14 October 2002
PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
115(3):650–669. 2002.

Redescription of two species of *Pseudodiaptomus* from Asia and Australia (Crustacea: Copepoda: Calanoida: Pseudodiaptomidae) with discussion of the female genital structure and zoogeography of Indo-West Pacific species

T. Chad Walter, Susumu Ohtsuka, Sumaitt Putchakarn,
Khwanruan Pinkaew, and Supawadee Chullasorn

(TCW) Smithsonian Institution, Department of Systematic Biology, Washington,
District of Columbia 20560-0163, U.S.A.;
(SO) Hiroshima University, Fishery Laboratory, 5-8-1 Minato-machi, Takehara,
Hiroshima 725 Japan;
(SP, KP) Burapha University, Institute of Marine Science, Bangsaen, Chon Buri 20131, Thailand;
(SC) Rhamkhamhaeng University, Department of Biology, Faculty of Science, Huamak,
Bangkok, 10240, Thailand

Abstract.—Many species of *Pseudodiaptomus* are known from the southeast Asia region. An ongoing review of this genus has produced 58 species from the eastern Indian Ocean and western Pacific Ocean coasts, from Japan to Australia. Range extensions for *P. ornatus* and *P. andamanensis* are noted for Australia and Japan, and for Thailand respectively. The previously unknown male of *P. ornatus* and the female genital structure of both species are described; the zoogeography of the genus is discussed.

Pseudodiaptomidae Sars (1902) contains three recognized genera, two of which are monotypic and freshwater, *Archidiaptomus aroorus* Madhupratap & Haridas, 1978 reported only from Cochin, India and *Calanipeda aquaedulcis* Kritschagin, 1873 which appears to be restricted to the European continent and Ponto-Caspian region. *Poppella guerni* Richard, 1888 and *Siatella durbini* Labbé, 1927 have been synonymized with *C. aquaedulcis.* The genus *Pseudodiaptomus* Herrick, 1884 currently consists of 74 species extending world-wide (approximately 50°N–50°S). Species are found in shallow, coastal, freshwater to hypersaline conditions, and they are demersal. *Mazellina* Rose, 1957, *Schmackeria* Poppe & Richard, 1890, *Weismannella* Dahl, 1894, and *Heterocalanus* T. Scott, 1894 are synonyms of *Pseudodiaptomus.*

Species of *Pseudodiaptomus* have very similar mouthparts; swimming legs rarely vary in shape, spination or setation and are of little use in the determination of species. The main characters used to distinguish the species are: fusion or not of the cephalosome and first pedigerous somite, shape of fifth pedigerous somite, urosome shape and ornamentation, especially the female genital double somite, and the fifth swimming leg (leg 5) of males and females.

Pseudodiaptomus ornatus and *P. andamanensis,* redescribed in this paper, belong to the Improcerus species group as defined by Walter (1986a). The left male leg 5 has a simple left endopod that is usually large and variably spatulate, while the female leg 5 basis possesses small, bluntly triangular processes at the distomedial corners. Redescriptions are necessary because *P. ornatus* (Rose 1957) was previously known only from females and *P. andamanensis* Pillai, 1980 requires a more detailed description and report of range extension. The use of the Scanning Electron Microscope (SEM) has revealed some additional fea-

tures especially for the female genital aperature structures. The collections of demersal plankton from Japan and Thailand, from Australia and from the Philippines provide specimens for this research, as well as for several new species to be described in subsequent papers.

The United States National Museum is abbreviated USNM. All measurements were done with a calibrated ocular micrometer in millimeters. Morphological terminology basically follows that of Huys & Boxshall (1991). Prosome length was measured laterally from the cephalon to the posterior margin of the prosome, and urosome length was measured from the insertion point to the distal tip of the caudal rami. Because the posterior corners of the fifth pedigerous somite overlap the prosome-urosome articulation, total length may be less than combined lengths of prosome and urosome. Mouthparts and swimming legs 1–4 are not described because they do not differ from those reported by Reddy & Radhakrishna (1982), Nishida (1985), Walter (1986a) and Soh et al. (2001).

General description of the species.—The following characteristics are common to both species. Cephalosome separate from first pedigerous somite, somites 4–5 completely fused dorsally, with posteriorly directed processes on each side of the articulation between prosome and urosome. Male fused somite with rounded posterior corners. Female urosome comprised of 4 somites, the first to third with row of small dorsoposterior scale-like spines, genital double somite ventral surface with paired genital flaps, spinule rows anterior to gonopore, pair of posterior spinulose hair-sensillae, and pair of fine setae. Genital double somite without seminal receptacles, with 1 or 2 pairs of hair-sensillae present ventrolaterally. Single egg sac. Male urosome of 5 somites, the second to fourth with row of small dorsoposterior scale-like spine rows.

Female and left male antennule with 21 segments; male right antennule with 20 segments, segment 6 is a compound segment with a suture visible (Fig. 5E). Female and left male antennule, segment 19 has a modified "barbed seta" which is a heavily chitinized spine, serrate along distal half and extending to almost the tip of segment 21 (Fig. 5F). Armature elements for segments 1–13, 16, 20, 21 as follows [segment number = seta(e) number + (spine or process)]: 1 = 3, 2 = 3, 3 = 3 + (1 rudimentary), 4–5 = 3, 6 = 3 + (1 spiniform), 7–8 = 2, 9 = 2 + (1 spiniform), 10–16 = 2, 17–18 = 1, 19 = 1 + (1 distally serrate spiniform), 20 = 1 + (1 rudimentary), 21 = 6 with aesthetasc. Male right antennule: 7–9 segments irregularly modified, geniculation between 17–18 segments. Armature elements as follows: segments 1–3, 6, 8–13, 15, 19–20 with aesthetasc. 1 = 2 + (1 rudimentary), 2 = 3, 3 = 2, 4 = 1, 5 = 3 + (1 rudimentary), 6 = 3, 7 = 1 + (1 spiniform), 8–10 = 2, 11–12 = 2 + (1 spiniform), 13 = 2, 14–15 = 2 + (1 spiniform), 16 = 1 + (1 process), 17 = 1 + (comb-row process, Fig. 4A), 18 = 2 + (1 rudimentary, 1 large spiniform), 19 = 2 + (2 rudimentary), 20 = 6. Proximal spiniform seta on 12th segment recurved, reaching distal margin of segment 13.

