

REVIEW OF THE NEW WORLD SPECIES OF
PSEUDODIAPTOMUS (COPEPODA: CALANOIDA),
WITH A KEY TO THE SPECIES

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ABSTRACT

This present study continues a review of the genus *Pseudodiaptomus* and clarifies the status of the American species. Two new species, *P. longispinosus*, and *P. panamensis*, and an unidentified species, along with the recent introduction of *P. marinus*, bring to 15 the number of species in this region. Previously misidentified species are placed in synonymy and extended zoogeographical ranges are presented. The Americanus species group and subgroups including 13 species are defined. A key to all species found in American coastal waters is presented.

The demersal copepods of the genus *Pseudodiaptomus* are circumglobal in tropical and temperate, shallow coastal waters. The genus was established by Herrick (1884) for *P. pelagicus* from specimens collected near the mouth of the Mississippi River. Prior to the present study 72 species were reported (Walter, 1986a; 1986b; 1987) with 14 species recorded from American waters. A synonymy of this genus presented in Walter (1986a) incorporated *Schmackeria* Poppe and Richard and *Mazellina* Rose and is amended herein to include *Weismanella* Dahl as a junior synonym of *Pseudodiaptomus*. The subgenus *Pseudodiaptallous* was established by Johnson (1939) to include the species *P. euryhalinus* since females possessed only two instead of the typical three or four urosomal segments common to other American pseudodiaptomids. Atlantic species were reported from Nova Scotia, Canada, south to La Plata, Argentina, while Pacific species were known from southern California south to Guayaquil, Ecuador.

The initial description and illustrations of *P. pelagicus* did not accurately identify the species and led to confusion among subsequent authors in determining east coast North American species. Marsh (1933) provided a general synopsis of the 22 species known world-wide at that time and noted the close similarities between *P. pelagicus* and *P. coronatus*. This was followed by a key to the species (Brehm, 1934). The South American species were reviewed by Wright (1936). Subsequently, Wright (1937) proposed to include the seven known species into an "Americanus" species group, a decision supported by Johnson (1948) and Walter (1986a). The species group name appropriately signifies the geographical range of the American species.

MATERIAL AND METHODS

Much of the material used in this study was obtained from collections deposited by C. B. Wilson at the National Museum of Natural History, Smithsonian Institution (USNM). In addition, among uncatalogued collections donated by Mildred S. Wilson I discovered undeposited type material of C. D. Marsh which had been given to M. S. Wilson. The rest of the study material was obtained from copepod researchers from North, Central, and South America.

Specimens were stained in a weak solution of chlorazol black and alcohol, and placed in lactic acid. Habitus and appendages were examined and measured using a compound microscope and drawn with camera lucida, to determine species and provide detailed drawings. Reference slides of appendages were prepared using polyvinyl lactophenol and deposited at USNM.

Abbreviations used in the text to describe morphological features are: A1 = first antenna, P1-P5 = swimming legs 1-5, Pdg1-Pdg5 = pedigers 1-5, Pr = prosome, Ur = urosome, Ur1-Ur5 = urosome



segments 1–5, CR = caudal rami, B1–B2 = basipods 1–2, Re = exopod, Ri = endopod, Se = outer spine and Sp = spermatophore.

In several species sexual variants referred to as "intersex" specimens were observed. The use of the word intersex does not imply a capability to change sex, only that polymorphisms exist in which morphological characters of both sexes are present in an individual. This expression of variation appears to occur more frequently among males than females. Intersex adult females vary from normal females in that they tend to have a reduced Ur1 and genital boss, the CR usually is shorter, and P5 spinulation is variable. Intersex adult males generally are larger than typical males, right A1 may not be geniculate and P5 may possess additional segments or spines.

Lengths of prosome and urosome were taken dorsally from the anterior margin of head to the posterior corner of Pdg5, and from anterior margin of Ur1 to posterior tip of CR. The ratio of Re2:Re3 for the female P5 is measured from the proximomedial margin to the distal tip of each segment. All measurements are in millimeters.

GENERAL DESCRIPTION AND APPENDAGE MORPHOLOGY

American pseudodiaptomids are characterized by a head that is bluntly rounded in lateral view and generally separated from the Pdg1. Rostrum typically with two long slender filaments, except in *P. gracilis*. Female and left male A1 of the American species group with 22 segments, male right A1 with 20, and the proximal segments not fused (Fig. 1A–B). *P. gracilis* (Nudus group) female and left male A1 with 20 segments, right male A1 with 17, and proximal segments fused (Fig. 1C–D). Segments 6–7 partly fused but counted separately, the terminal segment of male right A1 elongate and composed of two fused segments (Walter, 1986a; 1987). Pdg4–5 typically separate. Female urosome with two to four segments, and egg sacs paired, except in *P. gracilis*. Male urosome with five segments. CR variable in length, usually asymmetrical in female, and possess four terminal and one lateral strong, jointed, and distally plumose setae (except in *P. gracilis*), and one short dorsal seta. P1–4 and mouthparts as figured in Gonzalez and Bowman (1965), Grice (1969), and Walter (1986a).

The following are characteristics common to the male and female P5 of all species included and will not be repeated in the descriptions. Female P5 both rami with two basal and three exopodal segments. B2 and Re1 anterior surface with distal spinule row, B2 posterior surface with one large seta, and Re1 with Se. Re2 with Se and medially produced to form a spiniform process with serrate hyaline margins. Re3 with small acute medial basal process, and plumose on both margins. Male P5 both rami with two basal segments; right ramus with three and left ramus with two exopodal segments. Posterior surface: Right leg, B1 disto-medial corner variably produced. B2 with one large surface seta. Re1 segment may be twisted medially so that medial spinule patch and papilla appear to arise from anterior surface, while distolateral spiniform process appears medial. Re2 Se hirsute and medial margin with knob and seta. Re3 with two proximal setae, small proximomedial protrusion, and inner margin hirsute. Left leg, B1 not produced, B2 with large surface seta. Re2 irregularly shaped with apical spines. Anterior view: Right leg, B2 lateral spinule row usually extends onto surface, B2 and Re1 with a spinule row along distal margin. Left leg, B2 and Re1 same except for variably shaped Ri on B2. Re2 with surface hair patch.

Pseudodiaptomus pelagicus Herrick Figures 2A–J, 3A–K

- Pseudodiaptomus pelagicus* Herrick, 1884: 181.—1887: 10–11, p1. 1, fig. 8, p1. 2, figs. 1–8.—1895: 53–54, p1. 1, figs. 11–17.—Marsh, 1933: 38, p1. 19, figs. 5–6, p1. 20, fig. 2.
Pseudodiaptomus coronatus Williams, 1906: 640–644, figs. 1–7.—Sharpe, 1910: 412–413, fig. 4.—Willey, 1923: 320–324.—Wilson, 1932a: 101–103, fig. 68.—1932b: 30–31, p1. 2.—Marsh, 1933: 32–33, p1. 16, figs. 3–6.—Wright, 1936: 17–19, p1. 2, fig. 4.—1937: 158–159, p1. 1, fig. 3.—

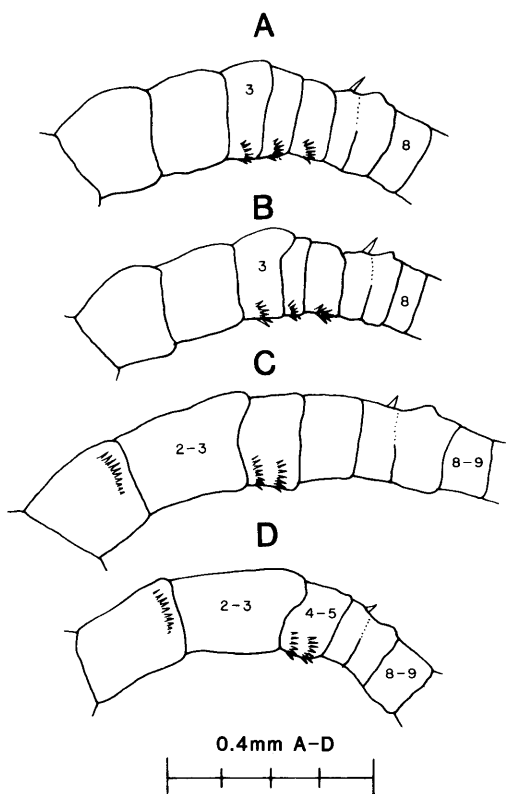


Figure 1. Segmentation of proximal segments of A1 for *Pseudodiaptomus*. A–B, Americanus species group, A, female A1; B, male A1; C–D, *P. gracilis*, C, female with fused segments; D, male A1 with fused segments.

Davis, 1948: 82–83, fig. 1.—Schmitt, 1954: 440—Jacobs, 1961: 443–446.—Grice, 1960: 224, tbl. 1.—1969: 291–301, figs. 1–83.—Björnberg, 1971: 348–349.—Perry and Christmas, 1973: 214, 217, 218.—McAden, 1977: 34, 56–61.—Walker, 1979: 69.—Jacoby and Youngbluth, 1983: 77–86, fig. 1b–f.

Pseudodiaptomus americanus Wright, 1937: 157–162, pl. 1, fig. 2.

Material.—UNITED STATES: *Massachusetts*, Woods Hole, R. Rathburn, USNM 59567, 04 Sep 1881, 28f, 7m; USNM 59590, 16 Sep 1882, 258f, 5m; C. B. Wilson, USNM 59744, 16 Jul 1925, 4m; USNM 60332, 30 Jul 1925, 2f, 2m; USNM 60342, 23 Jul 1926, 2f, 35m; F. A. Hopper, USNM 107765, 17 Aug 1960, 10f, 1m; *Long Island Sound*, P. S. Galtsoff, USNM 79875 and 79877, Jan 1923, 58f, 20m; *mouth of Delaware Bay*, C. M. Finney, USNM 213966, 10 Nov 1975, 8f, 13m; *Virginia*, Assateague Island, A. Cohen, USNM 228285, 05 Aug 1977, 68f, 1m; *North Carolina*, Beaufort, A. B. Williams, USNM 101850, 09 Nov 1956, 65f, 22m; W. H. Sutcliffe, USNM 87088, 29 Sep 1947, 2f, 5m; Beaufort, no collector/date, USNM 228286, 1m; *South Carolina*, 33°32'N, 078°55'W, USNM 98609, "T.N. GILL" Cruise 1, 03 Mar 1953, 30f, 1m; *Florida*, Indian River, Ft. Pierce, M. Youngbluth, USNM 213188, 29 Jun 1982, 10f, 10m; L. Walker, USNM 228279, 13 Dec 1973, 29f, 2m; Flamingo Key, L. P. Thomas, USNM 106197, 25 Mar 1960, 6f, 7m; Cedar Key, E. L. Pierce, USNM 88084, 29 Nov 1946, 3m; *Mississippi*, Ocean Springs, J. P. Steen, USNM 228280, 13 Jul 1976, 252f, 23m; *Louisiana*, Cocodrie, M. J. Dagg, USNM 228281, 05 Nov 1984, 2f, 1m; *Texas*, Corpus Christi and Aransas Bays, R. D. Kalke, USNM 228282, Nov 1972, 34f, 11m; Galveston Bay, E. Brown, USNM 228284, 03 Apr 1976, 8f, 16m; D. McAden, USNM 228521, 27 Aug 1974, 44f, 10m. MEXICO: Vera Cruz, Laguna LaMancha, M. Paez-Rodriguez, USNM 228283, 19 Nov 1981, 24f, 35m.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	60	1.30–1.57	1.48	0.94	0.57	1.6:1
Male	50	0.92–1.13	0.95	0.69	0.36	1.9:1

Description.—Female (Fig. 2A–F): Pdg2–4 posterior margins with small lateral scales that extend slightly dorsad. Pdg4–5 separate, Pdg5 corners slightly produced with dorsal and lateral spinules, hairs, and two long setae. Urosome with three segments. Ur1 large, constricted at midlength, posterodorsally swollen; dorsal surface heavily spinulose, with several long hairs at right corner between paired posterior scale rows; genital boss pronounced. Right and left lateral surfaces with anterior and posterior hair and spinule patches. Lateral view shows deep groove between Ur1–2. Ur2 partly fused (Stage V with Ur2–3 separate and Ur3–4 fused); right side with elongate posteriorly directed narrow wedge of spinules, left side with small circular hair patch. Ur3 with fine lateral hairs and four to five posterodorsal spinules. CR long, asymmetrical; right 5× and left 6× longer than wide. Ur segments and CR with proportions 31:21:17:31 = 100.

Female P5 (Fig. 2F): Re2 only slightly produced. Ratio Re2:Re3 = 1:1.3.

Male (Fig. 2G–J): Pdg4–5 separate, Pdg5 corners slightly produced. Ur2 posterior scale row not complete dorsally; ventrally with 2 spinule rows. Ur3–4 scale rows complete. Ur segments and CR with proportions 15:20:15:19:13:18 = 100.

Male P5 posterior view (Fig. 2I): Right leg, B1 with distal spinule row, distomedial corner produced into medially curved spiniform process lined with spinules. B2 proximomedial margin with spinules and circular spinule patch near midlength. Re1 small surface papilla with apical seta, and distolateral corner produced into medially curved spiniform process. Re2 with one surface seta, short Se, and medial knob with apical seta. Re3 with small basal protrusion. Left leg, B1 distomedial corner rounded. B2 medial margin incised and lined with spinule rows. Ri distally hirsute with spinules and hairs. Re1 small papilla with seta, Se short. Re2 with four strong spines and one seta near apex. Anterior view (Fig. 2J): Right leg, B1 with fine proximal hairs, one seta and subapical spinule row. B2 and Re1 with spinules along distal margin. Left leg, B1 with five large blade-like spines, four fine surface hair rows, seta, and subapical row of large spinules along suture. B2 and Re1 distal margin with spinules.

Remarks.—Herrick (1884) established the genus *Pseudodiaptomus* for *P. pelagicus* collected from the Mississippi Sound. That description was not completely accurate and the illustrations of the species, published by Herrick (1887; 1895), did not clearly depict morphological features of the habitus and fifth legs.

Examination of the above material from Massachusetts to Mexico allows for the following amendments to Herrick's description: 1) P1 Re1 with Se. female 2) Pdg2–4 posterior margins lined with posterolateral scale rows that extend slightly dorsad, Pdg4–5 not fused. 3) Female A1 and left male A1 with 22 segments; right male A1 with 19 segments. 4) Egg sacs paired, the right sac is reduced, containing only two to four eggs, the left with 10–24 eggs. 5) P5 B1–2 not fused, Re1 with Se directed distolaterally not medially. 6) CR asymmetrical. 7) Ur with three segments not two as in (1887) illustration. In specimens obtained from Texas and Mexico the right egg sac typically has more eggs (3 to 11), and the long posterior setae on female Ur1 are shorter and fewer in number. 8) male P5 right B1 with distomedial spiniform process on posterior surface, right Re1 distolateral corner produced into medially directed spiniform process, left Ri not heavily serrate. 9) Spermatophore is elongate, not oval, as Herrick mistakenly referred to the female right egg sac as a spermatophore.

During this study several occurrences of male and female intersex individuals were noted in samples from Massachusetts, North Carolina, Florida, and Texas (Fig. 3A–K). Examination of several hundred specimens produced 8 males and 15 females that had some kind of intersex variation. Intersex females: i) Pdg5 not

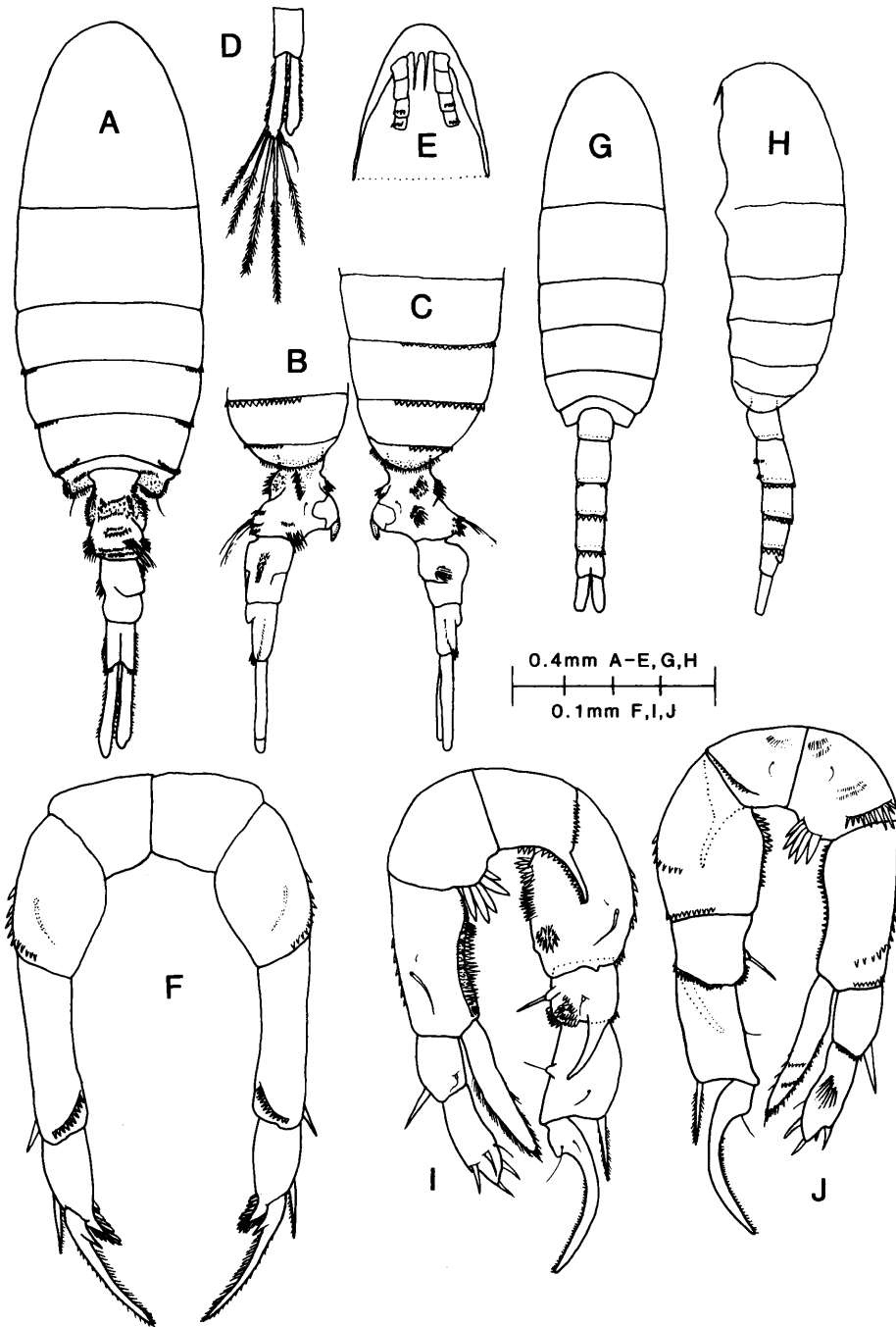


Figure 2. *Pseudodiaptomus pelagicus* Herrick. A-E, adult female: A, dorsal view; B, lateral view of Ur right side; C, lateral view of Pr and Ur left side; D, CR with bifid setae; E, ventral view of head; F, anterior view of P5. G-J, adult male: G, dorsal view; H, lateral view left side; I, posterior view of P5; J, anterior view of P5.

