is thanked for serving as a student field assistant on St. John Island. We are grateful to Dr. Hubert Höfer (curator of The Kiefer Collection of the State Museum of Natural History Karlsruhe, Germany) for all the information about Kiefer's (1934) material and for scanning Kiefer's (1934) original drawings of *C. dominicanus*, and to Dr. Karen van Dorp (Senior Collections Manager, Naturalis Biodiversity Center, The Netherlands) for the information about Chappuis' material.

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