Female leg 5 both coxae fused with intercoxal sclerite to form a common base (anterior surface with proximal setae), basis asymmetrical with 2 pairs of small surface setae and one large setulose seta. Exopods 3-segmented, segments 1–2 with distolateral spine, segment 1 with 2 pairs of small surface setae, and medial surface lined with fine setules. Segments 2–3 acutely produced distally, segment 2 with pair of fine surface setae, segment 3 spine-like with small proximomedial process, all fringed with setules. Male urosome of 5 somites, somites 2–4 with row of small posterodorsal, scale-like spine rows. Male leg 5 asymmetrical, in posterior view coxae and intercoxal sclerite fused to form common base, distomedial corners acute, (anterior surface with proximal setae). Basis with 2 small surface setae, one large setulose seta and lateral spinule row that continues onto anterior surface at mid-length (both legs with

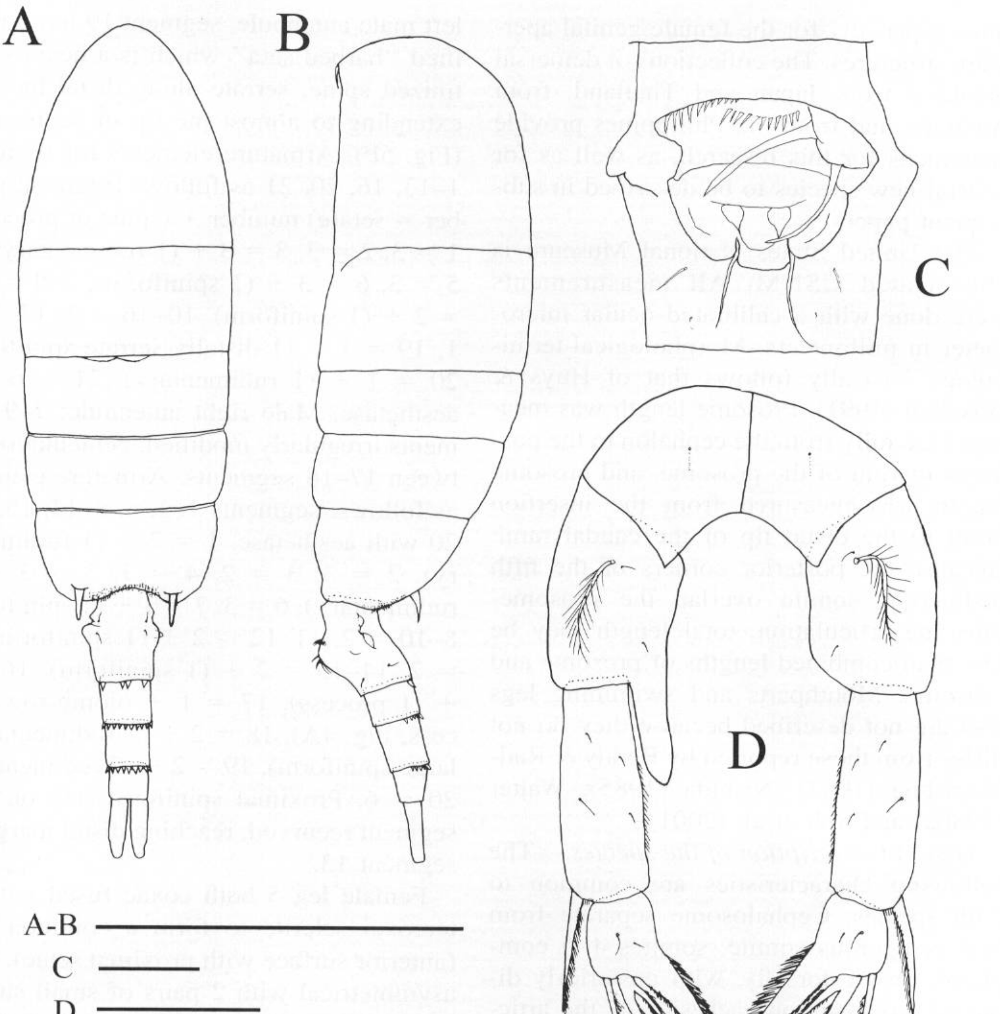

Fig. 1. *Pseudodiaptomus ornatus*, female (A–D). A, Habitus, dorsal view; B, Habitus, left lateral view; C, Genital double somite, ventral view; D, Leg 5, posterior view. Scale bars: A–B, scale = 1.0 mm, C–D, scale = 0.1 mm.

anteriorly inserted endopods). Right endopod short with terminal seta and left endopod larger with variable shape. Right leg: 3-segmented exopod, segment 1 with acutely produced distolateral margin and 3 surface setae, segment 2 with distolateral spine and 2 surface setae, segment 3 simple, proximal end swollen medially, curved and setulose, with 2 proximal surface setae. Left leg: 2-segmented exopod, segment 1 with large elongate distolateral spine and 2 small surface setae, segment 2 large, variably shaped, with lateral spine and 6–8 surface setae (anterior surface with fine spinule patches).

Pseudodiaptomus ornatus (Rose, 1957)

(Figs. 1A–D, 2A–E, 3A–B, 4A–C)

Mazellina ornata Rose, 1957:332–336, figs. 10–12 (female only).