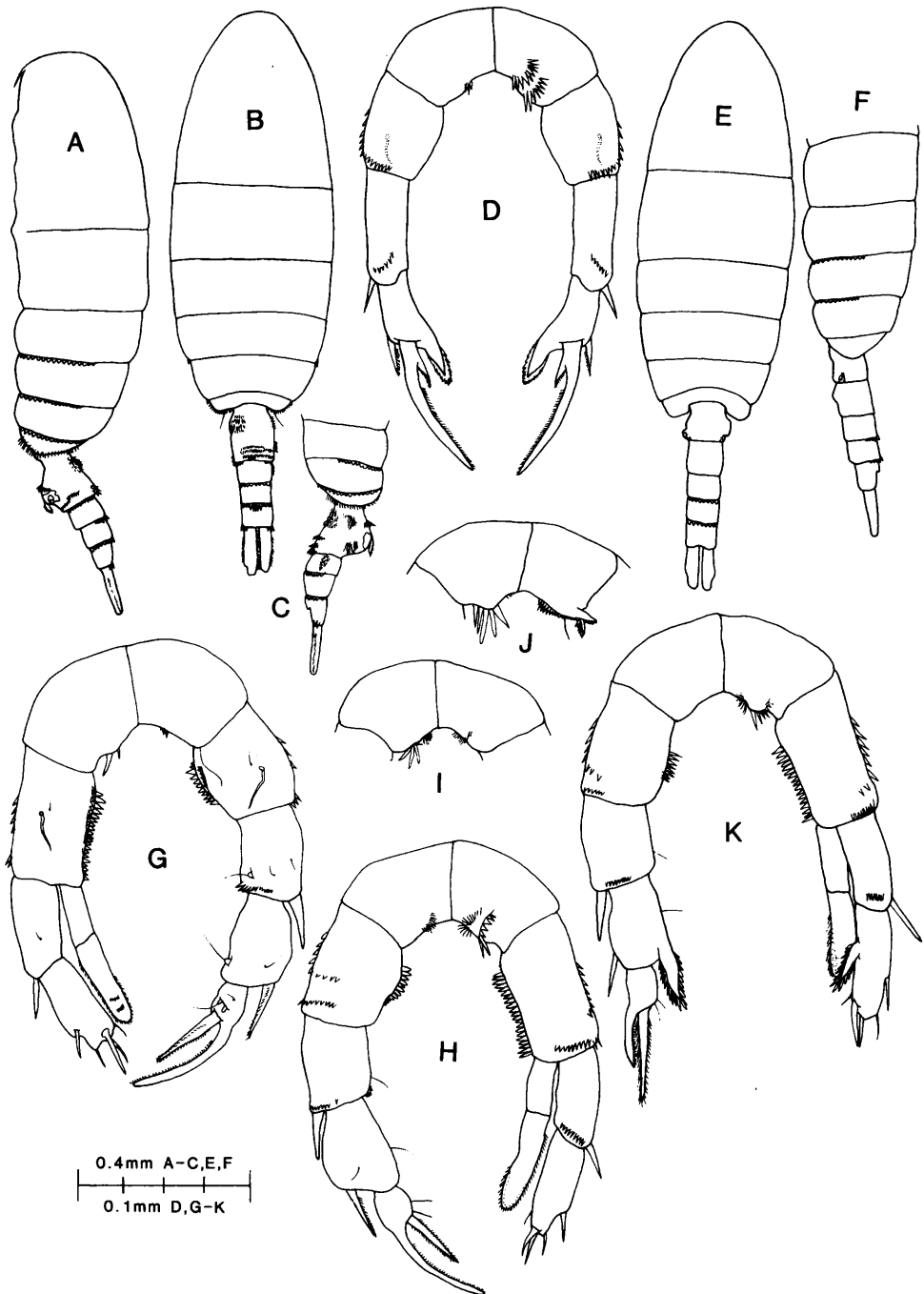


Figure 3. *Pseudodiaptomus pelagicus* (intersex variation). A–D, adult female: A, lateral view left side; B, dorsal view; C, lateral view of Ur right side; D, anterior view of P5. E–K, adult male: E, dorsal view; F, lateral view left side; G, posterior view of P5; H, anterior view of P5; I–J, variations noted in posterior B1; K, additional male variant, anterior view of P5.

produced, lacking surface spinule and hair patterns. ii) Ur with four segments; Ur1 reduced in size, lacking typical spinule patterns with small genital boss, Ur2 without left lateral hair patch, and Ur2-3 with posterior spine rows. iii) CR short. iv) P5 B1 with spinules, and Re2 spiniform process larger. Intersex males: i) Larger size (1.25-1.52 mm) than typical males. ii) Pdg2-3 with posterolateral scale rows. iii) Ur1 enlarged and in some individuals the appearance of reminiscent seminal receptacles was noted; Ur2 without posterodorsal spine row. iv) P5 right Re1 with laterally directed spiniform process, Re3 with large hirsute medial spine, left Re2 with larger apical spines. v) Typically right A1 not geniculate or only incompletely so; if geniculate the P5 left B1 medial spines show variations in spine size and number, right B1 with reduced spiniform process (Fig. 3J), and left Ri with one or two segments; if not geniculate P5 variations as in Figure 3G-I, K.

All of the material obtained for this species had previously been identified as *P. coronatus* by researchers. The misidentification of this species appears to be based on Herrick's inadequate description and inaccurate drawings, and the fact that subsequent researchers thought that the range of *P. pelagicus* was limited to the Mississippi Sound. The description of *P. coronatus* from Narragansett Bay (Williams, 1906) and Woods Hole (Wilson, 1932b) indicated females with four Ur segments and its latter report from the Gulf of Mexico (Marsh, 1933; Wright, 1936; 1937; Schmitt, 1954) also added to the confusion. However, these authors also suggested that this species is probably synonymous with *P. pelagicus*. This confusion led all other researchers to report only *P. coronatus* from Nova Scotia (Willey, 1923) to Mississippi (Perry and Christmas, 1973), and Texas (Chase, 1977; McAden, 1977; Steen, 1981). Another species, *P. americanus* Wright, based on a single male also reported from the Gulf of Mexico, is identical to that in Figure 3G-H. Unfortunately, the descriptions of both *P. coronatus* and *P. americanus* were based on intersex specimens and were not of new species. The report of these intersex specimens and the fact that I found only one species present from Massachusetts to Mexico confirms the synonymy of *P. coronatus* and *P. americanus* with *P. pelagicus*.

Pseudodiaptomus cokeri Gonzalez and Bowman
Figure 4A-J

Pseudodiaptomus cokeri Gonzalez and Bowman, 1965: 250-253, figs. 6-9.—Bacon, 1971: 85.—Björnberg, 1971: 384.—Yeatman, 1976: 217, figs. 79-80.—Jacoby and Youngbluth, 1983: 77-85, figs. 1A, 2A-C.

Material.—PUERTO RICO: Bahia Fosforescente, coll. by R. E. Coker, 13 Apr 1957, USNM 107790, Holotype, 1f; USNM 107791, Allotype, 1m; USNM 107792, Paratypes, 46f, 63m; 15 Jan 1958, USNM 107788, 47f, 157m; Canal de Maguayes, coll. by T. E. Bowman, 26 Feb 1959, USNM 107789, 1f; coll. by J. G. Gonzalez, 1957, USNM 111341, 5f, 1m. JAMAICA: Kingston, Hunts Bay, coll. by J. Grahame, 22 Oct 1971, USNM 150696, 31f, 3m; Montego Bay, coll. by H. Yeatman, 01 Jun 1964, USNM 233588, 1f on 1 slide. ANTIGUA: St. Johns, harbor entrance, coll. by Smithsonian Bredin 1959 Expedition, Sta. #82-59, 22 Apr 1959, USNM 234201, 15f, 15m. ST. LUCIA: Marigot Bay, coll. by T. E. Bowman, 14 Apr 1959, USNM 107933, 14f, 39m. TRINIDAD: Caroni Swamp, coll. by P. F. Bacon, 08 Jan 1966, USNM 128931, 2f, 3m. VENEZUELA: Margarita Island, Punta de Piedras, coll. by L. Gonzalez Cebrero, 19 Jul 1984, USNM 233657, 10f, 16m. PANAMA: Galeta Island, 09°24'N, 079°51'W, coll. by M. Jones, 16 Apr 1971, USNM 231285, 2f, 5m; Cristobal Harbor, coll. by R/V ALPHA HELIX, 05 Jul 1977, USNM 231289, 2f, 3m. BELIZE: Carrie Bow, 16°50'N, 088°05'W, coll. by K. Ruetzler, 03 Nov 1984, emergence trap, USNM 228522, 14f, 43m; coll. by F. Ferrari, 27 May 1985, surface tow, USNM 228523, 6f, 16m; 30 Mar 1986, USNM 228860, 30f, 27m.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	25	1.38-1.48	1.44	0.92	0.50	1.8:1
Male	30	0.94-1.00	0.97	0.68	0.32	2.1:1

Description.—Female (Fig. 4A–E): Pdg2–4 posterolateral scale row extends completely dorsad. Pdg4–5 separate, Pdg5 corners somewhat rounded with dorsal and lateral hairs and spinules. Urosome with four segments. Ur1 large, dorsal surface with anterior hair patches, 4 posterior rows of scales and patch of fine hairs at right posterior margin. Right and left lateral surfaces with anterior spinule patches; right side with posterior crooked spine (Fig. 4C–D) typically hidden in spinule and hair patch. Ur2 posterior margin with pair of lobes and small anterolateral spinule patch on right side. Ur4 with fine lateral hairs and posterolateral spinules at margin. CR with lateral hairs, asymmetrical with right shorter. Right CR $5.5\times$ and left $6\times$ longer than wide. Ur segments and CR with proportions $32:17:10:12:29 = 100$.

Female P5 (Fig. 4E): Re2 medial spiniform process enlarged, with ratio of Re2:Re3 = 1:1.1.

Male (Fig. 4F–J): Pdg4–5 separate. Pdg5 corners rounded. Ur2 posterior scale row not complete dorsally; ventrally with one spinule row. Ur3–4 scale rows complete. CR $2.5\times$ longer than wide. Ur segments and CR with proportions $15:20:15:15:15:20 = 100$.

Male P5 posterior view (Fig. 4H): Right leg, B1 distomedial corner bifid, lined with spinules, and laterally directed at apex. B2 with proximomedial spinules and small surface spinule patch at midlength. Re1 distomedial corner laterally compressed terminating in bifid process, medial fork spinulated and lateral fork with seta at apex. Left leg, B2 with small surface seta and medial groove lined with rows of spinules. Re1 with small distomedial spine. Re2 narrows distally to form acute apex with four spines and one seta. Anterior view (Fig. 4I): Left leg, B1 with short row of fine surface spinules and row of larger subapical spinules; medial margin with three or four large blade-like spines. Ri with distal spinules and apical seta.

Remarks.—The female of *Pseudodiaptomus cokeri* is readily distinguished from *P. pelagicus* by the pair of Ur2 posterodorsal lobes and paired egg sacs of equal size. The male requires closer examination of the P5 to separate species, with *P. cokeri* lacking the large right B1 medial spiniform process and possessing the posterior right distomedial Re1 scaled, bifid process.

This species was originally described as having a 3-segmented urosome with Ur2–3 appearing fused. However, after re-examining the type material and females from other localities, I believe that the separation between Ur2–3, though faint, is complete and results in four segments.

Examination of material from regions outside the type locality revealed some minor variations in the female Ur, particularly the size of the Ur1 right posterolateral spine and Ur2 lobes. Gonzalez and Bowman (1965, fig. 6C) indicated the posterolateral spine, but made no mention of it in the description. Examination of the type material showed that it is present, though much reduced and easily missed among the profusion of hairs and spinules. Specimens from the southern Caribbean Islands and Venezuela possess a larger lateral spine that is sometimes set upon a slight basal protrusion. Yeatman (1976) reported an atypical female with this spine from Jamaica, though this specimen lacked the Ur2 lobes and had shortened CR. This specimen is *P. cokeri*, though it is probably an intersex specimen with shortened CR. Females from Jamaica possess additional spinules on the lateral lobe (Fig. 4D) and lack the long posterodorsal setae on Ur1. The lateral spine is not present in females from Belize or Panama and the Ur2 lobes are reduced with the lateral lobe lightly scaled. Specimens from Jamaica, St. Lucia, and Trinidad show the Ur2 medial lobe variably reduced. Females from Venezuela

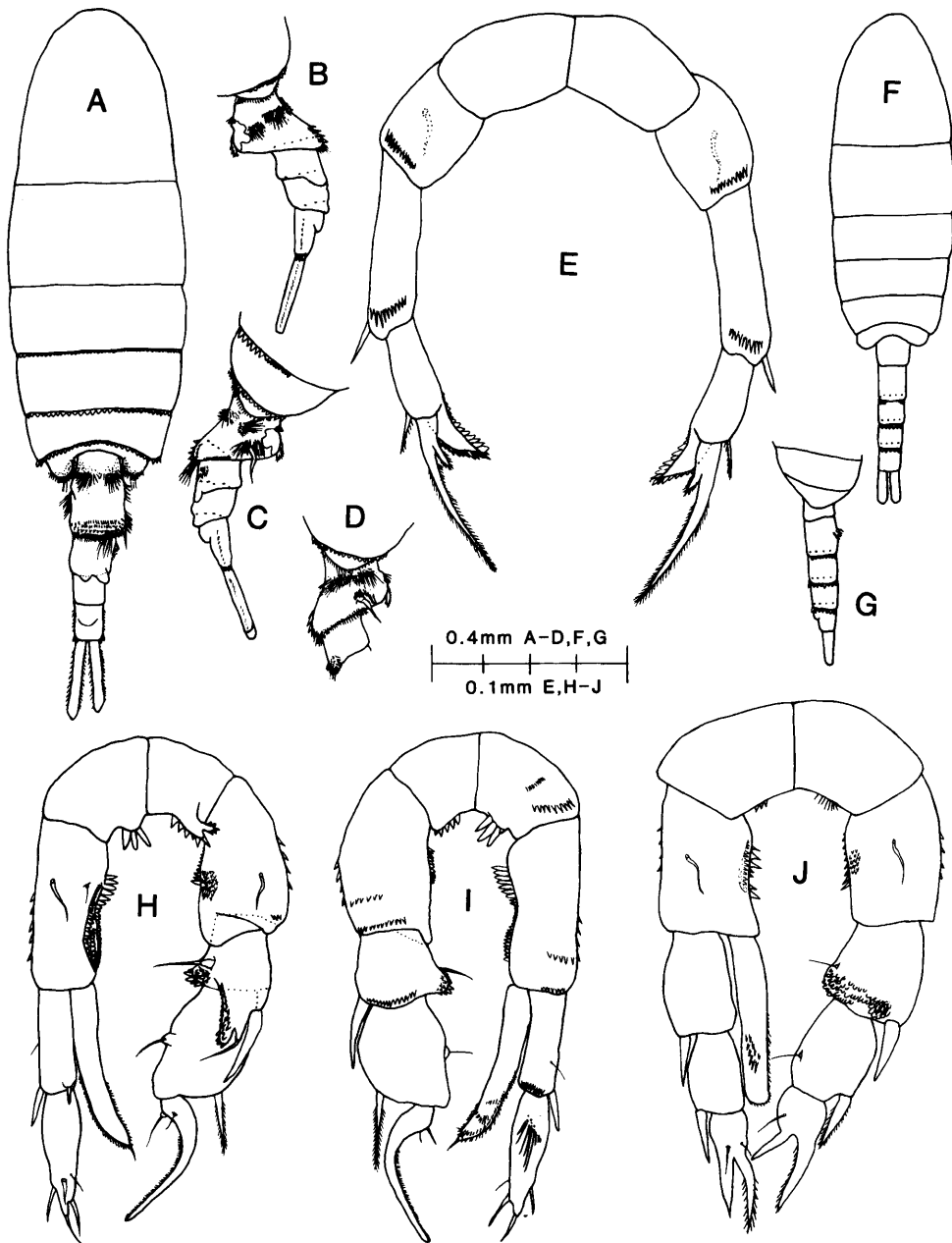


Figure 4. *Pseudodiptomus cokeri* Gonzalez and Bowman. A-E, adult female: A, dorsal view; B, lateral view of Ur left side; C, typical lateral view of Ur right side; D, Jamaican form lateral view of Ur right side; E, anterior view of P5. F-J, adult male: F, dorsal view; G, lateral view of Ur right side; H, posterior view of P5; I, anterior view of P5; J, variant form, posterior view of P5.

appear similar to those from Puerto Rico in that both lobes are pronounced. Even with these variations, all males appeared identical, except that in some specimens the left P5 B1 had two or three blade-like medial spines. An intersex male (1.30 mm in length) was recorded from Panama (Fig. 4J) with both P5 rami having three Re segments.

The range of *P. cokeri* is now known to extend throughout the Caribbean arc region to Venezuela and north to Belize. To date no overlap of this species and *P. pelagicus* has been observed, with the latter found as far south as Vera Cruz, Mexico and *P. cokeri* only extending as far north as Belize.

Pseudodiaptomus euryhalinus Johnson
Figure 5A–H

Pseudodiaptomus euryhalinus Johnson, 1939: 349–355, pl. 1, figs. 1–9, pl. 2, figs. 10–20.—Johnson, 1948: 319–330, pl. 1, figs. 1–7, pl. 2, figs. 8–22, pl. 3, figs. 23–35, pl. 4, figs. 36–56.—Fleminger, 1967: 28–29.—Dawson and Knatz, 1980: 96, pl. 83, figs. a–l.—Fleminger and Kramer (1988: 539).

Material.—UNITED STATES: California, Scripps Inst. Oceanography Pier, coll. by M. W. Johnson, 09 Mar 1938, Holotype, USNM 77393, 1m, Allotype, USNM 77394, 1f, Paratypes, USNM 77395, 1m on slide; San Francisco Bay, evaporation ponds near Alviso, coll. by T. Fast, 18 Jul 1950, USNM 92196, 500+ f, m; Carlsbad, coll. unknown, 11 Oct 1938, USNM 92940, 31f, 33m.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	25	1.24–1.32	1.27	0.80	0.47	1.7:1
Male	25	0.83–0.91	0.87	0.55	0.33	1.7:1

Description.—Female (Fig. 5A–D): Pdg2–4 posterior margin with small lateral scales that extend partly dorsad. Pdg4–5 separate; Pdg5 with surface, posterior, and acute lateral scales and hairs. Urosome with two segments; however, the posterior segment is composed of two partly fused segments. Ur1 large, constricted at midlength with dorsal and lateral hairs and spinules; genital boss reduced. Ur2 posterodorsal margin produced, posterolateral surface with hair row; dorsal view appears separate, while lateral view appears partly fused. CR about 6× longer than wide, appear symmetrical, and hirsute both medially and laterally. Ur segments and CR with proportions 33:22:14:31 = 100.

Females P5 (Fig. 5D): Re1 distal margin produced to extend onto Re2. Ratio of Re2:Re3 = 1:1.2

Male (Fig. 5E–H): Pdg4–5 separate, Pdg5 corners rounded and lined with scales. Ur1–2 left lateral surface with spinules. Ur2–3 with posteroventral spinule row. Ur2 left posterior margin with enlarged scales, right margin lacking scales. CR 3× longer than wide. Ur segments and CR with proportions 16:20:16:16:16:16 = 100.

Male P5 posterior view (Fig. 5G): Right leg, B1 proximomedial margin with long spinules and small distal projection covered with fine hairs near acute distal corner. B2 proximomedial margin greatly expanded forming large triangular process lined with large strong spinules and proximal circular surface patch of small spinules. Re1 distolateral spiniform process medially curved near apex. Left leg, B1 with subapical spinules. B2 with large seta arising from medial groove, distomedial corner large and overlaps onto Re1. Re1 Se naked and longer than Re2. Re2 small, oblong, bifid at medial apex. Anterior view (Fig. 5H): Right leg, B1 with subapical spinules. Left leg, B1 with three to five medial spinules and subapical spinules. Ri medially hirsute, proximally enlarged, curved medially, and apex appearing slightly bifid with apical seta.

Remarks.—In establishing this species, Johnson (1939) proposed a new subgenus *Pseudodiaptallous* because of the 2-segmented Ur of the female. In lateral view

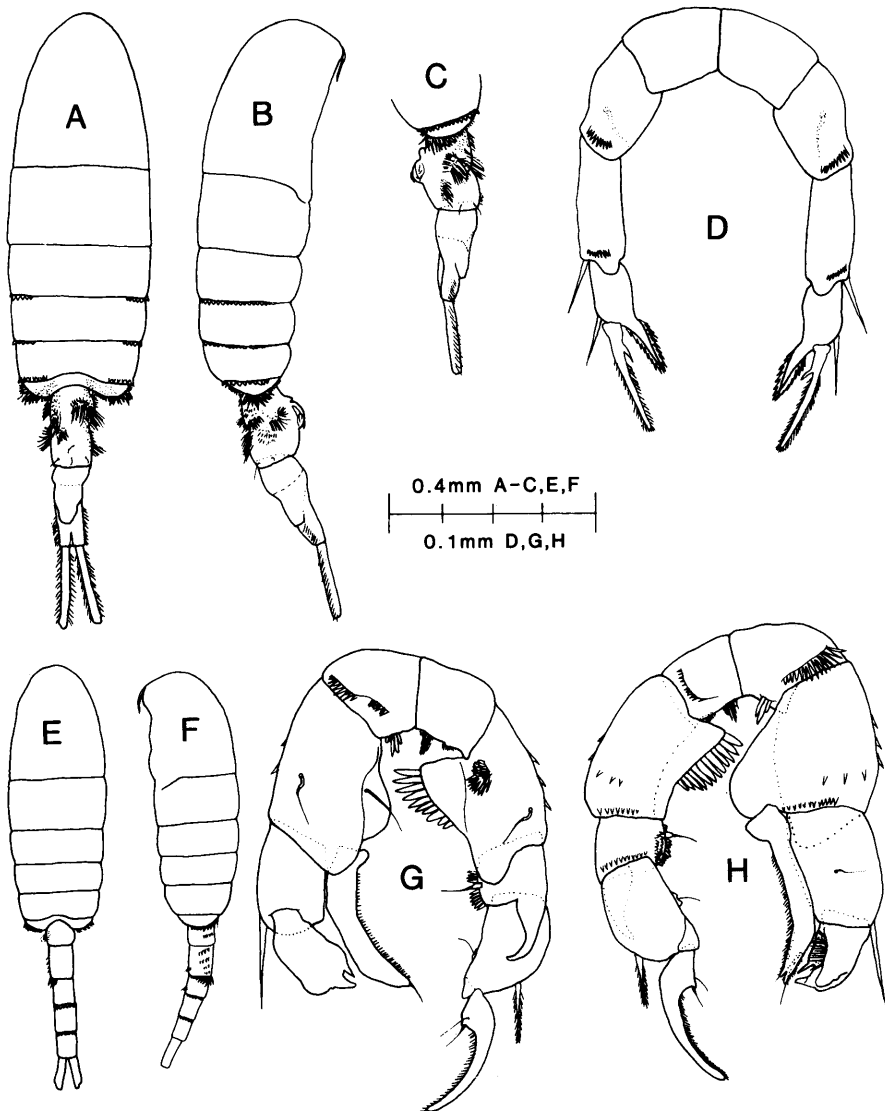


Figure 5. *Pseudodiaptomus euryhalinus* Johnson. A-D, adult female: A, dorsal view; B, lateral view right side; C, lateral view of Ur left side; D, anterior view of P5. E-H, adult male: E, dorsal view; F, lateral view left side; G, posterior view of P5; H, anterior view of P5.

the Ur2 appears incompletely fused, while separate in dorsal view, thereby appearing as three segments. However, for descriptive purposes the urosome is considered 2-segmented, with this species being the only member of the genus with this type of urosome.

The species most closely related to *P. euryhalinus* appears to be *P. culebrensis*, though it is easily distinguished in that: i) Male and female Pdg5 corners strongly scaled. ii) Female urosome 2-segmented. iii) Male P5 left Re2 apex bifid and directed medially, right B2 proximomedial margin triangular, and Re1 distolateral process longer and strongly curved towards mediad.

The range of this species still appears to be limited from San Francisco Bay south to the northern coastline of Baja California, Mexico.

Pseudodiaptomus culebrensis Marsh
Figure 6A–H

Pseudodiaptomus culebrensis Marsh, 1913: 4–6, pl. 1, figs. 1–7.—1933: 33–35, pl. 17, figs. 4–6, pl. 18, figs. 1–3.—Dodds, 1926: 23.—Wright, 1936: 14–15, pl. 3, fig. 6.—1937: 159–161, pl. 1, fig. 8.—Comita, 1951: 375–376, pl. 1, figs. 16–17.—Brinson and Nordlie, 1975: 1477, tbl. 4. (non) *Pseudodiaptomus culebrensis*.—Collado et al., 1984: 116, tbl. 3.

Material.—PANAMA: Rio Culebra, branch of Rio Chepo, coll. by Messrs. Meek and Hildebrand, 1911–1912, Syntype, USNM 233800, 9f, 7m, all on slides. COLOMBIA: Nariño State, Bucheli, coll. by M. F. Suarez, Nov 1986, USNM 229964, 21f.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	15	1.15–1.27	1.22	0.80	0.47	1.7:1
Male	4	0.83–0.93	0.90	0.59	0.32	1.8:1

Description.—Female (Fig. 6A–D): Pdg4–5 separate with Pdg3–4 lateral scale rows extending slightly dorsad. Pdg5 corners slightly produced, with hairs. Urosome with three segments, Ur1–3 lack posterior scale row. Ur1 left and right anterolateral surface swollen with spinules that extend dorsad and dorsal hair patch. Ur2 longer than Ur1. Ur3 with lateral spinule rows. CR with medial hairs, asymmetrical with left 6×, right 5× longer than wide. Ur segments and CR with proportions 27:31:10:32 = 100.

Female P5 (Fig. 6D): Ratio of Re2:Re3 = 1:1.7.

Male (Fig. 6E–H): Pdg4–5 separate with Pdg5 corners rounded. Ur2 left dorsolateral scale row with enlarged scales. Ur2–3 with ventral spinule row. Ur segments and CR with proportions 10:21:17:21:14:17 = 100.

Male P5 posterior view (Fig. 6G): Right leg, B1 with few fine medial hairs followed by large medial spinules extending to enlarged distomedial corner. B2 with two rows of strong proximomedial spinules. Re1 distolateral process short, medially curved, about ¼ the length of Re2, with one large surface seta. Re2 Se long. Left leg, B1 with distolateral spinule row. B2 with 10–12 long slender spines along medial margin. Ri clavate with rounded, slightly hirsute apex. Re2 triangular, narrowing distally with one lateral spine, and two small apical spines, the medial-most spine larger. Anterior view (Fig. 6H): Left leg, Re1 Se very short.

Remarks.—The Panama specimens were originally collected and described by Marsh (1913), but were never deposited. Recently, they were rediscovered among Mildred S. Wilson collections which she donated to the National Museum of Natural History. The specimens from Colombia were slightly larger than those from Panama.

Amendments to Marsh's description as follows: i) Male Ur2 with enlarged left distolateral scales. ii) Male P5 Ri narrower and distally enlarged, left Re1 with Se and triangular Re2. *Pseudodiaptomus culebrensis* is similar to *P. marshi*, though it may be distinguished from the latter in that: i) Female Ur1 lacks right lateral knob, Ur2 without surface spine cluster. ii) Left CR longer than right. iii) Male P5 with, more and larger, right and left B2 spines, right Re1 spiniform process shorter. Re3 not as large, and left Re2 triangular and apically pointed.

P. culebrensis is confined to the Pacific coast extending from Colombia north to Acapulco, Mexico (Comita, 1951). Specimens of this species reported from the Caribbean side of Costa Rica (Collado et al., 1984) are *P. marshi*.

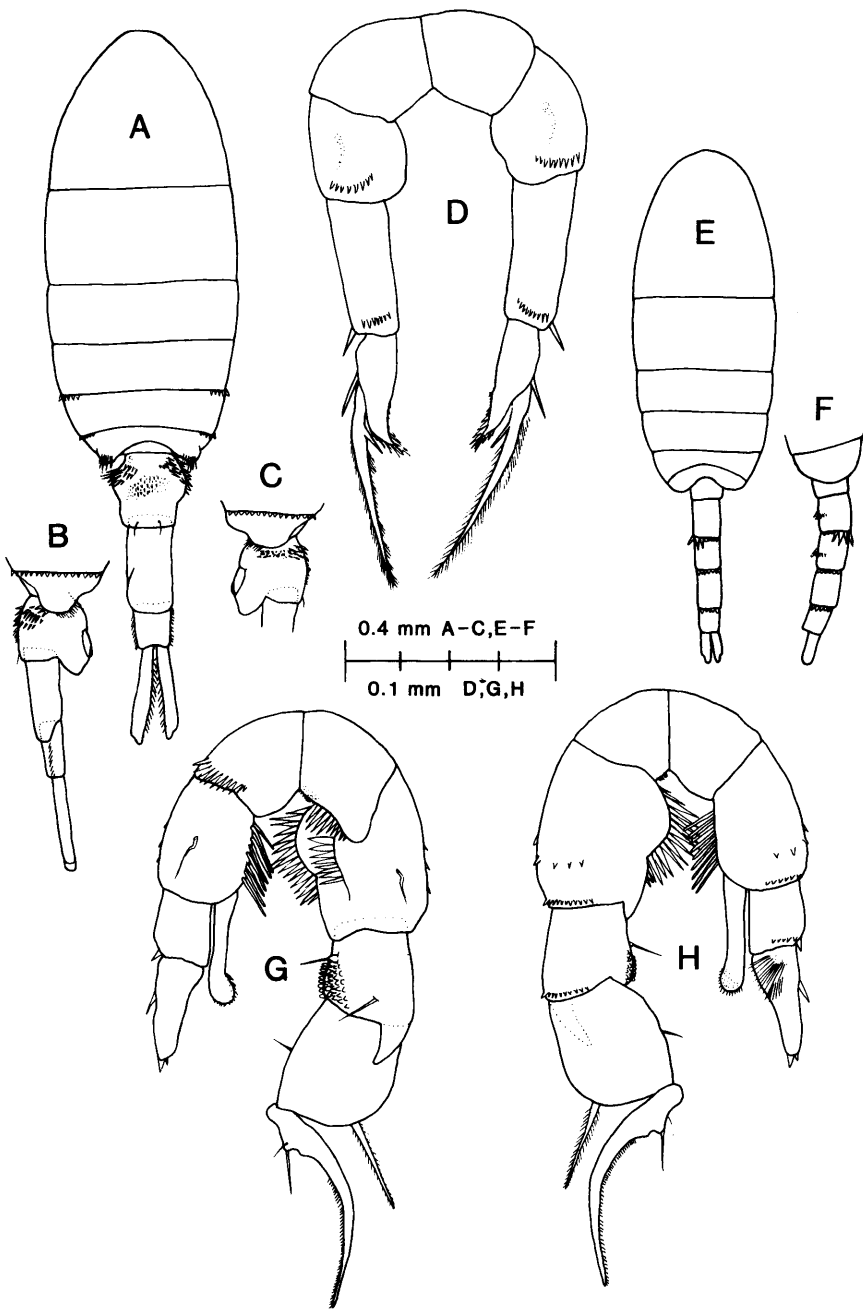


Figure 6. *Pseudodiaptomus culebrensis* Marsh. A-D, adult female: A, dorsal view; B, lateral view of Ur right side; C, lateral view of Ur left side; D, anterior view of P5. E-H, adult male: E, dorsal view; F, lateral view of Ur left side; G, posterior view of P5; H, anterior view of P5.

Pseudodiptomus cristobalensis Marsh

Figure 7A–D

Pseudodiptomus cristobalensis Marsh, 1913: 6–8, pl. 2, figs. 1–3, 5.—1933: 33, pl. 16, fig. 7, pl. 17, figs. 1–3.—Björnberg, 1963: 100.—Grindley, 1984: 226, fig. 1(3).—Collado et al., 1984: 116, tbl. 3.

(?) *Pseudodiptomus wrighti* Johnson, 1964: 38–40, figs. 23–25 (male variant only).

(non) *Pseudodiptomus cristobalensis*. Carvalho, 1952: 146–147, pl. 1, figs. 25–27.

Material.—PANAMA: Old French Canal, coll. by C. D. Marsh, 1912, Holotype, USNM 233801, 1m P5 and Ur on slide. COSTA RICA: Gulf of Nicoya, Pajaro Beach, coll. by Scripps Inst. Oceanography, 09 Dec 1953, USNM 234240, 6m with 2m P5 on slide (deposited as *P. cf. wrighti*). ECUADOR: Gulf of Guayaquil, 02°35'S; 080°06'W, coll. by F. Arcos, 19 Mar 1980, USNM 234241, 1m with P5 on slide (deposited as *P. cf. wrighti*).

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Male	6	1.25–1.30	1.27	0.88	0.46	1.4:1

Description.—Female unknown.

Male (Fig. 7A–B): Pdg2–3 with scale rows, Pdg4 scales incomplete dorsally. Pdg5 corners large, acute and posteriorly directed. Ur2–3 ventral surface with spinule row at midlength. Ur segments and CR with proportions 13:25:20:18:11:13 = 100.

Male P5 posterior view (Fig. 7C): Right leg, B1 with three surface spinule rows and medial spinule patch. B2 medial margin with elongate spinule cluster at midlength and distomedial corner enlarged, appears hyaline, with fine subapical hairs. Re1 distolateral spiniform process about half the length of Re2. Re2 enlarged, with lateral margin strongly convex, and small Se. Left leg, B1 with two surface spinule rows. B2 with medial spinule. Re1 with large surface seta. Re2 ovate with lateral spine, distolateral seta, fine hairs, and two distal spines, larger medial one hirsute. Anterior view (Fig. 7D): Right leg, B2 with distomedial spinule rows. Re1 distolateral spinules larger. Left leg, Ri simple and slender, hirsute apex with seta. Re2 with large distomedial spinule and slightly sclerotized, thickened distal margin.

Remarks.—Marsh (1913) described this species from one male found in the Old French Canal along the Panama Canal, but did not deposit the specimen. This specimen was found among the Mildred S. Wilson collection, and based on Marsh's notes and his 1913 drawings, I deposited this slide as the Holotype.