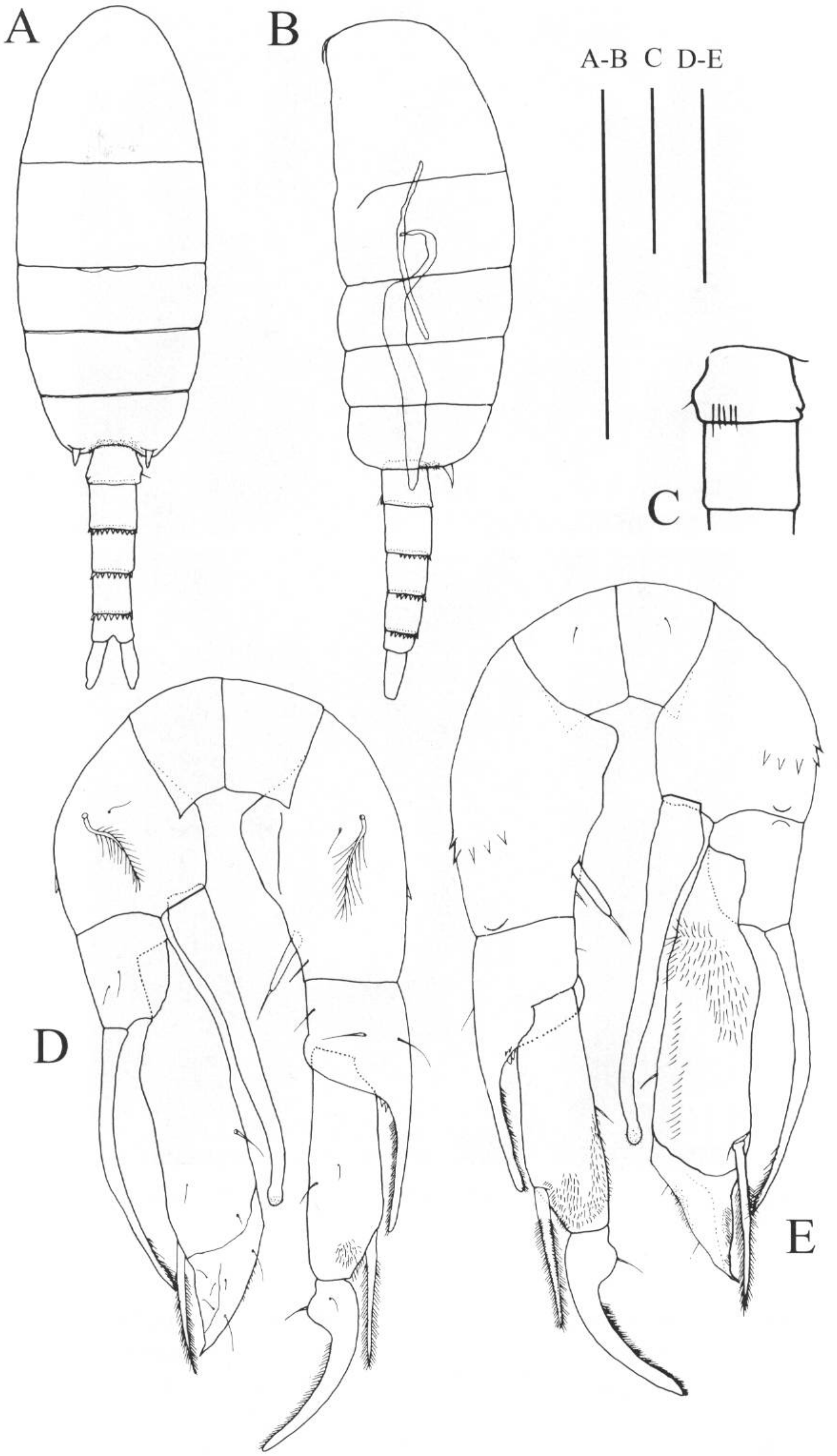

Fig. 2. *Pseudodiaptomus ornatus,* male (A–E). A, Habitus, dorsal view; B, Habitus, left lateral view; C, Urosomites 1–2, ventral view; D, Leg 5, posterior view; E, Leg 5, anterior view. Scale bars: A–B, scale = 1.0 mm, C, scale = 0.5 mm, D–E, scale = 0.1 mm.

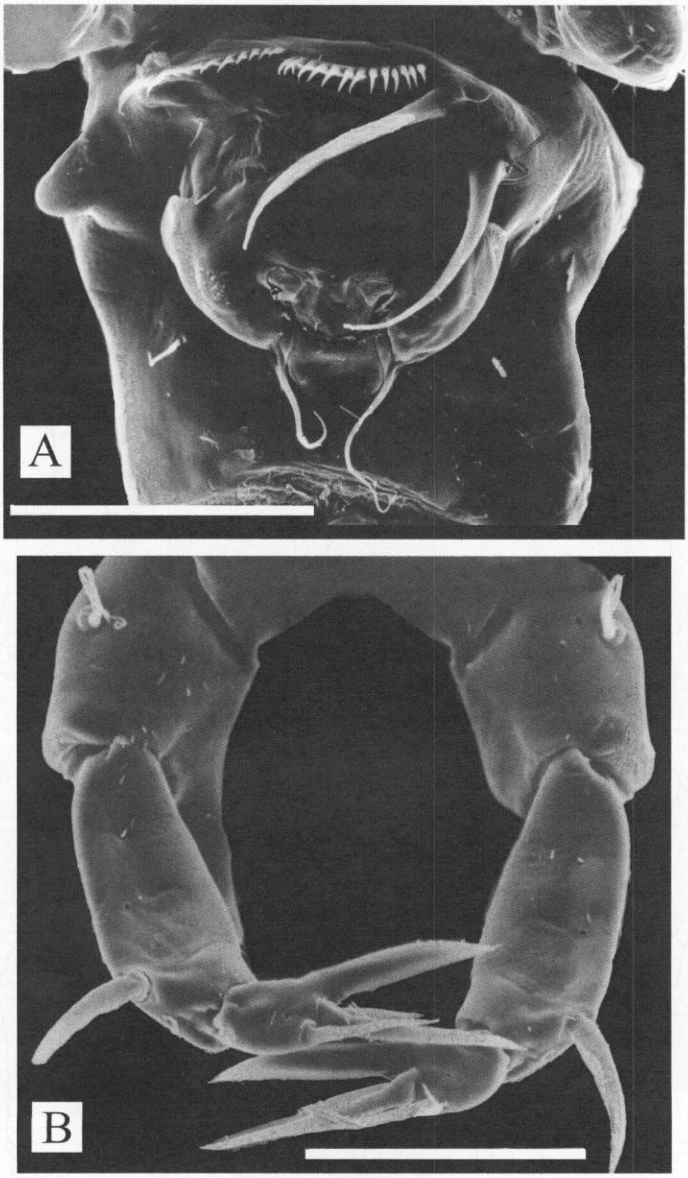

Fig. 3. *Pseudodiaptomus ornatus,* female (A–B). A, Genital double somite, ventral view; B, Leg 5, posterior view; Scale bars: A–B, scale = 0.1 mm.

Pseudodiaptomus ornatus Walter, 1986a: 141–142, fig. 5A–D (female only).

Pseudodiaptomus trispinosus Walter, 1986a:142–144, fig. 6E–I (male only), [new synonomy].

Material.—*P. ornatus* North Pacific Ocean, Japan, Okinawa Islands, Kerama Retto, Agenasiku Island, coll. by S. Ohtsuka, 4–9 m, 20 May 1989, USNM 250697, 22 females, 29 males; Okinawa Islands, Aguni Island, coll. by S. Ohtsuka, 9–12 m, 30 May 1999, USNM 288078, 2 females, 1 male; Okinawa Islands, Aguni Island, coll. by S. Ohtsuka, 9–12 m, 30 May 1999, USNM 309756, 1 male; Philippines, Luzon Island, Quezon province, Tayabas Bay, Pa-