Subsequently, in collections from Costa Rica and Ecuador, containing only *P. wrighti*, large atypical males as described by Johnson (1964) were found. These atypical males are identical to Marsh's type material of *P. cristobalensis* and resemble *P. wrighti* in all respects, except for larger size and minor P5 variations. One differentiating feature of the larger (\bar{x} = 1.27 mm) atypical males is the presence of large amounts of spermatogenic material and spermatophores which are twice the size of the typical *P. wrighti* spermatophore. Examination of hundreds of *P. wrighti* female urosomes revealed that both large and regular spermatophores (Figs. 7A, 12D) were attached, indicating mating with atypical males. The smaller normal males did not possess large spermatophores. It is for this reason that I could not synonymize these males with *P. cristobalensis*; they were deposited as *P. cf. wrighti*. In addition, the lack of a large female does not allow me to synonymize *P. cristobalensis* with *P. wrighti*. Further material from the holotypic area is needed to determine if *P. cristobalensis* males are simply a large morph of *P. wrighti*.

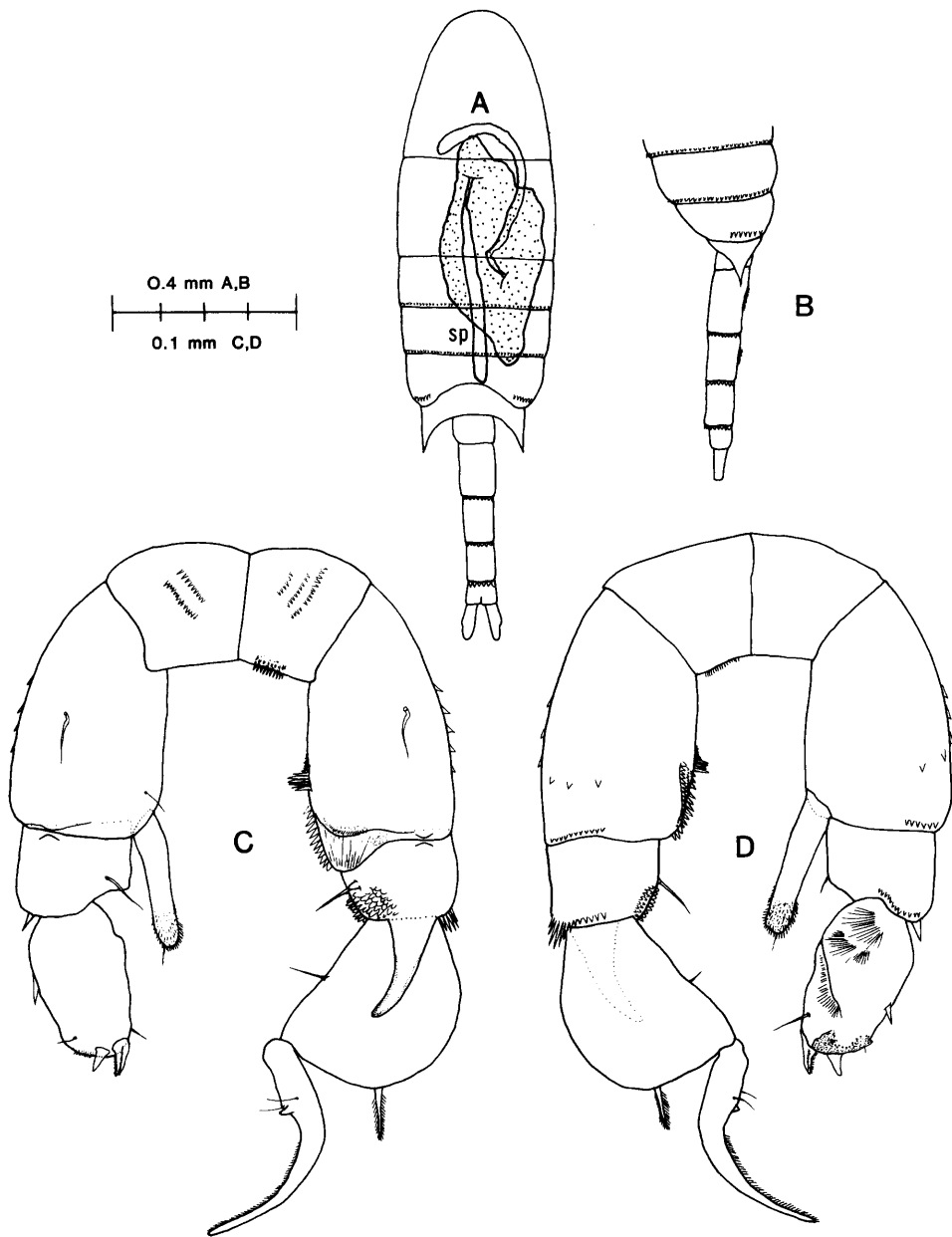


Figure 7. *Pseudodiptomus cristobalensis* Marsh. A-D, adult male: A, dorsal view; B, lateral view right side; C, posterior view of P5; D, anterior view of P5.

Pseudodiptomus marshi Wright
Figure 8A-J

Pseudodiptomus marshi Wright, 1936: 13-15, pl. 3, figs. 1-5, 7.—1937: 159-161, pl. 1, figs. 6-7.—Bacon, 1971: 85, tbl. 2.—Björnberg, 1981: 645-646, fig. 216(3).—Dussart, 1984: 63.—Dussart and Fernando, 1985: 39-41, figs. 1-9.—Prado-Por and Lansac-Tôha, 1984: 148.
Pseudodiptomus culebrensis.—Collado et al., 1984: 116, tbl. 3.

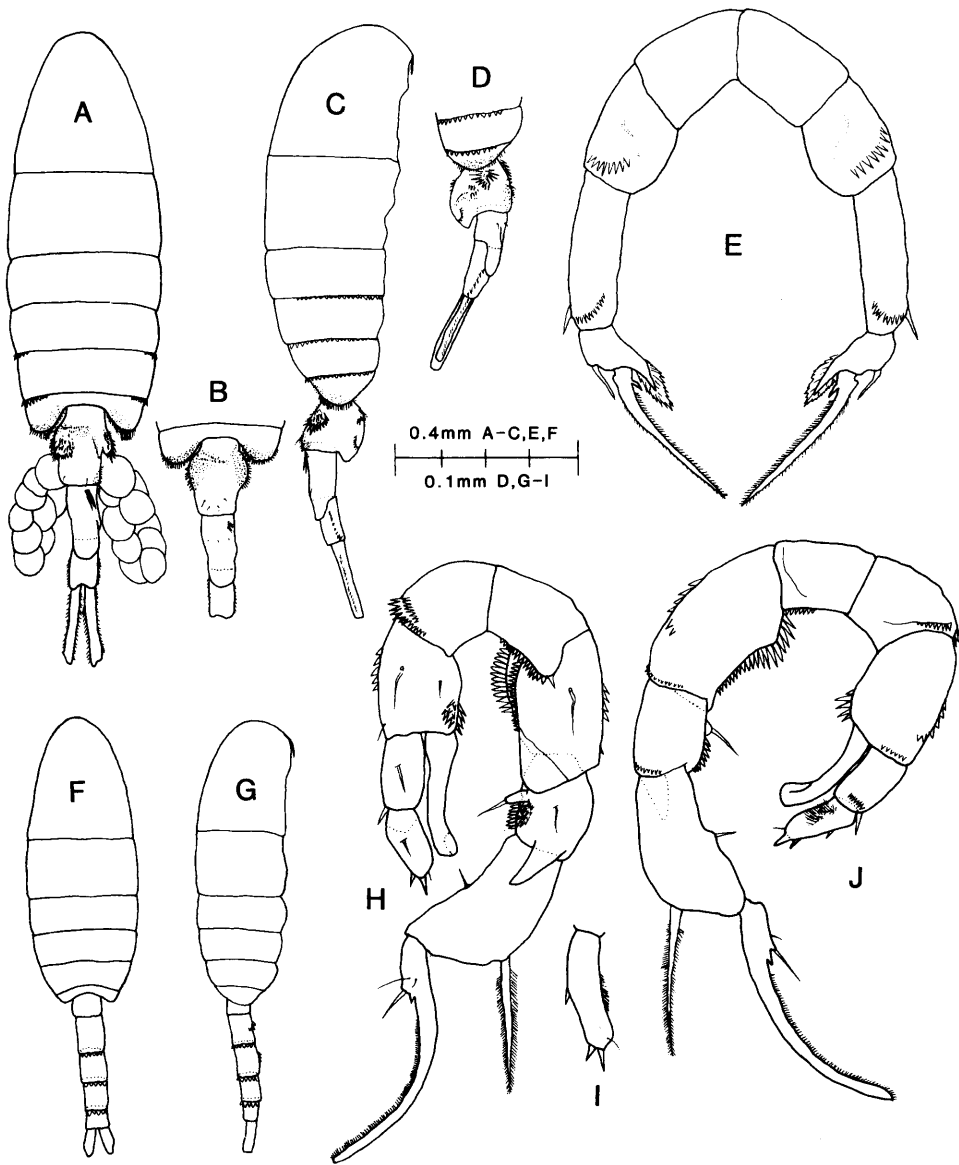


Figure 8. *Pseudodiaptomus marshi* Wright. A-E, adult female: A, dorsal view; B, dorsal view of Pdg5 and Ur from Brazil and Trinidad; C, lateral view of right side; D, lateral view Ur left side; E, anterior view of P5. F-J, adult male: F, dorsal view; G, lateral view right side; H, posterior view of P5; I, lateral view of P5 left Re2; J, anterior view of P5.

Material.—BRAZIL: Sergipe State, Pomonga River, coll. by C. E. F. da Rocha, 14 Nov 1979, USNM 231365, 5f, 18m. TRINIDAD: Caroni Swamp, coll. by P. F. Bacon, 1966, USNM 128930, 100+ f, m. COSTA RICA: Limon, coll. by A. Goss, June 1986, USNM 231366, 1f with P5 on slide, 1m on slide. BELIZE: Southern Lagoon, 17°13.2'N, 088°15.5'W, coll. by R/V ALPHA HELIX, 17 Jul 1977, USNM 231367, 1f, 4m with 2m P5 on slide.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	25	1.29–1.51	1.38	0.86	0.49	1.8:1
Male	25	0.95–1.06	0.98	0.65	0.37	1.8:1

Description.—Female (Fig. 8A–E): Pdg 2–3 with lateral scale rows. Pdg4–5 separate with Pdg4 lateral scale rows extending slightly dorsad. Pdg5 with dorsal and lateral spinules and hairs. Urosome with three segments. Ur1 left and right anterolateral surface with spinules and hairs, right lateral margin with or without knob at midlength (Fig. 8A–B) and set with spines; genital boss swollen posteroventrally with anterior spinules. Ur2 as long as Ur1, right anterodorsal surface with three to five spines, and posterodorsal margin extends onto Ur3. Ur3 with lateral spinule row. Ur1–3 lack posterior scale row. CR asymmetrical with right $6\times$, left $5\times$ longer than wide. Ur segments and CR with proportions $30:28:12:30 = 100$.

Female P5 (Fig. 8E): Ratio of Re2:Re3 = 1:2.0.

Male (Fig. 8F–J): Pdg4–5 separate with Pdg5 corners somewhat acute. Ur2–3 with ventral spinule row. Ur segments and CR with proportions $15:22:18:15:12:18 = 100$.

Male P5 posterior view (Fig. 8H): Right leg, B1 with medial spinules increasing in size toward enlarged distomedial corner. B2 with two rows of proximomedial spinules. Re1 with surface seta and distolateral process small and distally directed. Re2 Se long. Re3 very long with small proximomedial projection distal to medial seta. Left leg much shorter than right leg. B1 with distolateral spinule rows. B2 with small patch of distomedial spinules and small surface seta. Re1 with surface seta and small Se. Re2 as long as Re1, elongate, oblong with one lateral spine, two apical spines, the medial spine larger, and one medial seta. Anterior view (Fig. 8J): Left leg, B1 with subapical spinule row. Ri slender and medially curved.

Remarks.—Wright (1936) originally described this species from the Amazon region of Brazil. Subsequently, it has been reported from Trinidad (Bacon, 1971), Costa Rica (Dussart and Fernando, 1985; Collado et al., 1984) and Belize in this paper. *Pseudodiaptomus marshi* is restricted to the Atlantic coast of Central and South America. Material from these localities indicates that there are two morphological forms of females as evidenced during examination of the Ur1. Specimens from Brazil and Trinidad possess symmetrical Ur1 as described by Wright (Fig. 8B), while the Ur1 of the Central American females (Costa Rica and Belize) is asymmetrical (Fig. 8A) with an anterolateral knob present on the right side. Males from the four locations were identical in all respects, with no other species present in the samples, indicating that the females were conspecific.

The male P5 of *P. marshi* is unusual among pseudodiaptomids in that the right foot is markedly longer than the left. In addition, the left Re2 typically is directed anteriorly, thereby appearing shortened; the lateral spine appears to be a surface spine, though its actual size is apparent in Figure 8I. As previously discussed, this species is easily confused with *P. culebrensis*, its Pacific relative. The above information does not support the determination of Dussart and Fernando (1985) that specimens collected from Acapulco, Mexico by Comita (1951) were *P. marshi*, an Atlantic species.

Pseudodiaptomus panamensis new species

Figure 9 A–G

Material.—PANAMA: Panama Canal, Naos Marine Station, coll. by M. Jones, 04 Nov 1971, Holotype USNM 231558, 1m, Allotype USNM 231559, 1f, Paratypes USNM 231560, 1f, 6m. COSTA RICA: Gulf of Nicoya, Chira Flats, coll. by Scripps Inst. Oceanography, 29 Dec 1953, USNM 234227, 50f, 30m.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	20	1.49–1.59	1.53	0.86	0.56	1.5:1
Male	20	0.92–0.95	0.93	0.65	0.32	2.0:1

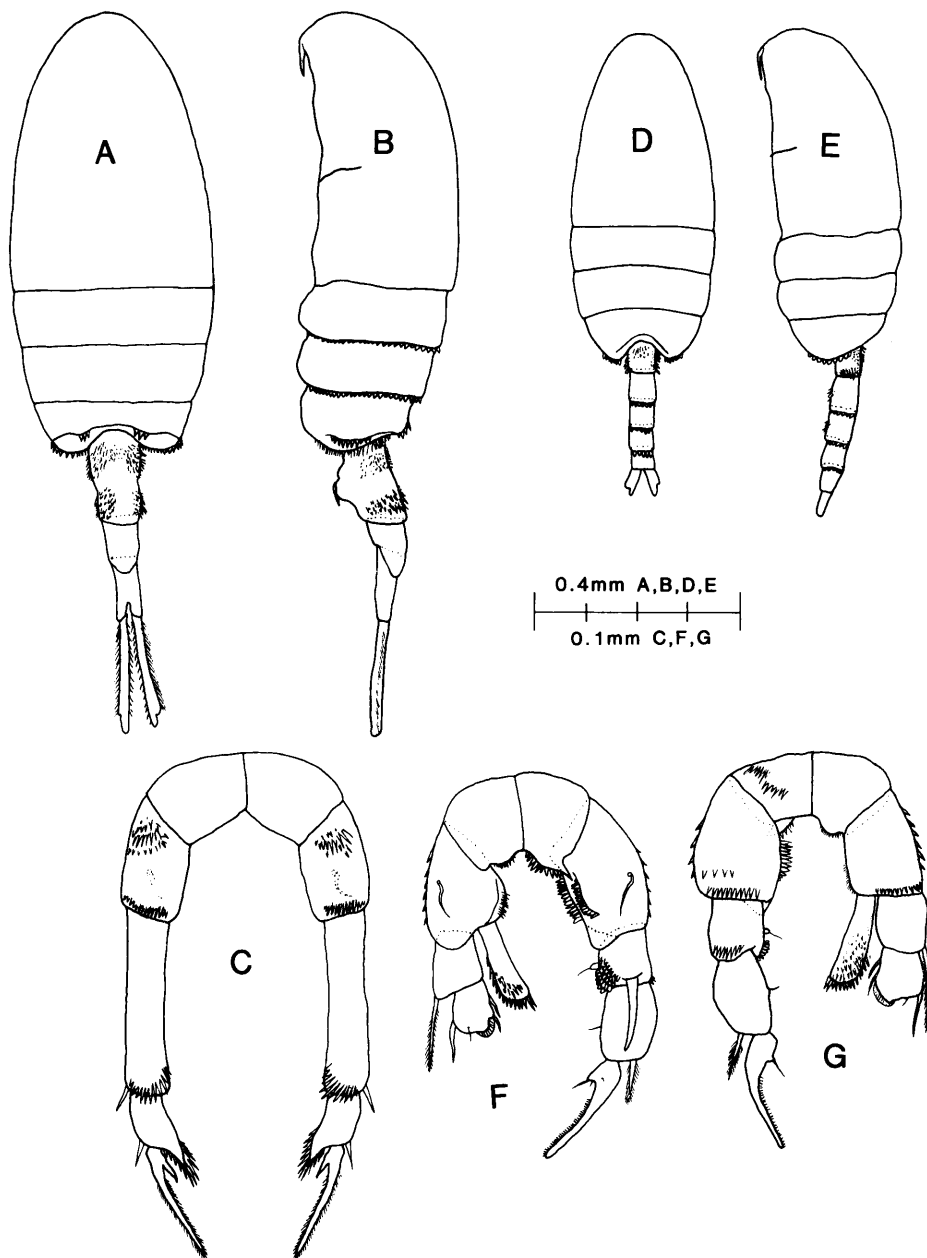


Figure 9. *Pseudodiaptomus panamensis* sp. nov. A–C, adult female: A, dorsal view; B, lateral view left side; C, anterior view of P5. D–G, adult male: D, dorsal view; E, lateral view left side; F, posterior view of P5; G, anterior view of P5.

Description.—Female (Fig. 9A–C): Head and Pdg1 fused. Pdg2–3 with lateral scale rows. Pdg4–5 incompletely fused along lateral margin. Pdg4 with postero-lateral scales and three or four dorsal scales. Pdg5 with rounded corners and scales along margin. Urosome with three segments. Ur1 with anterior and posterior hair

and spinule patches; genital boss insignificant. Ur2 posterodorsal margin overlaps onto Ur3. CR slightly asymmetrical, right $7.5\times$ and left $8.0\times$ longer than wide. Ur segments and CR with proportions $31:13:18:38 = 100$.

Female P5 (Fig. 9C): B2 anterior surface with proximal spinules. Ratio Re2:Re3 = 1:1.3.

Male (Fig. 9D–G): Head and Pdg1 fused. Pdg4–5 incompletely fused lateral margin. Pdg5 with rounded corners and posterolateral scale row. Ur1 with dorsal and lateral hairs and spinules. Ur2–3 with ventral spinule row. Ur segments and CR with proportions $18:22:17:13:13:17 = 100$.

Male P5 posterior view (Fig. 9F): Right leg, B1 medial margin lined with spinules and distomedial corner pointed. B2 medial margin with two spinule rows. Re1 posterolateral spiniform process almost the length of Re2. Re2 Se short. Left leg, B1 small medial protrusion lined with fine hairs. B2 medial margin with hairs. Ri clavate with rounded spinulated apex. Re1 Se long and hirsute. Re2 small, quadrate with one long distolateral spine, distal seta, distomedial hyaline comb, and two small medial spines. Anterior view (Fig. 9G): Right leg, B1 with two spinule rows.

Remarks. — *Pseudodiptomus panamensis* is unique among the American species in that: i) Head and Pdg1 are fused. ii) Proportional body sizes of male to female are exceptionally smaller than the typical male-female size ratios. iii) Female P5 possesses anterior B2 spinule patches. iv) Male P5 is easily distinguished from all other species in its reduced size, long hirsute left Re1 Se, which is about twice Re2 length, and left Re2 reduced with long distolateral spine and distomedial hyaline comb.

This species is found along the Pacific coastline from Costa Rica and Panama.

Pseudodiptomus longispinosus new species

Figure 10A–H

Material. — ECUADOR: Gulf of Guayaquil, $02^{\circ}15.6'S$, $079^{\circ}54.5'W$, coll. by F. Arcos, 28 Mar 1983, Holotype USNM 231555, 1m, Allotype USNM 231556, 1f, Paratypes 231557, 20f, 25m.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	15	1.10–1.15	1.14	0.77	0.42	1.8:1
Male	15	0.90–0.97	0.94	0.62	0.34	1.8:1

Description. — Female (Fig. 10A–D): Pdg2–3 posterior margin with lateral scales that extend completely dorsad. Pdg4–5 separate. Pdg5 with hairs and spinules along rounded posterior corners. Urosome irregularly shaped consisting of four segments. Ur1 large, asymmetrical, with anteriorly produced genital boss. Left anterodorsal margin swollen, covered with hairs and spinules; right posterodorsal corner notched, forming a knob adorned with several large spinules, and posterior margin slightly overlapping Ur2. Left anterolateral surface with hairs and fine spinules that extend dorsad, and ear-shaped process; right lateral surface with two anterior spinule patches. Ur2 posterior margin twisted and slightly overlaps Ur3, with ventral and dorsal surfaces notched at midlength. Ur3 slightly overlaps Ur4, the latter with dorsal and lateral spinules. CR symmetrical, short, $3\times$ longer than wide. Ur segments and CR with proportions $38:16:20:10:16 = 100$.

Female P5 (Fig. 10D): Ratio Re2:Re3 = 1:2.

Male (Fig. 10E–H): Pdg4–5 separate. Ur2 posterodorsal scale row incomplete on right side; ventrally with two spinule rows. Ur3 with ventral spinule row. Ur segments and CR with proportions $13:25:17:21:12:12 = 100$.

Male P5 posterior view (Fig. 10G): Right leg, B1 with medial protrusion, dis-

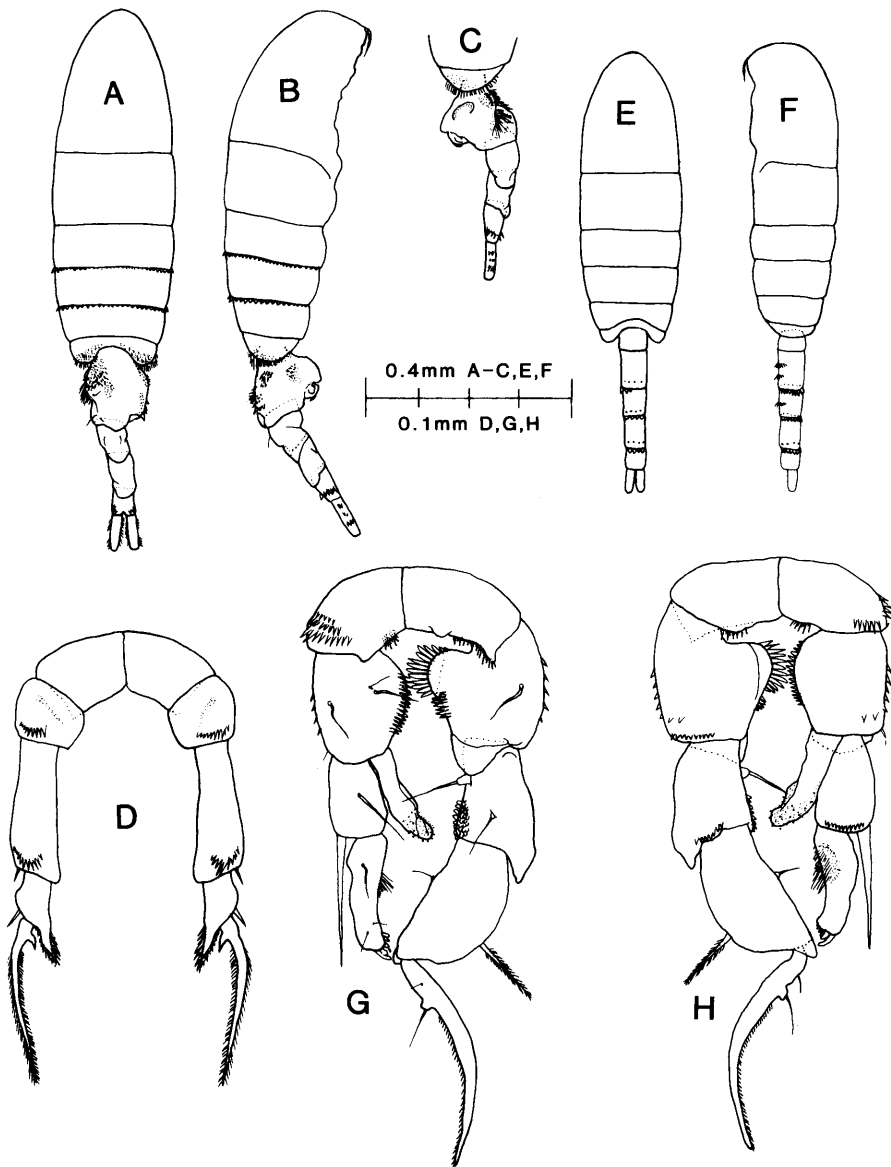


Figure 10. *Pseudodiaptomus longispinosus* sp. nov. A-D, adult female: A, dorsal view; B, lateral view right side; C, lateral view of Ur left side; D, anterior view of P5. E-H, adult male: E, dorsal view; F, lateral view left side; G, posterior view of P5; H, anterior view of P5.

tomedial corner acute and lined with fine spinules. B2 proximomedial corner greatly extended, with large spinules, set of smaller medial spinules, and hyaline distomedial corner overlapping Re1. Re1 with one small surface papilla, and distolateral spiniform process distally directed, short and triangular. Re3 long. Left leg, B1 with three rows of subapical spinules, distomedial corner only slightly produced. B2 with two surface setae and spinules along medial margin. Re1 with one large surface seta, and naked Se equal in length to Re2. Re2 laterally com-

pressed and medially curved with one large proximal surface seta, two subapical setae and four to five small irregular papillae-like projections at apex. Anterior view (Fig. 10H): Left leg, B1 with subapical spinules. B2 Ri medially directed, medial margin with low projection above midlength, narrowing to rounded, finely pilose apex.

Remarks.—*Pseudodiptomus longispinosus* was collected in the Gulf of Guayaquil, Ecuador. The only other eastern Pacific coastline species found below the equator is *P. wrighti*, from which the former is easily distinguished by: i) Female smaller in size with a four-segmented urosome, and rounded Pdg5 corners. ii) Male also smaller with rounded corners, P5 right Re1 lateral process reduced, and left Re2 elongate and laterally flattened.

Pseudodiptomus gracilis (Dahl)

Figure 11 A–I

Weismanella gracilis Dahl, 1894: 10–11, pl. 1, figs. 12–14.

Schmackeria gracilis Poppe and Mrázek, 1895: 127.

Pseudodiptomus gracilis Giesbrecht and Schmeil, 1898: 65.—Stingelin, 1904: 588.—Wright, 1928: 589–592, text figs. 1–2, pl. 12, fig. 4;—1936: 3–6, pl. 1, figs. 1–8.—Marsh, 1933: 35–36, pl. 18, figs. 4–6.—Brehm, 1934: 93.—Cipólli and Carvalho, 1973: 97–98, 100.—Björnberg, 1981: 645–646, fig. 216(2).—Dussart, 1984: 27, 43, fig. 2.—Prado-Por and Lansac-Tôha, 1984: 148, tbl. 1.

Material.—BRAZIL: no station data, coll. by S. Wright, USNM 60559, 1m slide; USNM 60600, 1f slide; USNM 92945 1f slide; Pará State, Baía do Marajo, Rio Guama, Nov–Dec 1984, coll. by M. L. Carvalho, USNM 228785, 14f, 15m; Capim River, 12 Aug 1970, coll. by M. A. J. de Carvalho, USNM 228784, 4f, 5m; Belem, Belem Harbor, 01°27.8'S, 048°29.2'W, 11–14 Jun 1977, coll. by R/V ALPHA HELIX, USNM 231288, 47f, 45m.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	25	1.03–1.15	1.10	0.73	0.39	1.8:1
Male	25	0.89–0.95	0.92	0.67	0.31	2.1:1

Description.—Female (Fig. 11A–E): Head with ventrolateral horns, and posterolateral margins with row of scales; rostrum with short truncate filaments. Pdg2–4 posterolateral margins with scale rows complete to dorsad. Pdg4–5 separate with Pdg5 corners rounded and naked. Urosome consists of four segments. Ur1 genital boss slightly produced. Ur1–3 posterodorsal scale row extending slightly laterad. CR symmetrical, 3 × longer than wide, with CR setae plumose and jointed except for naked, spine-like, lateral seta (Fig. 11D). Ur segments and CR with proportions 32:18:18:14:18 = 100. Egg sac single and centrally carried. A1 as in Figures 1C, 11B–C.

Female P5 (Fig. 11E): Re1 and Re2 Se large and thickened. Ratio Re2:Re3 = 1:2.1.

Male (Fig. 11F–I): Rostrum, head and Pdg1–5 as in female. Ur2 with ventral spinule row. Ur segments and CR with proportions 12:24:16:16:16:16 = 100. A1 as in Figure 1D.

Male P5 posterior view (Fig. 11H): Right leg, B1 with two rows of subapical spinules, posteromedial corner acute. B2 with few proximomedial hairs. Re1 with medial cluster of large spinules, distolateral spiniform process long and distally directed. Re2 narrow. Left leg, B1 with two rows of subapical spinules. B2 with one surface seta and fine hairs along medial margin. Lacks Ri. Re1 with very short Se and one surface seta. Re2 large, ovate, with two surface setae and one apical spine. Anterior view (Fig. 11I): Right leg, B1 with medial spinules along groove.

Remarks.—Of the American pseudodiptomid species, *P. gracilis* stands out as an odd species in that it possesses the following characteristics: i) Head with

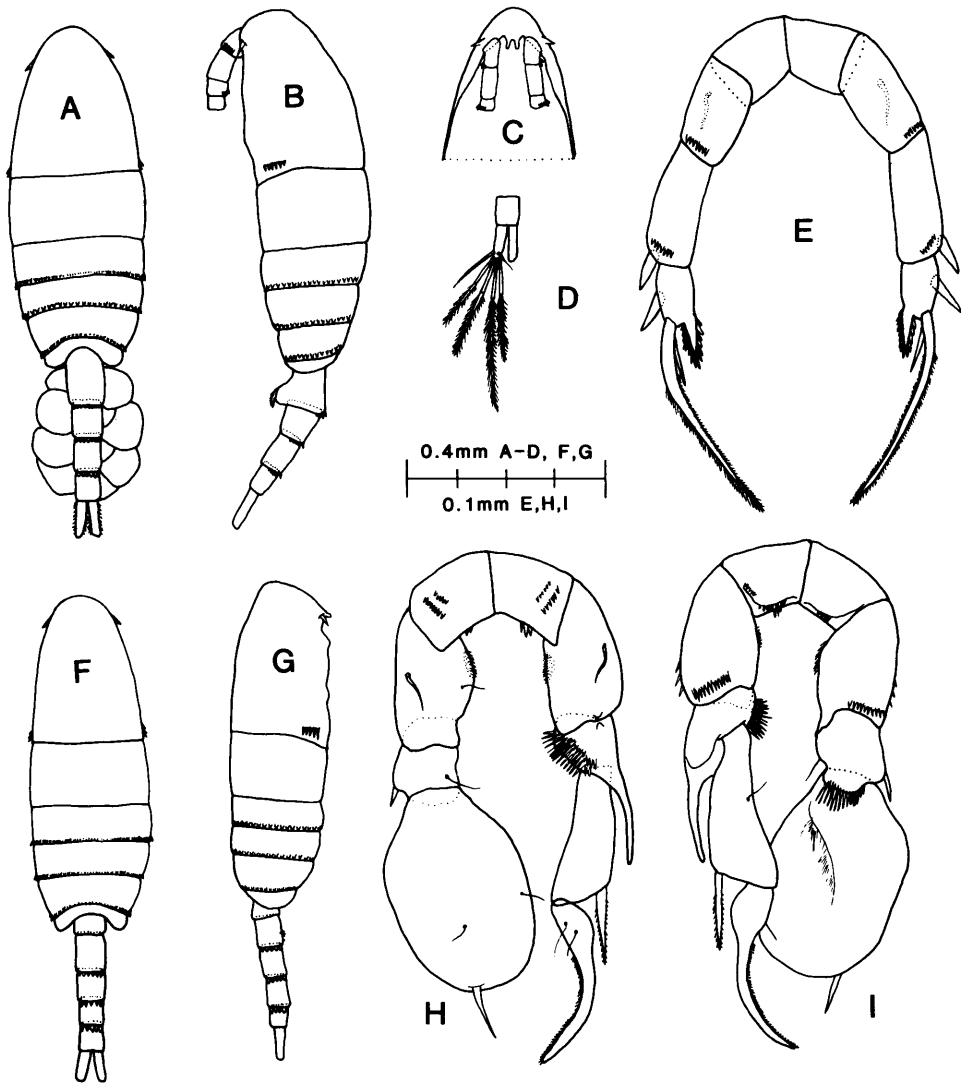


Figure 11. *Pseudodiaptomus gracilis* (Dahl). A-E, adult female: A, dorsal view; B, lateral view left side; C, ventral view of head; D, CR showing naked lateral spine-like seta; E, anterior view of P5. F-I, adult male: F, dorsal view; G, lateral view right side; H, posterior view of P5; I, anterior view of P5.

anterolateral hooks and posterolateral spines. ii) Rostral filaments shortened and truncate. iii) Lateral CR seta is spine-like, not jointed and plumose. iv) Female with single egg sac. v) Male P5 with large ovate left Re2 and lacks left Ri.

All early reports of *P. gracilis* indicated that it was endemic to the Amazon region of Brazil. Recently, Dussart (1984) found it near Tucupita, Venezuela. This species is typically found in low to very low saline inland waters, though after heavy rains it may be flushed seaward and temporarily displaced to more marine environments.

Only one other pseudodiaptomid, *P. clevei* from the Indo-Pacific region, is known to lack both a left and right Ri. Both these species are assigned to the

Nudus species group and appear to be allopatric species, though several major differences exist between the species (Walter, 1986a).

Pseudodiaptomus wrighti Johnson
Figure 12A–H

Pseudodiaptomus wrighti Johnson, 1964: 34–40, figs. 1–25.—Fleminger, 1967: 35.—Dussart, 1984: 63.

Pseudodiaptomus acutus var. *leptopus* Löffler, 1963: 208–209, fig. 9a.

Pseudodiaptomus galapagensis Arcos, 1978: 50, tbl. 3.

Material.—MEXICO: Boca de Canasal, Baja California, coll. by M. W. Johnson, 4 Jul 1963, USNM 110260, Holotype, 1f on slide; USNM 110261, Allotype, 1m on slide; USNM 110262, 2f, 2m on slides. COSTA RICA: Gulf of Nicoya, Pajaro Beach, coll. by Scripps Inst. Oceanography, 09 Dec 1953, USNM 234239, 85f, 63m. PANAMA: Perlas Islands, 08°24'N 079°05'W, coll. by M. Jones, 30 Apr 1971, USNM 231563, 39f, 35m; Gulf of Panama, coll. by D. Ayguabibas, 1967, USNM 139474, 10f. ECUADOR: Gulf of Guayaquil, 03°08'S, 080°04'W, coll. by Santoro, 22 Feb 1963, USNM 149799, 6f, 6m; 02° 35'S, 080°06'W, coll. by F. Arcos, 19 Mar 1980, USNM 231561, 9f, 7m; 01°32'N, 079°00'W, coll. by R/V A. AGASSIZ, 15 Nov 1965, USNM 234228, 44f, 7m. PERU: 04°32'S, 081°34'W, coll. by Yale South American Exped., 18 Mar 1953, USNM 231562, 42f, 36m.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	25	1.38–1.52	1.45	1.02	0.54	1.9:1
Male	25	1.12–1.20	1.15	0.85	0.42	2.0:1

Description.—Female (Fig. 12A–C): Pdg2–3 posterior margin with lateral scale row that extends completely dorsad, Pdg4 scale row not complete dorsally. Pdg4–5 separate, Pdg5 corners large, acute, and posterolaterally directed with surface hair and spinules. Urosome with four segments. Ur1 both anterolateral surfaces with spinules that extend dorsad, right side with small hirsute ball-shaped knob at midlength, and few very fine posterolateral hairs; genital boss deeply extended. Ur2–3 partly fused and counted separately, Ur3 with posterior scale row. CR symmetrical and $2.5 \times$ longer than wide. Ur segments and CR with proportions 42:37:5:16 = 100.