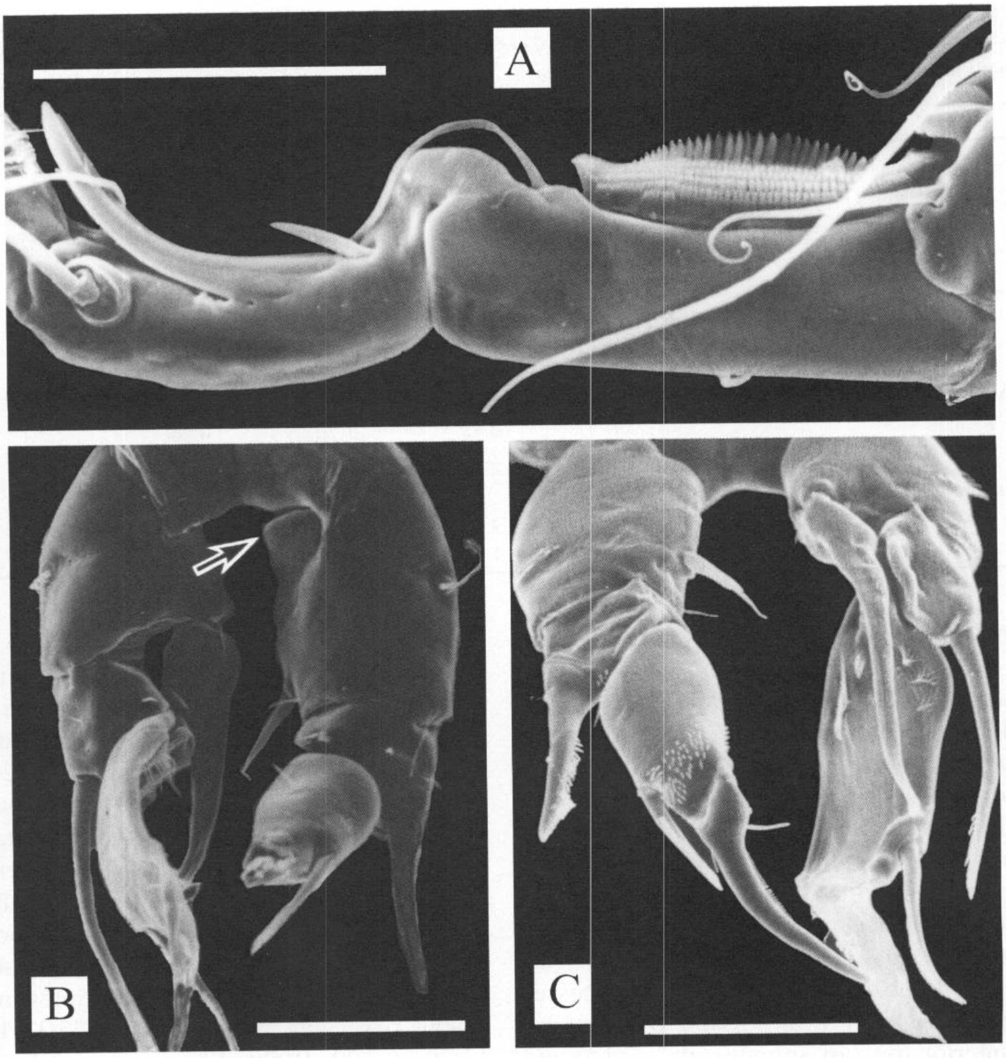

Fig. 4. *Pseudodiaptomus ornatus,* male (A–C). A, Antennule at geniculation of segments 17–18; B, Leg 5, posterior view, arrow indicates produced right basis proximomedial corner; C, Leg 5, anterior view. Scale bars: A, scale = 0.05 mm, B–C, scale = 0.1 mm.

dre Burgos, 13°53′N 112°47′E, coral reef, coll. by T. C. Walter, 3 m, 10 January 1981, USNM 210656, 1 female; USNM 210657, 2 females (leg 5 on slide); South Pacific Ocean, Australia, Queensland, Great Barrier Reef, Davies Reef, coll. by A. D. McKinnon, 8 m, 01 December 2000, USNM 310675, 2 females, 2 males. *Pseudodiaptomus trispinosus,* North Pacific Ocean, Philippines, Luzon Island, Quezon province, Padre Burgos, coll. by T. C. Walter, 3 m, 7–10 January 1981, USNM 210660, 1 male, holotype, USNM 210662, 3 males, paratypes.

Description.—Female (Figs. 1A–D, 3A–B, Table 1). Additions to Walter's (1986a) description as follows. Genital double somite asymmetrical with 2 pairs of dorsal setae, right anterolateral surface slightly produced forming a knob-like process at midlength, left anterolateral surface more strongly produced with a double knob-like process extending onto dorsal surface and forming U-shaped cleft between knobs

Table 1.—Body measurements of *P. ornatus* and *P. andamanensis*. (No. = number of specimens measured, x̄ = average length of individuals measured, Pr x̄ = prosome, average length in (mm), Ur x̄ = urosome, average length in (mm), Pr : Ur = prosome : urosome ratio.

Sex	No.	Length (mm)	x̄	Pr x̄	Ur x̄	Pr : Ur
P. ornatus						
Okinawa						
Female	22	2.30–2.38	2.34	1.62	0.75	2.1:1
Male	29	1.95–1.99	1.97	1.30	0.60	2.2:1
Philippines						
Female	3	2.10–2.32	2.20	1.58	0.73	2.1:1
Male	4	1.86–1.90	1.88	1.28	0.58	2.2:1
Australia						
Female	2	2.40–2.50	2.45	1.70	0.78	2.2:1
Male	2	2.02–2.10	2.06	1.48	0.66	2.2:1
P. andamanensis						
Female	1	2.19	2.19	1.50	0.72	2.0:1
Male	1	1.80	1.80	1.24	0.60	1.9:1

(knobs and cleft absent on swollen process of Australian specimens), 2 pairs of dorsoanterior setae and 3 lateral setae on each side. Posterodorsal margin of somite with incomplete row of small triangular scale-like spines on specimens from Japan and Philippines; Australian specimens with a complete row of spines and additionally, urosomite 2 with an incomplete spine row. Ventral surface of genital double somite, left side (Figs. 1C, 3A) with 2 medially directed, large, curved spiniform processes protruding from swelling above gonopore, 2 anterior rows of spinules, on medial and on right side, and a slightly asymmetrical pair of posteriorly directed lamelliform processes at base of paired gonopores, left process slightly longer. Urosomites and caudal rami with proportions 30:15:20:13:22 = 100. Antennule as in *P. andamanensis* (Fig. 5E) except without fine anterior spinules on segment 1. Leg 5 slightly asymmetrical, posterior view (Figs. 1D, 3B), with distomedial corners of coxae acute, distomedial corner of left basis produced distally to form an elongate process, distomedial corner of right basis rounded. Exopod segment 1 (left and right) medial margin lined with fine setules and 2–3 small distolateral spinules between spine and exopod segment 2.

Male: (Figs. 2A–E, 4A–C, Table 1). Body similar to that of female. Urosomite 1, right lateral surface slightly produced at midlength with single seta, ventral surface with several fine posterior setae (Fig. 2C) on right side only on specimens from Japan; specimens from Philippines with 3 setae, setae lacking on the Australian specimens. Length of spermatophore more than half the length of prosome. Urosomite 4 with posterodorsal spine row incomplete ventrally as in original description. Urosomites and caudal rami with proportions 11:22:18:18:11:20 = 100. Right A1 armature at geniculation shows modified comb-row process on segment 17, anterior surface with small proximal and large distal curved spiniform processes on segment 18 (Fig. 4A).