Female P5 (Fig. 12C): Ratio of Re2:Re3 = 1:1.2.

Male (Fig. 12D–H): Pdg2–3 posterior margin with complete scale row, Pdg4 scale row not complete dorsally. Pdg4–5 separate, Pdg5 corners strongly acute and posteriorly directed. Ur2–3 with ventral spinule rows (Fig. 12F). Ur segments and CR with proportions 14:22:19:19:10:16 = 100.

Male P5 posterior view (Fig. 12G): Right leg, B1 with acute distomedial corner, two surface spinule rows, and small medial hirsute protrusion. B2 medial margin with hair and fine spinule rows, distomedial corner enlarged, and appears hyaline with fine hairs. Re1 medial spiniform process narrow and medially directed. Left leg, B1 with surface spinule row. Ri distally pointed and hirsute. Re2 circular with lateral spiniform process, lateral comb of eight to ten short teeth, two large apical spines, medial toothed, and distal seta. Anterior view (Fig. 12H): Right leg, B1 with subapical spinules. B2 medial groove with spinules. Left leg, B1 same. B2 with medial spinule crest.

Remarks.—Löffler (1963) reported male pseudodiaptomids from Ecuador, noting their similarity to the Atlantic species *P. acutus*, and established these Pacific males as *P. acutus* var. *leptopus*. Based on his report and drawing this species is undoubtedly *P. wrighti*. The range of *P. wrighti* is confined to the Pacific coast and now extends from Baja California, Mexico, south to the northern coast of Peru.

As mentioned under the remarks section of *P. cristobalensis*, Johnson (1964) reported three variant males of *P. wrighti* which were larger with minor P5 vari-

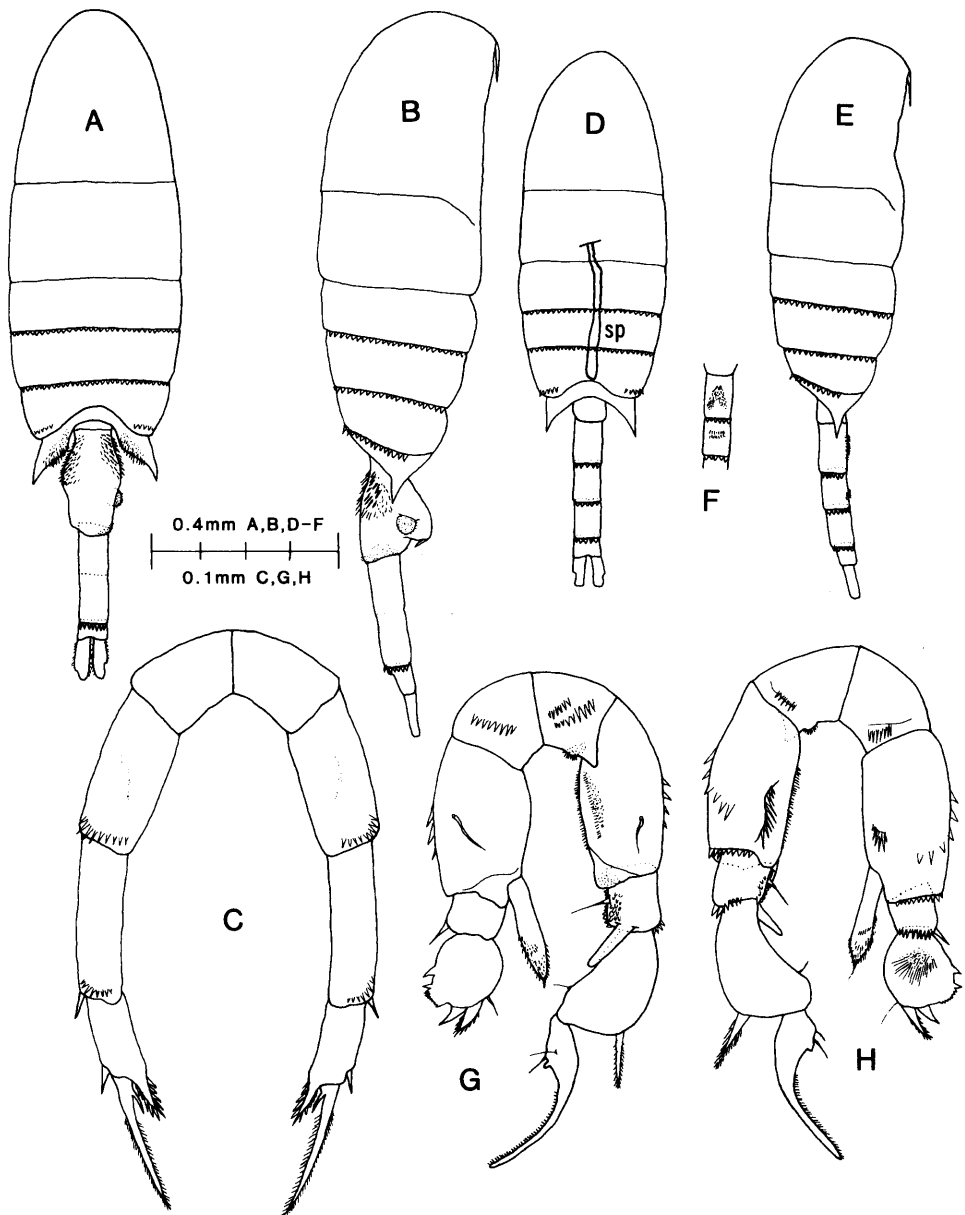


Figure 12. *Pseudodiaptomus wrighti* Johnson. A-C, adult female: A, dorsal view; B, lateral view right side; C, anterior view of P5. D-H, adult male: D, dorsal view; E, lateral view right side; F, ventral view of Ur2-3; G, posterior view of P5; H, anterior view of P5.

ations noted. In samples from Costa Rica and Ecuador containing only *P. wrighti*, I encountered these atypical males and, like Johnson, found no large conspecific females. It is possible that these large males are intersex specimens similar to variants noted with *P. pelagicus*. However, the P5 characters do not possess any female traits as seen in the intersex specimens of the latter. Spermatophores in

these males are twice as large as those of the normal males (Figs. 7A, 12D). Females of *P. wrighti* were observed with both types of spermatophores attached to their urosomes, indicating that they are capable of mating with the larger intersex males. Therefore, I am hesitant to assign these atypical males as *P. wrighti*, or synonymize them with *P. cristobalensis*, and have deposited them as *P. cf. wrighti* (USNM 234240, 234241) until additional material becomes available for study.

Pseudodiaptomus galapagensis Grice
Figure 13A-I

Pseudodiaptomus galapagensis Grice, 1964: 255-258, figs. 1-19.
(non) *Pseudodiaptomus galapagensis* Arcos, 1978: 50, tbl. 3.

Material.—Ecuador: Galapagos, Santa Cruz Island, Academy Bay, coll. by G. Grice, 13 Feb 1962, Holotype USNM 108360, 1f, Allotype USNM 108361, 1m, Paratypes USNM 108362, 4f, 5m, USNM 108164, 11f, 1m; coll. by F. Arcos, 15 Nov 1973, USNM 231624, 12f, 1m.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	10	1.67-1.70	1.68	1.03	0.66	1.6:1
Male	4	1.12-1.16	1.14	0.78	0.41	1.8:1

Description.—Female (Fig. 13A-E): Pdg2-3 posterior margin with lateral scale row that extends slightly dorsad. Pdg4-5 separate with Pdg5 posterior corners large, acute, and laterally directed with surface hair and spinules. Urosome with four segments. Ur1 asymmetrical, right posterior margin extends farther onto Ur2, right anterolateral margin triangular, left rounded, both surfaces with dorsal and lateral hairs and spinules; genital boss greatly enlarged posteriad. Ur2 left anterolateral margin slightly produced. Ur3 with partial scale row along right posterolateral margin. Ur4 left lateral surface spinulated. Most females possess a distinctive durable, hyaline-type spermatophore coupling apparatus (Fig. 13C-D). Apparatus opens ventrally and laterally along right posterior half of urosome, eggs carried under the apparatus, with spermatophore usually attached to Ur1. CR asymmetrical, rami broad (left 2× and right 1.5× longer than wide), with dorsal and lateral spinule rows. CR setae thickened at base. Ur segments and CR with proportions 34:21:21:9:15 = 100.

Female P5 (Fig. 13E): Ratio Re2:Re3 = 1:1.5.

Male (Fig. 13F-I): Pdg2-3 posterior margin with lateral scale row that extends dorsad. Pdg4-5 separate with Pdg5 corners rounded. Ur2-3 with ventral spinule row. Ur segments and CR with proportions 10:24:14:21:10:21 = 100.

Male P5 posterior view (Fig. 13H): Right leg, B1 medial margin with two rows of surface spinules, slight pilose protrusion, and rounded distomedial corner. B2 with short medial spinules, distomedial corner hyaline, and distally expanded. Re1 distomedial spiniform process short, about one-third length of Re2. Left leg, Ri distally hirsute, tapering to point at apex. Re2 somewhat oval with one small lateral spine, distal comb row of five-six small teeth, two distomedial spines equal in size, and one seta at medial indentation. Anterior view (Fig. 13I): Right leg, B1 with subapical spinules. B2 with narrow subapical spinule patch.

Remarks.—The only records for *P. galapagensis* indicate that it is confined to the Galapagos Islands. It is most closely related to *P. wrighti*, also a Pacific coast species, as evidenced by the male P5, though the latter is confined to continental waters. *Pseudodiaptomus galapagensis* is distinguished by: i) Female Pdg5 corners laterally directed, Ur2-3 completely separate, CR heavily spinulated with CR setae thickened at base. ii) Male Pdg5 corners rounded, P5 right Re1 spiniform process shorter, and left Re2 more oval in shape. The females short, heavily

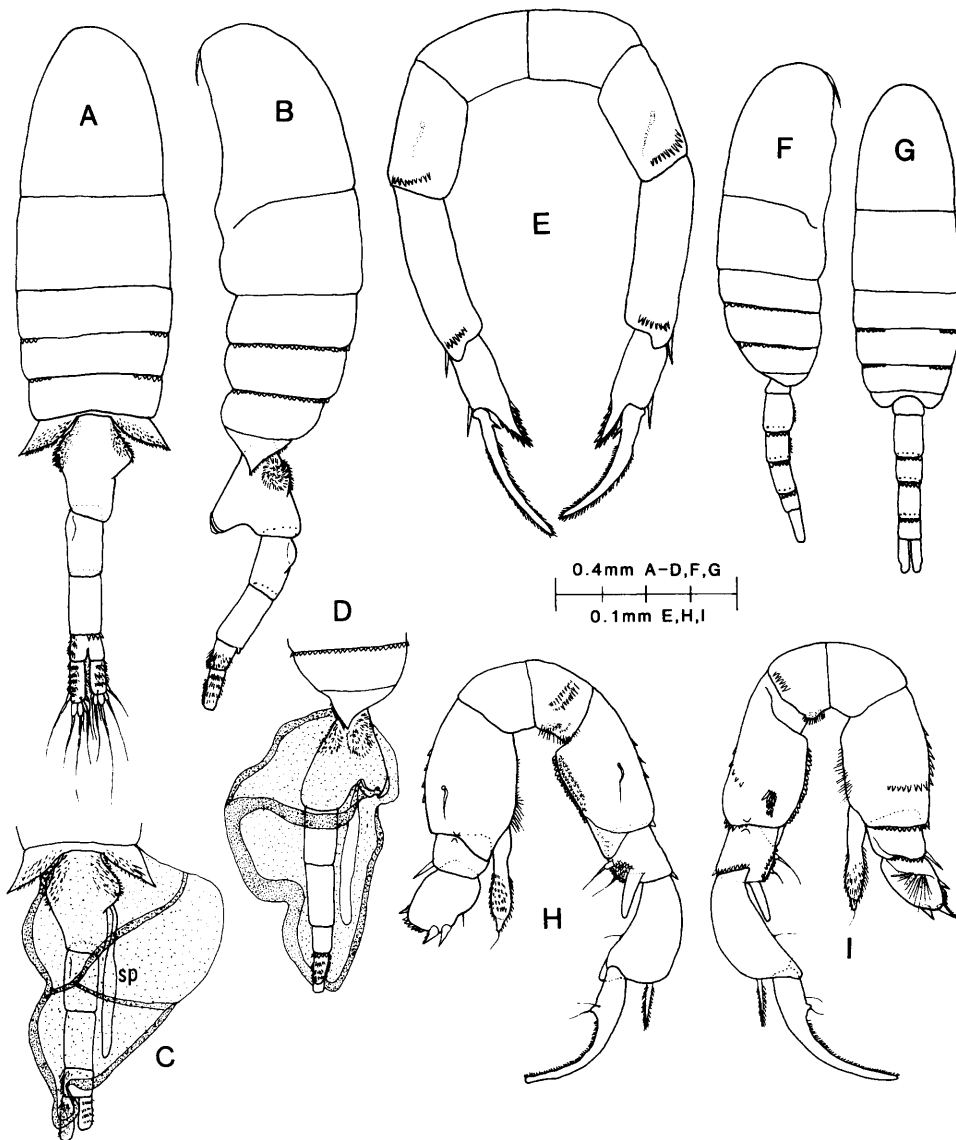


Figure 13. *Pseudodiaptomus galapagensis* Grice. A-E, adult female: A, dorsal view; B, lateral view left side; C, dorsal view of Ur showing hyaline-like shield; D, lateral view of Ur right side with shield; E, anterior view of P5. F-I, adult male: F, lateral view right side; G, dorsal view; H, posterior view of P5; I, anterior view of P5.

spinulated CR and Ur1 hyaline apparatus were not reported by Grice (1964) and appear to be unique to this species.

Pseudodiaptomus acutus (Dahl)
Figures 14A-H, 15A-B

Weismannella acutus Dahl, 1894: 10-11, pl. 1, figs. 9-11.
Schmackeria acutus Poppe and Mrázek, 1895: 127.

Pseudodiaptomus acutus. Giesbrecht and Schmeil, 1898: 64.—Marsh, 1933: 30, pl. 15, figs. 1, 2, 4.—Wright, 1936: 10–13, pl. 2, figs. 5–6, pl. 3, fig. 8.—1937: 159–161, pl. 1, fig. 4.—Carvalho, 1945: 95–96, pl. 8, fig. 7a–c.—1952: 146, pl. 1, figs. 20–24.—Björnberg, 1963: 45.—1968: 76–88, figs. 15–19.—1981: 646, fig. 216(4).—Cervigón and Marcano, 1967: 268, tpls. 7, 10.—Bowman, 1978: 249–252, figs. 1–2.—Jacoby and Youngbluth, 1983: 77, 79–85, figs. 1A, 2A, D, tpls. 1–3.—Montú, 1980: 57, tbl. 1.—Prado-Por and Lansac-Tôha, 1984: 148, tbl. 1.—Montú and Goeden, 1986: 79, fig. 24a–c.

Material.—BRAZIL: São Paulo, Cananéia, 16 Mar 1984, coll. by M. S. Prado-Por, USNM 231217, 3f, 4m; Cananéia, 26 Nov 1954, coll. by V. Sadowisky, USNM 231219, 28f, 24m; Baía do Marajo, Cabo Maguari, 22 Oct 1982, coll. by M. Carvalho, USNM 231218, 1f, 1m; *Sergipe State*, Piavi River, 18 Aug 1981, coll. by S. A. do Nascimento, USNM 232186, 6f, 2m. SURINAM: 06°09.2'N 054°21.5'W, 19 Jun 1977, coll. by R/V ALPHA HELIX, USNM 231287, 13f, 5m. VENEZUELA: Coche Island, 21 Nov 1980, coll. by L. Gonzalez Cebrero, USNM 233658, 14f, 20m. JAMAICA: St. Catherine Parish, 1975, coll. by J. Grahame, USNM 153826, 1f.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	25	1.14–1.36	1.25	0.85	0.45	1.9:1
Male	25	0.92–1.05	0.94	0.67	0.33	2.0:1

Description.—Female (Fig. 14A–D): Pdg2–4 posterior margin with complete scale row. Pdg4–5 separate. Pdg5 with medial surface hairs, posterior corners acute, and distally directed. Urosome with four segments. Ur1 asymmetrical, left and right proximolateral surfaces with hair and spinule patches, distally this segment is twisted to the right, dorsal surface with proximal and distal hairs and spinules; genital boss not greatly enlarged. Ur1–3 right distolateral margin with scale row that extends slightly dorsad. CR asymmetrical, the right 3× and left 4× longer than wide. Ur segments and CR with proportions 38:15:12:9:26 = 100.

Female P5 (Fig. 14D): Left anterior Re1 with five to seven large medially directed spinules at midlength. Re2 spiniform process recurved. Ratio Re2:Re3 = 1:1.3.

Male (Fig. 14E–H): Pdg2–4 with posterolateral scale row. Pdg4–5 separate. Pdg5 posterior corners small, acute and distally directed with few hairs along margin. Ur2–3 ventral surface with two and one spinule rows, respectively. Ur segments and CR with proportions 17:21:17:17:8:20 = 100.

Male P5 posterior view (Fig. 14G): Right leg, B1 distomedial corner acute. B2 proximomedial margin enlarged and lined with spinules. Re1 distomedial spiniform process slightly curved to mediad about one-half length of Re2. Left leg, Ri distally enlarged and hirsute, narrowing to a nipple-like apex. Re1 distomedial corner enlarged to overlap onto Re2. Re2 somewhat ovate with one small lateral spiniform process, lateral comb row of five to six teeth, and two distal spines; spine next to comb row with lateral hyaline margin, the other lined with fine spinules. Anterior view (Fig. 14H): Right leg, B1 with subapical spinules. B2 with several spinule rows along medial groove and proximal spinules decreasing in size distally.

Remarks.—Amendments to Dahl's description were first stated by Wright (1936) and include: i) Female P5 with surface spinules on left Re1, and B2 without lateral Se. ii) Male P5 left leg with B2 and Re1 separate. *P. acutus* figured by Carvalho (1952) inaccurately represents the male P5, as the right Re3 was placed on the left Re2. Among South American Atlantic species, *P. acutus* is readily distinguishable in that the female P5 possesses anterior surface spinules on B2, and the male Pdg5 corners are acute. A disjunct population of *P. acutus* was reported from Jamaica by Bowman (1978) who noted a minor variation in the female Pdg5 left corner which possessed two spines; all other characteristics were unchanged.

In samples from São Paulo, Brazil seven variant males were observed. These

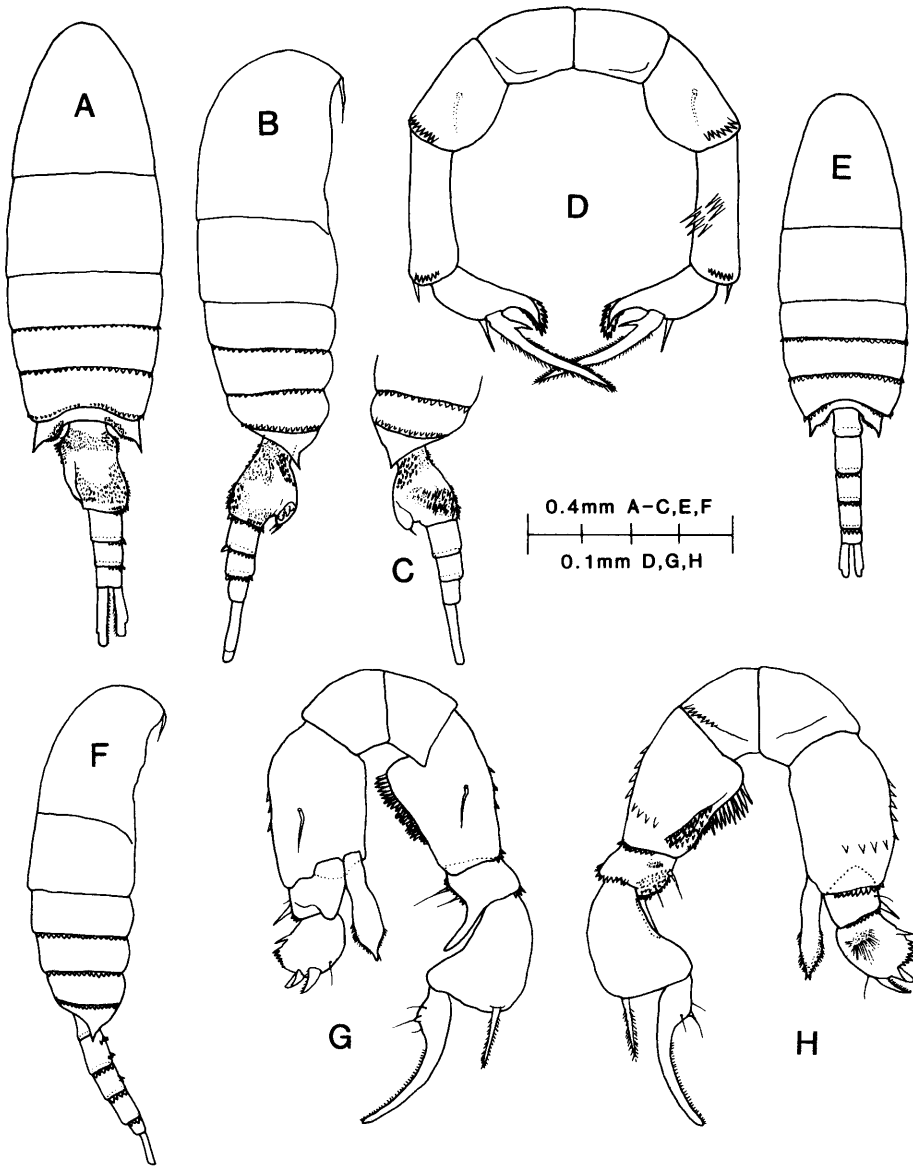


Figure 14. *Pseudodiaptomus acutus* (Dahl). A-D, adult female: A, dorsal view; B, lateral view right side; C, lateral view of Ur left side; D, anterior view of P5. E-H, adult male: E, dorsal view; F, lateral view right side; G, posterior view of P5; H, anterior view of P5.

variants (Fig. 15A-C) appeared identical to the normal male (0.93-0.95 mm) except that they were larger (1.10-1.18 mm) and the P5 more than twice as large with the following differences: i) Right B2 proximomedial margin not enlarged, with B2 and Re1 medial margin produced into knob. ii) Re2 greatly enlarged laterally. iii) Re3 with medial protrusions. iv) Left B2 with medial spinule row and Ri stouter. v) Left Re2 turned laterally with smaller distomedial spine. The

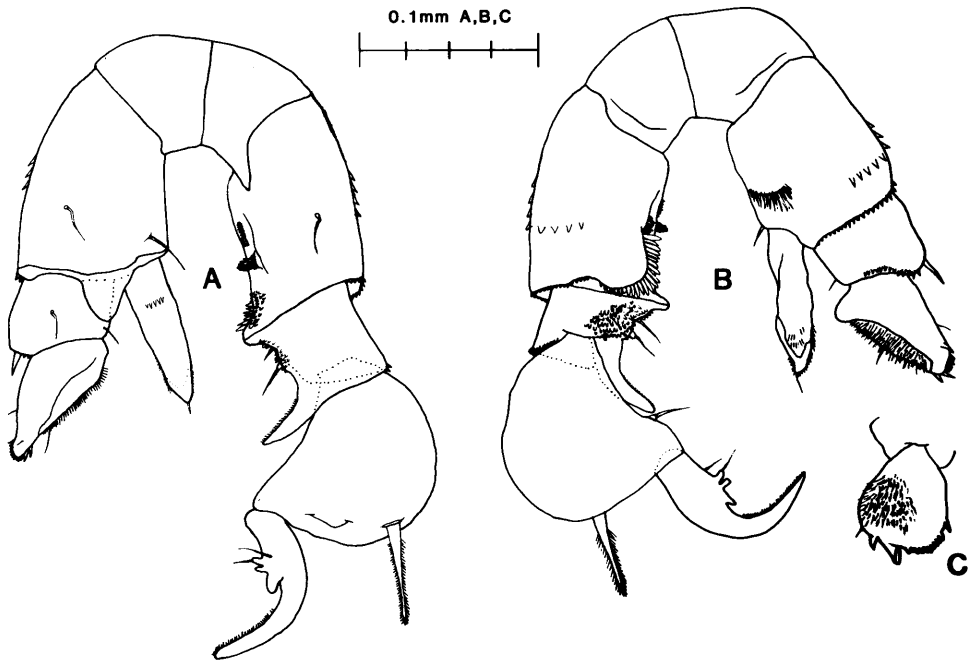


Figure 15. *Pseudodiptomus* cf. *acutus*. A-C, adult male P5: A, posterior view; B, anterior view; C, lateral view of left Re2.

large atypical males, as also noted in the *P. wrighti* variants, do not appear to be intersex specimens. Therefore, I have assigned these males as *P. cf. acutus* until such a time as additional material becomes available for study.

The range of *P. acutus* has been extended to the Caribbean Island arc with its report from Jamaica, and in this report from Surinam and Venezuela, south to Brazil.

Pseudodiptomus richardi (Dahl)

Figure 16A-L

Weismannella richardi Dahl, 1894: 20, pl. 1, figs. 6-8.

Schmackeria richardi Poppe and Mrázek, 1895: 127.

Pseudodiptomus richardi Giesbrecht and Schmeil, 1898: 64.—Mrázek, 1901: 14, pl. 1, fig. 14, pl. 2, fig. 39.—Pesta, 1927: 71, fig. 2b-d.—Marsh, 1933: 39, pl. 20, figs. 1, 3.—Brehm, 1965: 3, 8, 12.—Wright, 1936: 6-10, pl. 1, fig. 9, pl. 2, figs. 1-3.—1937: 159-161, pl. 1 fig. 5.—Carvalho, 1945: 96, pl. 8, fig. 8.—Björnberg, 1963: 46.—1981: 645, fig. 216(1).—Owre and Foyo, 1967: tbl. 6.—Cipólli and Carvalho, 1973: 100.—Montú, 1980: 57, 60, tpls. 1-3.—Prado-Por and Lansac-Tôha, 1984: 148-149, tbl. 1.—Reid and Esteves, 1984: 310, 311, 315, 317.—Dussart, 1984: 63.—Montú and Goeden, 1986: 77, fig. 24d-h.

Pseudodiptomus richardi inaequalis Brian, 1926: 187-188, figs. 15-16.—Ringuelet, 1958: 56.—Cicchino, 1975: 37-49, figs. 1-63.

Pseudodiptomus richardi emancipans Brehm, 1957: 53-58, figs. 64-66.

Pseudodiptomus cristobalensis Carvalho, 1952: 146-147, pl. 1, fig. 22 (not figs. 25-27).

Material.—ARGENTINA: Rio de la Plata, Rio Terito, near Tigré, coll. by S. Wright, 26 Nov 1936, USNM 92963, 4f, 5m; Balneario, Quilmes, Lago Artificial, coll. by S. Wright, 01 Jan 1937, USNM 233581, 21f, 9m. BRAZIL: *Pará State*, Belem, Baía de Marajó, coll. by M. L. Carvalho, 06 Jun 1984, USNM 233582, 6f, 11m; Bujarú, Rio Guama, coll. by M. L. Carvalho, 17 Dec 1983, USNM 233585, 2m; *Sergipe State*, Sergipe River, coll. by C. da Rocha, 22 Sep 1977, USNM 233578, 10f, 8m; Piavi

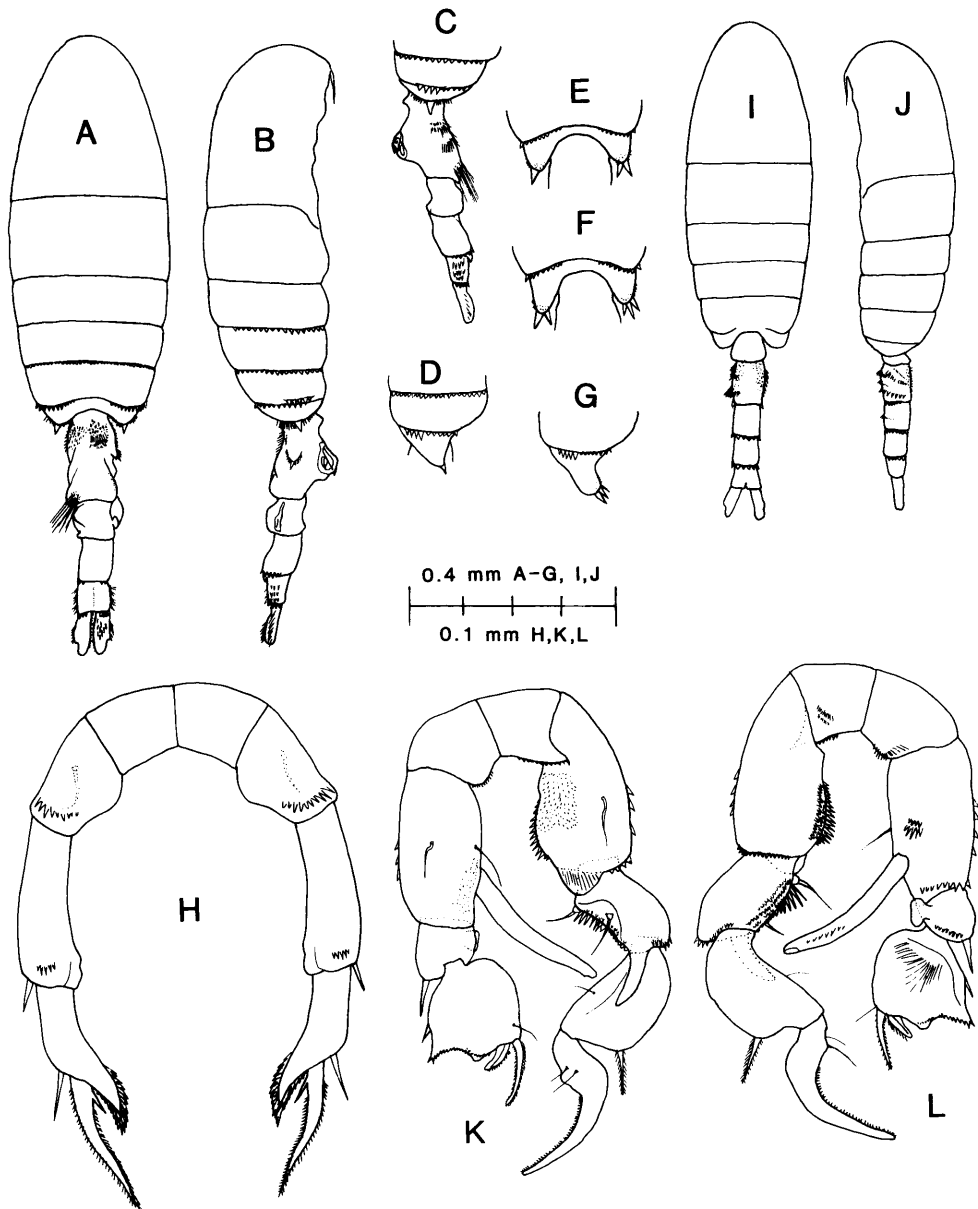


Figure 16. *Pseudodiaptomus richardi* (Dahl). A-H, adult female: A, dorsal view; B, lateral view right side; C, lateral view of Ur left side; D-G, variations of Pdg5 corners; D, G, lateral view left side; E, F, dorsal view; H, anterior view of P5. I-L, adult male: I, dorsal view; J, lateral view left side; K, posterior view of P5; L, anterior view of P5.

River, coll. by S. A. do Nascimento, 18 Aug 1981, USNM 233580, 1m; *Rio de Janeiro State*, Lagoa Coca-Cola, Iodada, 22°13'S 041°33'W, coll. by F. A. Esteves, 27 Feb 1985, USNM 233586, 3f, 1m. *São Paulo State*, Una do Prelado River, coll. by F. A. Tôha, 29 Dec 1982, USNM 233579, 15f, 15m; Jureia, coll. by M. S. Prado-Por, 10 Dec 1984, USNM 233584, 4f, 4m; *Santa Catarina*, Santa Catarina Island, Lagoa da Conceicao, coll. by M. Jones and T. P. Lowe, 17 Nov 1965, USNM 113704, 1m;

Rio Grande do Sul State, Lagoa dos Patos, coll. by G. Y. Shimizu, 08 Apr 1984, USNM 233583, 1f, 3m;

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	20	1.13–1.60	1.38	0.94	0.50	1.9:1
Male	20	0.92–1.23	1.08	0.71	0.40	1.8:1

Description.—Female (Fig. 16A–H): Pdg2 with posterolateral scale row, Pdg3–4 scale row extends dorsad, Pdg4 with four to six larger lateral scales. Pdg4–5 separate, Pdg5 corners small and rounded to large and lobate, with one to three posterior spines varying in size (Fig. 16A–G). Urosome with four segments. Ur1 asymmetrical, anterodorsal hair and fine spinule patches, left posterodorsal corner set with long hairs, right lateral protrusion at midlength with small spinules; genital boss enlarged. Ur2 anterodorsal margin dorsally depressed, right lateral surface indented forming knob-like process, left lateral indented at midlength. Ur3 with posterolateral scale row extending slightly dorsad. Ur4 with fine lateral spinule rows. CR symmetrical, 3× longer than wide with dorsal spinules on right ramus. Ur segments and CR with proportions 36:17:17:14:16 = 100.

Female P5 (Fig. 16H): Ratio Re2:Re3 = 1:1.1

Male (Fig. 16I–L): Pdg4–5 partially fused, Pdg5 corners somewhat rounded. Ur2 left ventral surface with two spinule rows extending laterad, right side with hair and fine spinules, posterior scale row not complete dorsally. Ur3 with one ventral spinule row. Ur segments and CR with proportions 16:22:18:16:12:16 = 100.

Male P5 posterior view (Fig. 16K): Right leg, B1 medial margin lined with small spinules, and pointed distomedial corner. B2 with proximal fine surface hair patch and enlarged, striated, hyaline distomedial corner. Re1 with medial papilla and seta, and spiniform process at distomedial corner. Left leg, B2 with medial seta and scattering of fine distomedial hairs. Re2 quadrate, with lateral spine, pointed distolateral corner, spinule comb row, small distal knob, one seta, and two hirsute distomedial spines, medial spine longer. Anterior view (Fig. 16L): Right leg, B1 with subapical spinules. B2 medial margin with spinule rows. Left leg, B1 with fine medial hairs that extend from medial margin. B2 with small medial spinule patch. Ri long and narrow. Re1 medial surface with knob-like protrusion.

Remarks.—Since Dahl's creation of *P. richardi*, two subspecies were established (*P. richardi emancipans* and *P. richardi inaequalis*) to account for variations noted in Argentine specimens (Brian, 1926; Brehm, 1957). The division into subspecies was based on the larger body size of females, larger Pdg5 corners with several spines, and differing sizes of egg sacs. Ringuelet (1958) synonymized *P. richardi emancipans* with *P. richardi inaequalis*: this was supported by Cicchino (1975). After a thorough examination of males and females from waters of northern Brazil to Argentina, I am able to further synonymize the latter with *P. richardi* (s. str.). Variation among female characters is present, with female Pdg5 corners being small and rounded (with one posterior spine) in northern Brazil to large and lobate (with two or three posterior spines) in southern Brazil and Argentina (Fig. 16A–G); no obvious variation in egg sac size was noted. Concurrently, body size also increased as latitude increased with the following mean sizes noted: Brazil; Belem (F = 1.14 mm, M = 0.95 mm), Sergipe River (F = 1.20 mm, M = 0.96 mm), Rio de Janeiro and São Paulo (F = 1.38 mm, M = 1.08 mm), Argentina; Rio de la Plata (F = 1.55 mm, M = 1.22 mm). In all cases males varied only in body size, with the P5 and other characters remaining identical. The lack of variation

among males, and the minor variation of Pdg5 corners among females, does not support the separation into subspecies by previous authors.