Leg 5, posterior view (Figs. 2D, 4B), right leg, basis with proximomedial corner largely produced with small distomedial seta, endopod anteriorly placed (Figs. 2E, 4C), short, digitiform, tapering distally with terminal spiniform setule. Exopod segment 1, distolateral corner produced distally reaching base of lateral spine of segment 2, armed with several small spinules proximally and medially setulose. Segment 2 with distolateral patch of fine surface spinules. Left leg, proximomedial corner of basis rounded with endopod anteriorly placed (Figs. 2E, 4C), proximally swollen, long, tapering distally, with few fine spinules at rounded apex, reaching ¾ the length of second exopodal segment. Exopod segment 1, small, triangular with lateral spine elongate and distally directed, with fine setules along distomedial margin. Segment 2 elongate with 8 surface setae and distolateral spine, distal third of segment hyaline in appearance marked by distal line (Fig. 2D,E). This segment variably shaped depending on view, in lateral view appears medially curved (Fig. 4B) from proximal end to midlength.

Remarks.—Rose (1957) established the new genus and species *Mazellina ornata* collected from Vietnam, based on his observations of the modified setae on the distal segments of the maxilliped. These modified setae are not unique to this genus and species, but are present in all species of the genus *Pseudodiaptomus.* The species was based only on the female. Rose reported females of 2.00 mm in length, which is slightly smaller than the size of specimens in this paper which ranged from 2.10–2.50 mm; the largest specimens are from Australia. Amendments to the redescription of *P. ornatus* by Walter (1986a) are as follows: ventral surface of female genital double somite with recurved pair of spines arising from a process on the left side anterior to the genital aperature; posterodorsal scale-like spines incompletely developed in specimens from Japan and Philippines, but complete in Australian specimens; female leg 5 basis with triangular process on the left leg, not right as stated in Walter (1986a).

The female specimens of *P. ornatus* studied by Rose are not extant (pers. comm. Dr. R. Vaissière, Musée Océanographique, Monaco). The redescription (Walter 1986a) of *P. ornatus* was based on female specimens only. In the same paper, the closely related new species *P. trispinosus* Walter, 1986 was described based on both females and males. The co-occurrences of females and males of *P. ornatus* in the present study indicate that the female allotype of *P. trispinosus* is not conspecific with the male holotype. The USNM male holotype and female allotype of *P. trispinosus* will retain their same USNM numbers and the original name, which is now a synonym of *P. ornatus.* Future collecting in the Philippines or adjacent areas of the Indo-Pacific should result in the discovery of the male which is conspecific with the now unnamed female allotype incorrectly referred to as *P. trispinosus* in Walter (1986a).

The original description of the male of *P. ornatus* (described as *P. trispinosus* Walter, 1986a) is amended as follows: Urosomite 1 right ventral surface with row of posterior setae (not present on Australian specimens), three small posterior setae (not spines) on the right lateral surface of urosomite 1 of Philippine specimens, urosomite 1 of specimens from Japan and Australia with one right lateral seta, leg 5 coxae are without distoposterior or proximoanterior spinule rows. The range of *P. ornatus* extends from the Okinawa Islands, Japan to Queensland, Australia.

Pseudodiaptomus andamanensis Pillai, 1980

Figs. 5–8

Pseudodiaptomus andamanensis Pillai, 1980:256–260, fig. 3.—Ohtsuka et al., 2000:135–137, fig. 4.

Material.—Indian Ocean, Andaman Sea, Thailand, Ko Aew Island, Phuket Island, coll. by S. Ohtsuka, 9–13 m, 19 December 1997, coral sandy bottom, 1 female, 1 male, USNM 253015.

Description.—Female (Figs. 5A–E, 7A–C, 8A–B, Table 1) body robust, with red-colored naupliar eye. Pedigerous somite 5, posterodorsal corners acute with right lateral posterior corner slightly smaller, with 2 dorsolateral acutely pointed posteriorly directed processes, minute setules along posterodorsal margin between dorsolateral processes (Fig. 5A–B). Genital double somite (Figs. 5C, 7A–C) with acute anterodorsal process on right side, posteriorly directed reaching proximal third of somite, ventral surface with 4 rows of spinules at midlength, right posteroventral row on rounded process, asymmetrical pair of posteriorly directed lamelliform processes at base of paired gonopores located beneath the genital operculum (Fig. 7B), left process longer and thicker, and pair of posteroventral spinulose hair-sensilla (Fig. 7C). Urosomite 3 with minute posterodorsal setules. Urosomites and caudal rami in the proportions 31:18:18:11:22 = 100. Antennule (Fig. 5E) with several fine anterior spinules on segment 1. The labrum (Fig. 8A) bilobed, each lobe with relatively long setules. Leg 5, posterior view (Figs. 5D, 8B), distomedial corners of coxae slightly rounded, distomedial corner of left basis produced and bifurcate, right smooth and less produced with pair of small setae at produced corner. First exopod segment with row of fine spinules along medial margin, and triangular patch of acute spinules (Fig. 8B) at distolateral corner. Second exopod segment with proximolateral fine setules proximal to spine.

Male (Fig. 6A–B, Table 1) prosome similar to that of female, except pedigerous somite 5 with rounded posterolateral corners. Urosomites and caudal rami in the proportions 16:18:18:18:12:18 = 100. Right antennule geniculate (Fig. 6E). Leg 5, posterior view (Figs. 6C, 8C), right leg: basis with endopod inserted anteriorly (Fig. 6D), short, tapering distally with terminal spiniform setule. Exopod segment 1 quadrate, acutely produced at distal corners, with 1 distomedial spine adjacent to base of exopod segment 2, 1 medial and 2 surface setae, distolateral corner acute with small spinule. Exopod segment 2 elongate, with small medially directed spinule at midlength and 1 surface seta, distolateral spine ¾ length of segment (inserted anteriorly). Left leg: basis with anteriorly inserted endopod (Fig. 6D), bulbous at base, indented at midlength, and with distal digitform process. Exopod segment 1 triangulate with large terminal stout recurved spine strongly spinulose. Exopod segment 2 inserted anteriorly, somewhat ovate, medially directed at right angle, distally acute, with 4 triangular sclerotized medial processes, 6–7 surface setules and thickened along midlength, (anterior surface with proximolateral stout spinulose spine, proximomedial patch of fine setules, and second lateral patch along midlength).