The report of *P. cristobalensis* from Brazil (Carvalho, 1952) is in error, as it is obviously a misidentification of *P. richardi*. In addition, Carvalho mistakenly referred the latter male P5 to figure 27 instead of the correct figure 22, and transposed both the left and right rami of the male P5. Finally, his drawings (figs. 25–26) indicate a *P. richardi* male with acute Pdg5 corners which is incorrect for this species.

Pseudodiptomus richardi is most closely related to *P. acutus*, but is easily distinguished from the latter by: i) Female and male Pdg5 corners not acutely pointed. ii) Female CR short, wide and symmetrical. iii) Female P5 Re1 lack spinules on left anterior surface. iv) Male Ur2 heavily spinulated. v) Male P5 Ri long and narrow, left Re1 with medial knob-like process, and left Re2 large and square-shaped with long distomedial spine.

The range of this species is known to extend from Belem, Pará State, in northern Brazil, south to the Rio de la Plata, Buenos Aires Province, Argentina.

Pseudodiptomus sp.

Figure 17A–C

Material.—COSTA RICA: Gulf of Nicoya, Pajaro Beach, coll. by Scripps Inst. Oceanography, 09 Dec 1953, 1f.

Sex	No.	Length	\bar{x}	Pr \bar{x}	Ur \bar{x}	Pr:Ur
Female	1	1.02	1.02	0.68	0.38	1:1.8

Description.— Female (Fig. 17A–C): Pdg3–4 posterior margins with lateral scales that extend dorsad. Pdg4–5 separate, Pdg5 corners rounded with fine hairs. Uro-some with four segments. Ur1 slightly asymmetrical, swollen at midlength, with dorsal surface hair row; right lateral with hair patch, left lateral with strong spines extending dorsad. Ur3 posterodorsal margin asymmetrical and overlaps onto Ur4 which has lateral spinules. CR slightly asymmetrical with right rami 4× and left 3.5× longer than wide. Ur segments and CR with proportions 31:17:21:10:21 = 100.

Female P5 (Fig. 17C): Re1 distomedial corners enlarged. Ratio Re2:Re3 = 1:2.

Remarks.— This female was found in a collection with *P. wrighti*. It is obviously not a member of the *acutus*-subgroup, as the Pdg5 corners are rounded and the CR are somewhat long and asymmetrical. No males other than *P. wrighti* were encountered in this sample. Unfortunately, this specimen was lost during preparation. This female does not resemble any of the *pelagicus*-subgroup females and is probably new and therefore must wait for a male in order to be described.

Additionally, an unidentified male was observed in samples from the Panama Canal. Its P5 closely resembles that of *P. cristobalensis*. Unfortunately this specimen also was lost during preparation before any preliminary drawings had been made. I feel that future collections from that area will reveal at least one new species.

Pseudodiptomus marinus Sato

This species described by Sato (1913) has been recently introduced from Japanese coastal waters into southern California waters near San Diego (Fleminger and Kramer, 1988). These authors noted the absence of the expected endemic

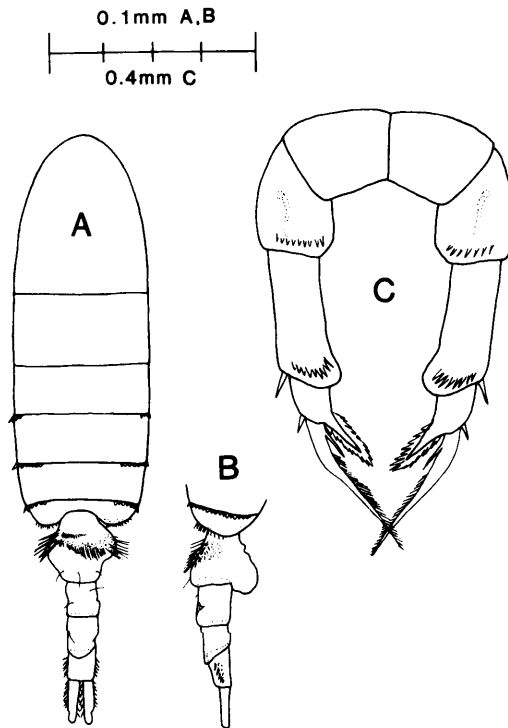


Figure 17. *Pseudodiaptomus*. A–C, adult female: A, dorsal view; B, lateral view of Ur right side; C, anterior view of P5.

P. euryhalinus in their collections. For a complete description and discussion of *P. marinus*, refer to Fleminger and Kramer (1988) and Walter (1986a).

SPECIES RELATIONSHIPS AND DISTRIBUTION

A recent review of south Indo-West Pacific pseudodiaptomids resulted in five new species (Walter, 1987) and brought to 72 the number of known species in the genus. However, with the 3 synonymies presented herein, plus the 2 new species, the number of species is now reduced to 71. Over the years several authors have attempted to divide this large genus into appropriate species groups (Pillai, 1980; Grindley, 1984; Walter, 1986a; 1986b).

In reviewing American species of *Pseudodiaptomus*, Wright (1937) proposed the establishment of the Americanus species group and presented a hypothetical family tree. He also noted that this group may further be divided into two subgroups, a decision supported by Johnson (1948). Wright did not name the subgroups and based his division only on the male P5 right Re1 spiniform process which proves inadequate to accurately divide all American species. The difficulty in using females to designate subgroups is compounded, since most female P5 appear identical, except for *P. acutus* and *P. panamensis*, thereby making integration into groups impossible. The only other female feature which could be used to differentiate species would be urosome segment number. Unfortunately, females with four-segmented urosomes occur in both subgroups and oceans. At least 15 species are now known from both American continents. The members of the Americanus

Table 1. American *Pseudodiptomus* species group and species subgroup assemblages. F = Reported from freshwater habitats; U = Specimens deposited at USNM; A = Atlantic Ocean species; P = Pacific Ocean species; Ur = Number of female urosomal segments

	F	U	A	P	Ur
Nudus					
1) <i>P. gracilis</i> (Dahl, 1894)	+	+	+	-	4
Americanus					
"acutus-subgroup"					
2) <i>P. acutus</i> (Dahl, 1894)	-	+	+	-	4
3) <i>P. cristobalensis</i> Marsh, 1913	-	+	-	+	?
4) <i>P. galapagensis</i> Grice, 1964	-	+	-	+	4
5) <i>P. richardi</i> (Dahl, 1894) [= <i>P. richardi inaequalis</i> Brian, 1926]	+	+	+	-	4
6) <i>P. wrighti</i> Johnson, 1964 [= <i>P. acutus</i> var. <i>leptopus</i> Loeffler, 1963]	-	+	-	+	4
"pelagicus-subgroup"					
7) <i>P. cokeri</i> Gonzalez and Bowman, 1965	-	+	+	-	4
8) <i>P. culebrensis</i> Marsh, 1913	-	+	-	+	3
9) <i>P. euryhalinus</i> Johnson, 1939	-	+	-	+	2
10) <i>P. longispinosus</i> sp. nov.	-	+	-	+	4
11) <i>P. marshi</i> Wright, 1936	-	+	+	-	3
12) <i>P. panamensis</i> sp. nov.	-	+	-	+	3
13) <i>P. pelagicus</i> Herrick, 1884 [= <i>P. americanus</i> Wright, 1937 and <i>P. coronatus</i> Williams, 1906]	-	+	+	-	3
14) <i>P. sp.</i> (female)	-	-	-	+	4
Ramosus					
"hickmani-subgroup"					
15) <i>P. marinus</i> Sato, 1913	-	+	-	+	4

species group are divided into two subgroups based on a combination of male and female characters as follows, with the species listed in Table 1. The recently introduced species *P. marinus* is included, but is not a member of the Americanus group.

NUDUS SPECIES GROUP. Lateral head horns. Female with rounded Pdg5 corners and a single egg sac. Male P5 without right or left Ri.

AMERICANUS SPECIES GROUP. Female urosome composed of two to four segments. Egg sacs paired, P5 with anterior spinule row on B2 and Re1. Male P5 lacks right Ri, left Ri simple and typically digitiform, right Re1 and left Re2 variable. a) *pelagicus*-subgroup: Female Pdg5 corners rounded, CR typically long and asymmetrical. Male Pdg5 corners rounded, P5 left Re2 spatulate or elongate, right Re1 with lateral spiniform process. b) *acutus*-subgroup: Female Pdg5 corners pointed, CR typically short and symmetrical. Male Pdg5 corners pointed or rounded, P5 left Re2 oval or rounded, right Re1 with medial spiniform process.

RAMOSUS SPECIES GROUP. (introduced) Female P5 Re1 without anterior surface spinule row. Male P5 with both left and right Ri, the right Ri variably forked.

There are eight species in the *pelagicus* and five species in the *acutus* subgroups (Table 1) composed of American members from both the Atlantic and Pacific oceans. Regarding the male P5 right Re1 spiniform process, it appears that medial rotation of the Re1 segment occurs in southern species which is characterized by this process appearing medial while in the northern species it is lateral. This rotation of the Re1 is also apparent in that the medial spinule patch and papilla

with seta appear to arise from the anterior surface rather than posterior in the southern species.

This paper clarifies the status of several species that have been wrongly identified for many years. The synonymy of *P. pelagicus*, *P. wrighti*, and *P. richardi* expands the known ranges of the species and allows for the easy identification of species. The following is a key for all American species:

KEY TO THE AMERICAN SPECIES OF *PSEUDODIAPTOMUS*

- 1a. Male P5 with left and right Ri; Female P5 lack Re1 anterior surface spinule row ... *P. marinus*
- 1b. Male P5 lacking right Ri; Female P5 with Re1 spinule row (2)
- 2a. Female with one egg sac; Male P5 lacking left Ri *P. gracilis*
- 2b. Female with paired egg sacs; Male P5 with left Ri (3)
- 3a. Head and Pdg1 fused in both sexes *P. panamensis*
- 3b. Head and Pdg1 not fused in both sexes (4)
- 4a. Female urosome composed of two segments; Male Pdg5 corners with scales *P. euryhalinus*
- 4b. Female urosome composed of three to four segments; Male Pdg5 corners lacking scales . . . (5)
- 5a. Female Pdg5 corners small and rounded without spines; Male Pdg5 corners rounded, P5 right Re1 with lateral spiniform process (6)
- 5b. Female Pdg5 corners large and pointed or rounded with spines; Male Pdg5 corners pointed or rounded, P5 right Re1 with medial spiniform process (9)
- 6a. Female urosome composed of three segments (7)
- 6b. Female urosome composed of four segments (8)
- 7a. Female Ur1 with long posterior hairs, Ur2 both margins with lateral spinules; Male P5 right B1 distomedial corner spiniform, left B1 with large medial blade-like spines *P. pelagicus*
- 7b. Female Ur1 lacking long hairs, Ur2 with right anterior cluster of several long surface spines, right CR longer than left; Male P5 right B1 distomedial corner rounded, left B1 without spines, left B2 with few small distomedial spinules *P. marshi*
- 7c. Female Ur1 lacking long hairs, Ur2 without spinules or spine cluster, left CR longer than right; Male P5 right B1 distomedial corner rounded, left B1 without spines, left B2 with many long medial spines *P. culebrensis*
- 8a. Female with long CR, Ur2 posterior margin typically with two lobes; Male P5 both legs equal in size, right Re1 with large bifid distolateral process and spine *P. cokeri*
- 8b. Female with short CR, Ur2 posterior margin without lobes; Male P5 right leg longer than left, right Re1 without bifid process or spine *P. longispinosus*
- 9a. Pacific Ocean species (10)
- 9b. Atlantic Ocean species (11)
- 10a. Female Ur1 with right lateral hirsute knob, Ur2-3 partly fused, CR naked; Male Pdg5 corners pointed, P5 left Re2 rounded with large apical spines, Ri apex pointed *P. wrighti*
- 10b. Female Ur1 without knob, Ur2-3 separate, CR heavily spinulated; Male Pdg5 rounded, P5 left Re2 oval with small apical spines, and Ri apex pointed *P. galapagensis*
- 10c. Female unknown; Male Pdg5 corners pointed, P5 about twice normal size, left Re2 oval with large apical spines, and Ri apex rounded *P. cristobalensis*
- 11a. Female Pdg5 corners pointed, CR long and asymmetrical, P5 with anterior Re1 surface spines; Male Pdg5 corners pointed, P5 left Re2 rounded with two small spines, Ri short and broad *P. acutus*
- 11b. Female Pdg5 corners rounded with varying number of spines, CR short and symmetrical, P5 lack Re1 spines; Male Pdg5 corners rounded, P5 left Re2 square-shaped with one long and short spine, Ri long and narrow *P. richardi*

The zoogeographical distribution of the species is presented in Figure 18 and amends that presented by Walter (1986b). Another review on pseudodiaptomid distribution (Grindley, 1984) also discussed the groupings and zoogeography of species, though the authors do not agree as to how to divide the species groups.

From the present study it is shown that only *P. pelagicus*, *euryhalinus* and *galapagensis* do not share their ranges with any other species. The recently introduced species, *P. marinus* (Ramosus species group) was endemic to Indo-Pacific waters (Walter, 1986a; 1987) and should not be considered a true American species. The most unusual American species, *P. gracilis*, of the Nudus species group is restricted to the Amazon brackishwater region. However, *P. clevei*, the only other member of the Nudus group, is a marine species and inhabits a wide range throughout Indo-Pacific waters (Walter, 1987).

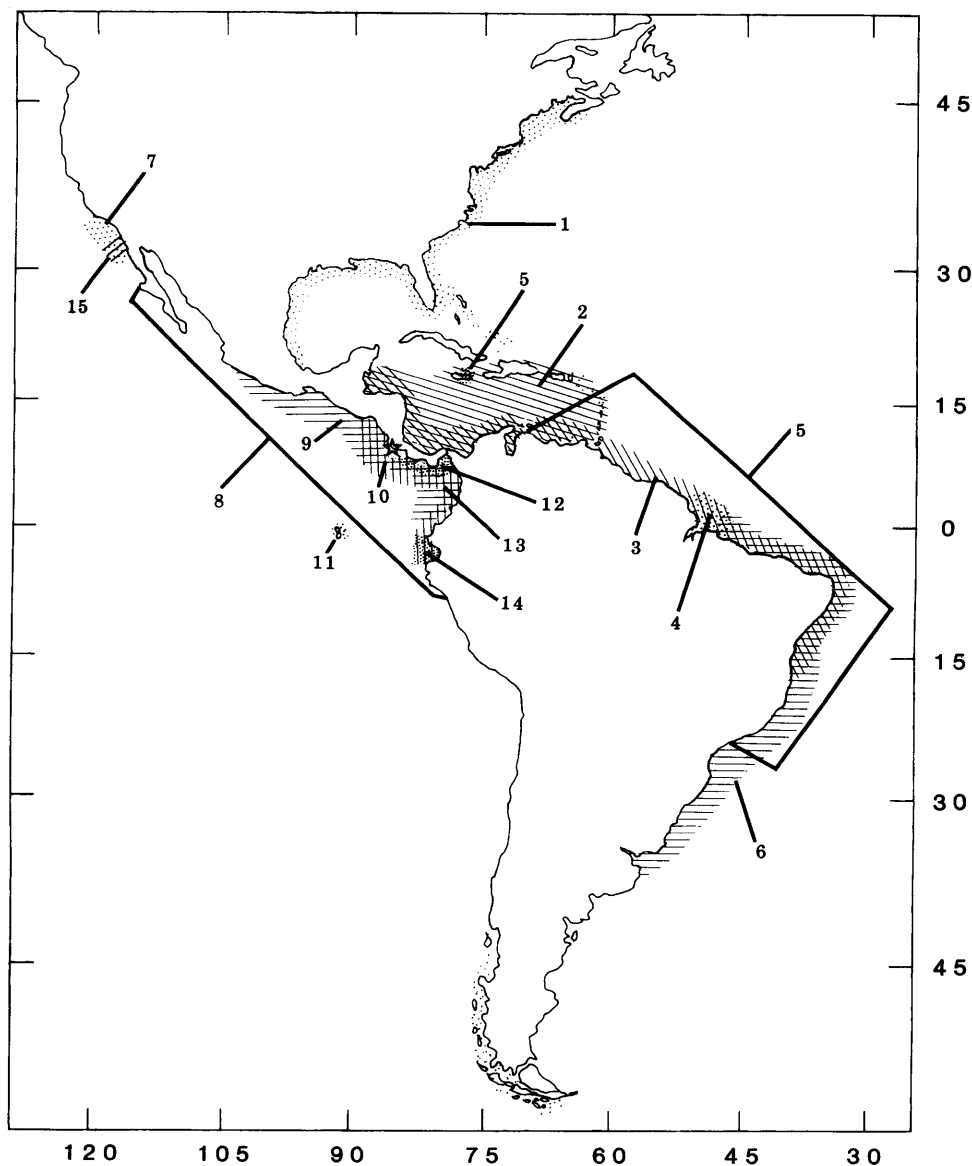


Figure 18. Map of American continents showing the zoogeography of *Pseudodiaptomus* species. The numbers correspond to the following species: (1) *pelagicus*, (2) *cokeri*, (3) *marshi*, (4) *gracilis*, (5) *acutus*, (6) *richardi*, (7) *euryhalinus*, (8) *wrightii*, (9) *culebrensis*, (10) *P. sp.*, (11) *galapagensis*, (12) *panamensis*, (13) *cristobalensis*, (14) *longispinosus*, (15) *marinus*.

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