Remarks.—Specimens collected from Phuket, Thailand, generally agree with the original description of Pillai (1980) for material from Port Blair, South Andaman Island, except as follows (descriptions in parentheses are those of Pillai). Female urosome somite 3 with fine dorsal setules (2 spines on mid-dorsal margin); anal somite without row of small triangular scale-like spines along posterior margin (with finely serrated shields, partly overlapping caudal rami anteriorly). Male genital somite smooth on left side (with small tubercle on left mid-margin); three segments of right antennule beyond geniculation (only 2 segments beyond hinge); right leg 5 endopod tapering distally, with terminal spiniform seta (bifid at tip).

Discussion

Female genital structure.—The female genital systems of calanoid copepods have recently been analysed in detail by Cuoc et al. (1989, 1997), Huys & Boxshall (1991), Ohtsuka et al. (1994), Barthélémy et al. (1998a,b), Barthélémy (1999) and Defaye et al. (2000) in order to re-evaluate the systematics, phylogeny, and evolution of the order Calanoida. Scanning electron microscopy has clearly revealed that these copepods are much more diversified than previously reported, and distinctly exhibit several evolutionary tendencies. For example, most of relatively advanced calanoids bear a single genital operculum, beneath which paired gonopores and copulatory pores are located, while the early divergent superfamily Arietelloidea shows a wide variety of

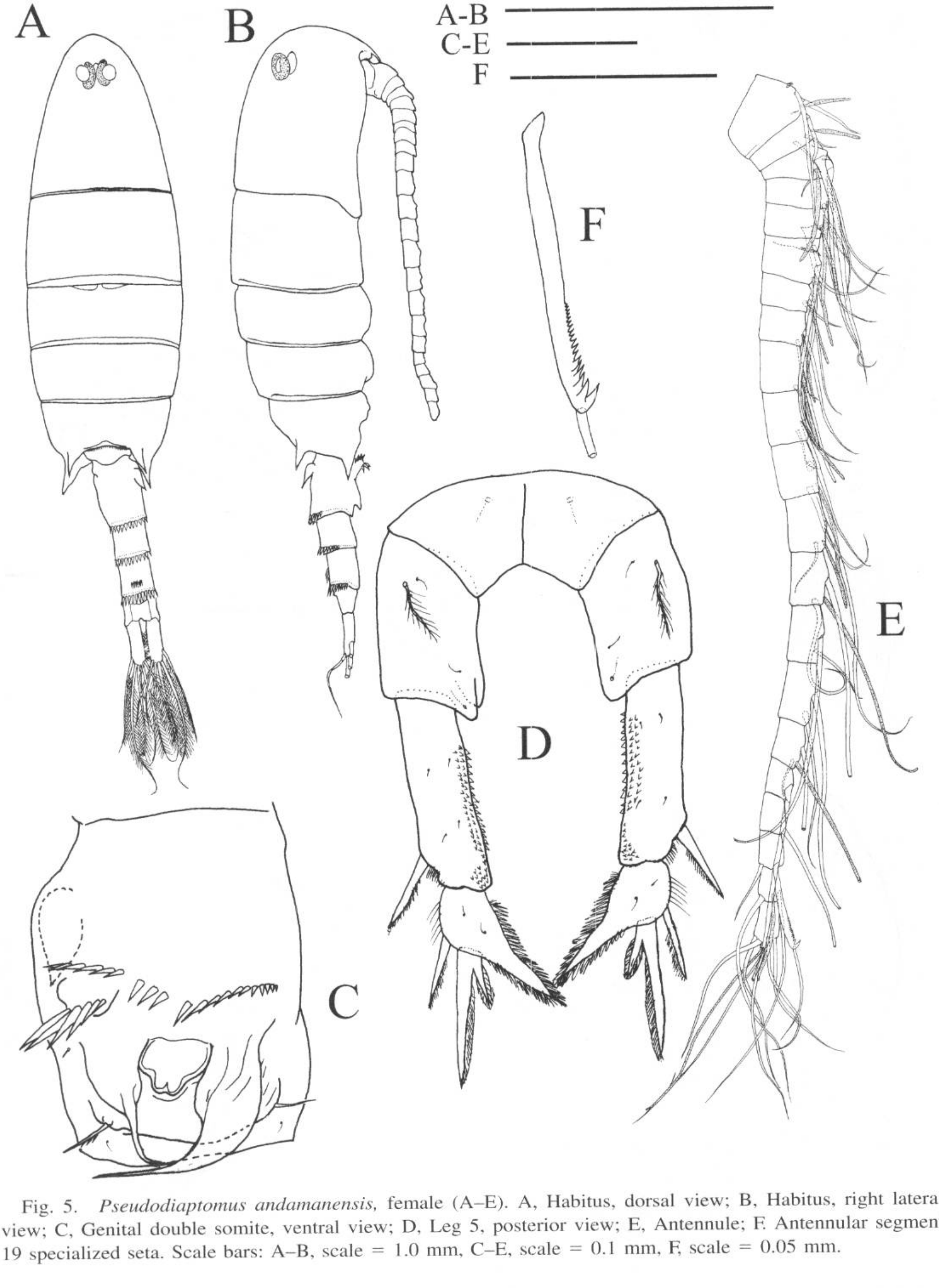

Fig. 5. *Pseudodiaptomus andamanensis,* female (A–E). A, Habitus, dorsal view; B, Habitus, right lateral view; C, Genital double somite, ventral view; D, Leg 5, posterior view; E, Antennule; F. Antennular segment 19 specialized seta. Scale bars: A–B, scale = 1.0 mm, C–E, scale = 0.1 mm, F, scale = 0.05 mm.

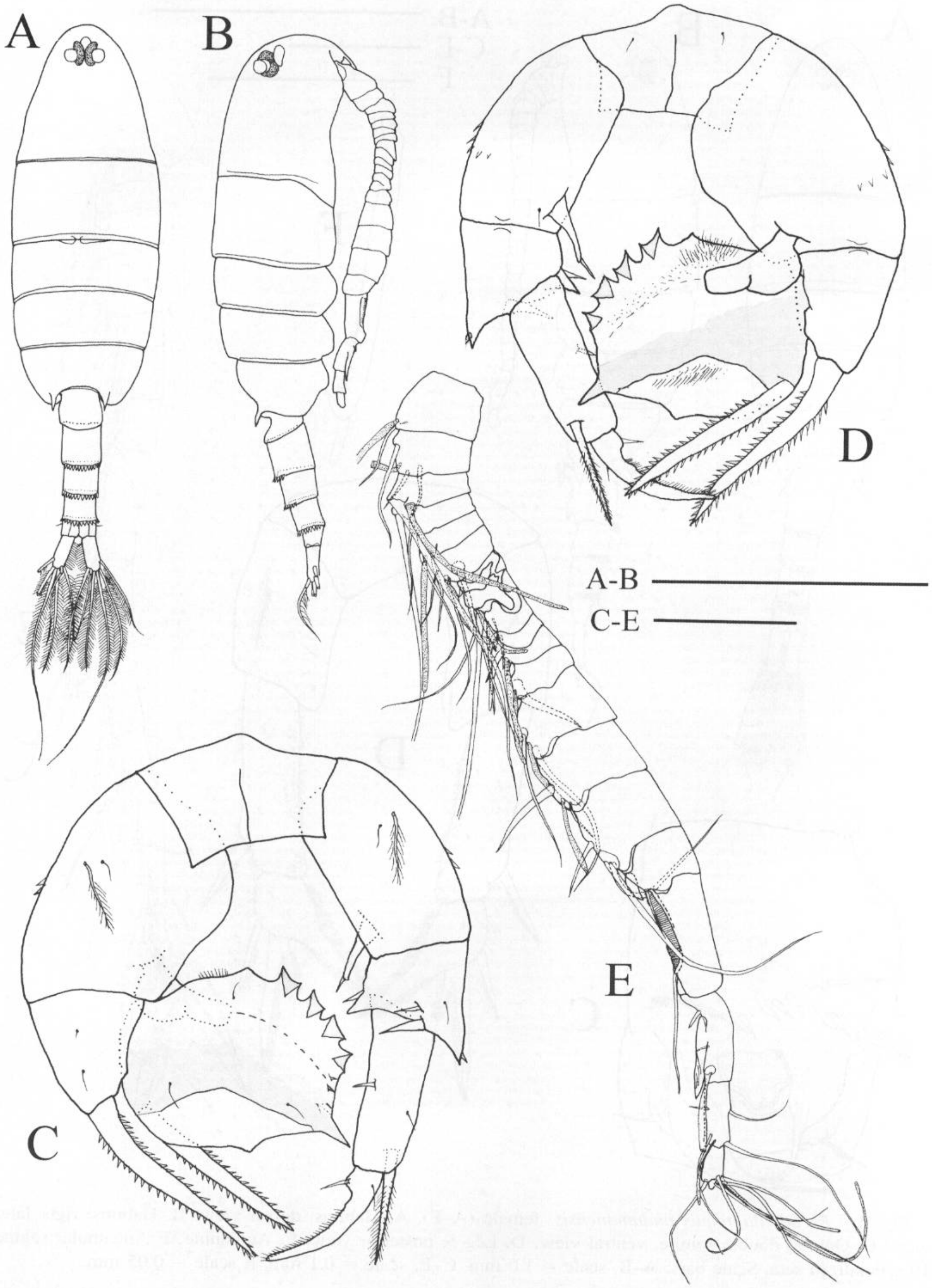

Fig. 6. *Pseudodiaptomus andamanensis,* male (A–E). A, Habitus, dorsal view; B, Habitus, right lateral view; C, Leg 5, posterior view; D, Leg 5, anterior view; E, Antennule. Scale bars: A–B, scale = 1.0 mm, C–E, scale = 0.1 mm.

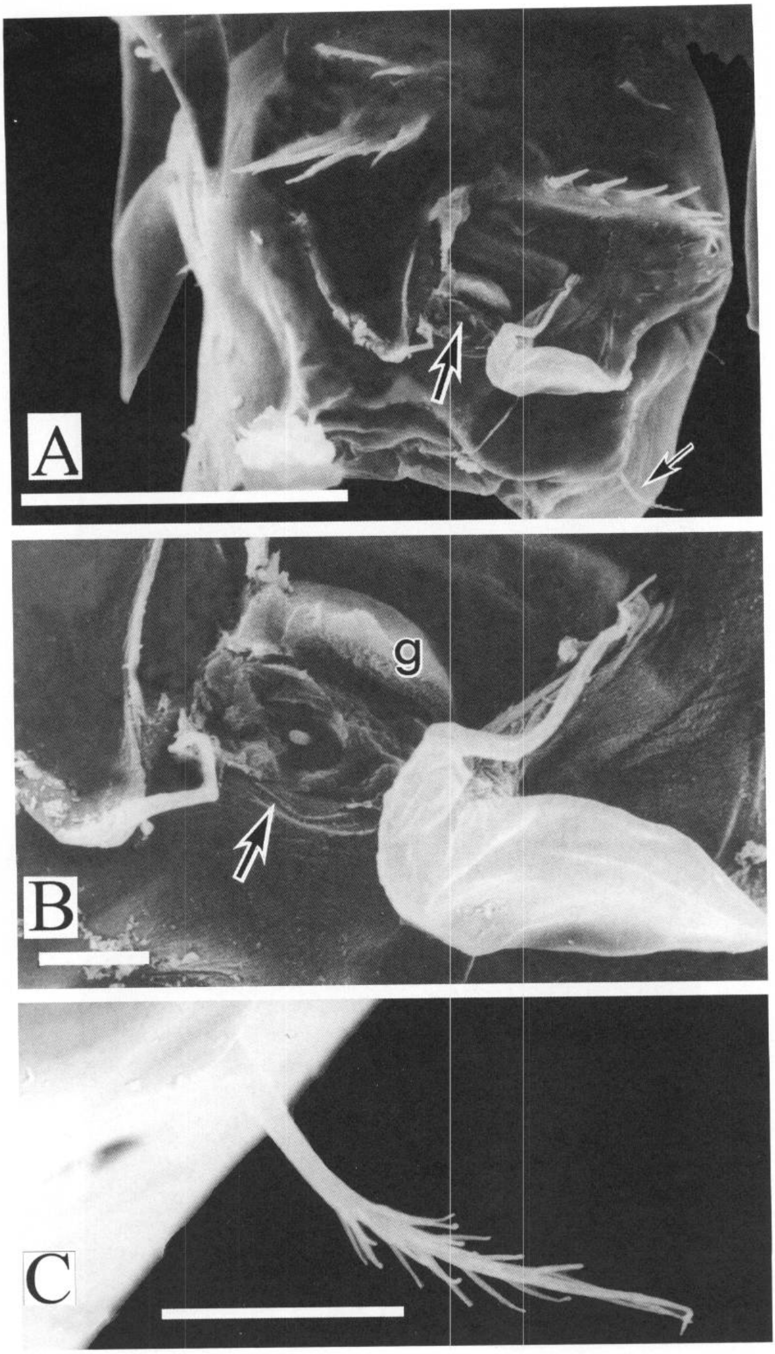

Fig. 7. *Pseudodiaptomus andamanensis,* female (A–C). A, Genital double somite, ventral view, genital atrium indicated by large arrow, left hair-sensillum by small arrow; B, Genital double somite, ventral view, magnified, (g) genital operculum, genital atrium indicated by large arrow; spermatophore remnant to the right of arrow; C, Genital double somite, ventral view of left hair-sensillum (magnification of A, indicated by small arrow). Scale bars: A–B, scale = 0.1 mm, C, scale = 0.01 mm.

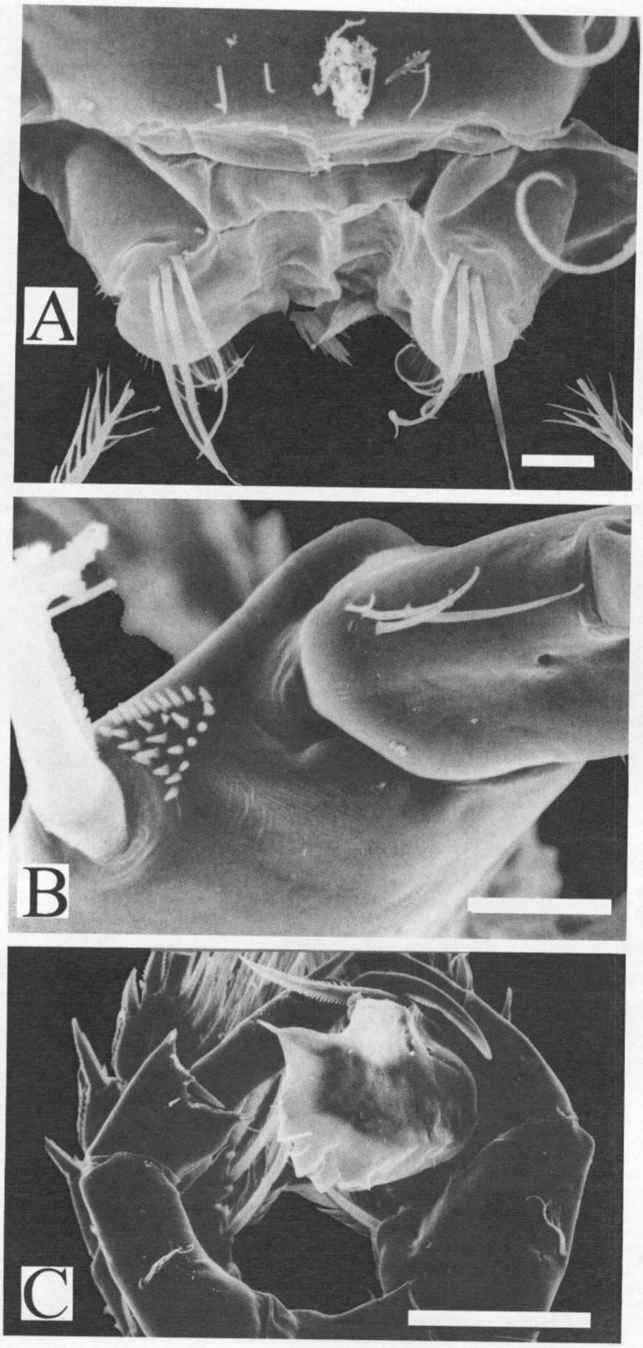

Fig. 8. *Pseudodiaptomus andamanensis,* female (A–B). A, Labrum, ventral view; B, Leg 5, distolateral view of first segment; Male C, Leg 5, posterior view. Scale bars: A–C, scale = 0.1 mm.

Table 2.—Number of egg-sac(s) for the species groups of *Pseudodiaptomus*.

Species group	No. of egg-sac(s)	References
Nudus	single	Walter (1989); present study
Americanus	paired	Walter (1989); present study
Burckhardti	unknown	
Improcerus	single (mostly)	Grindley (1963), present study
	paired (*P. pauliani*)	Dussart (1982)
Lobus	paired	Soh et al. (2001); present study
Hyalinus	single	Ohtsuka et al. (2000); present study
Ramosus	single	Soh et al. (2001); present study

evolutionary trends (Ohtsuka et al. 1994, Cuoc et al. 1997). The superfamily Centropagoidea, which includes the families Pseudodiaptomidae and Acartidae, exhibits a similar genital system pattern, with the exception of the genus *Acartia* (Barthélémy 1999). The centropagoid egg-laying ducts typically open via an adjacent pair of gonopores into the genital atrium, which is covered with a single genital operculum and opens to the outside through a distal atrial slit; there are no seminal receptacles (Barthélémy et al. 1998a). Light and scanning electron microscopic observations (Ohtsuka et al. 2000, Soh et al. 2001, present study) suggest that pseudodiaptomids are similar to this pattern of the Centropagoidea. However, the paired genital flaps flanking the genital operculum and the combination of single or paired egg sacs appear to be unique for species of the Pseudodiaptomidae. Species of Diaptomidae, *Eurytemora* (Temoridae), *Boeckella,* and *Osphranticum labronectum* Forbes, 1882 (Centropagidae) carry only one egg-sac and lack genital flaps in the female (Huys & Boxshall 1991, Barthélémy et al. 1998a). Genital flaps of Pseudodiaptomidae may play a role in the formation and guidance of the egg-sac(s) after eggs are released from the genital atrium or the gonopores. For example, the genital flaps of the Hyalinus species group (Walter 1984, 1986a, 1987; Ohtsuka et al. 2000) are typically long and spiniform processes that taper distally at the tip. They may be analogous to the ovigerous spines of monstrilloids on which one or more egg masses are attached (Huys & Boxshall 1991). The morphology of the female genital double somite of *Pseudodiaptomus* appears to be species-specific and should prove useful for the taxonomy of the genus. Features that are significant are symmetry of the genital structures; relative position of the paired gonopores; presence or absence of a genital operculum; shape of genital flaps; and number and distribution of swellings, prominences, and hair-sensilla (Ohtsuka et al. 2000, Soh et al. 2001, present study).

Females of some species of *Pseudodiaptomus* carry only a single egg-sac, while others carry a pair. The number of egg-sacs (Table 2) appears constant within six of the seven pseudodiaptomid species-groups, established by Walter (1986a). A single egg-sac is found in the Nudus, Hyalinus, and Ramosus groups; paired egg sacs are found in the Americanus and Lobus groups. The Improcerus group contains both with *P. pauliani* Brehm, 1951 bearing paired egg-sacs in contrast to the others with a single one; the number of egg-sacs of *P. andamanensis* or *P. batillipes* Brehm, 1954 is not known. Comparison of SEM ventral views of the female genital double somite of *P. ornatus* and *P. andamanensis* (Improcerus group: Fig. 3A, Fig. 7A, respectively), *P. clevei* A. Scott, 1909 (Nudus group: Fig. 9E–F), *P. trihamatus* Wright, 1937 and *P. bowmani* Walter, 1984 (Hyalinus group: Fig. 10A, Fig. 10B, respectively), *P. nihonkaiensis* Hirakawa, 1983 and *P. marinus* Sato, 1913 (Ramosus group: see Soh et al.

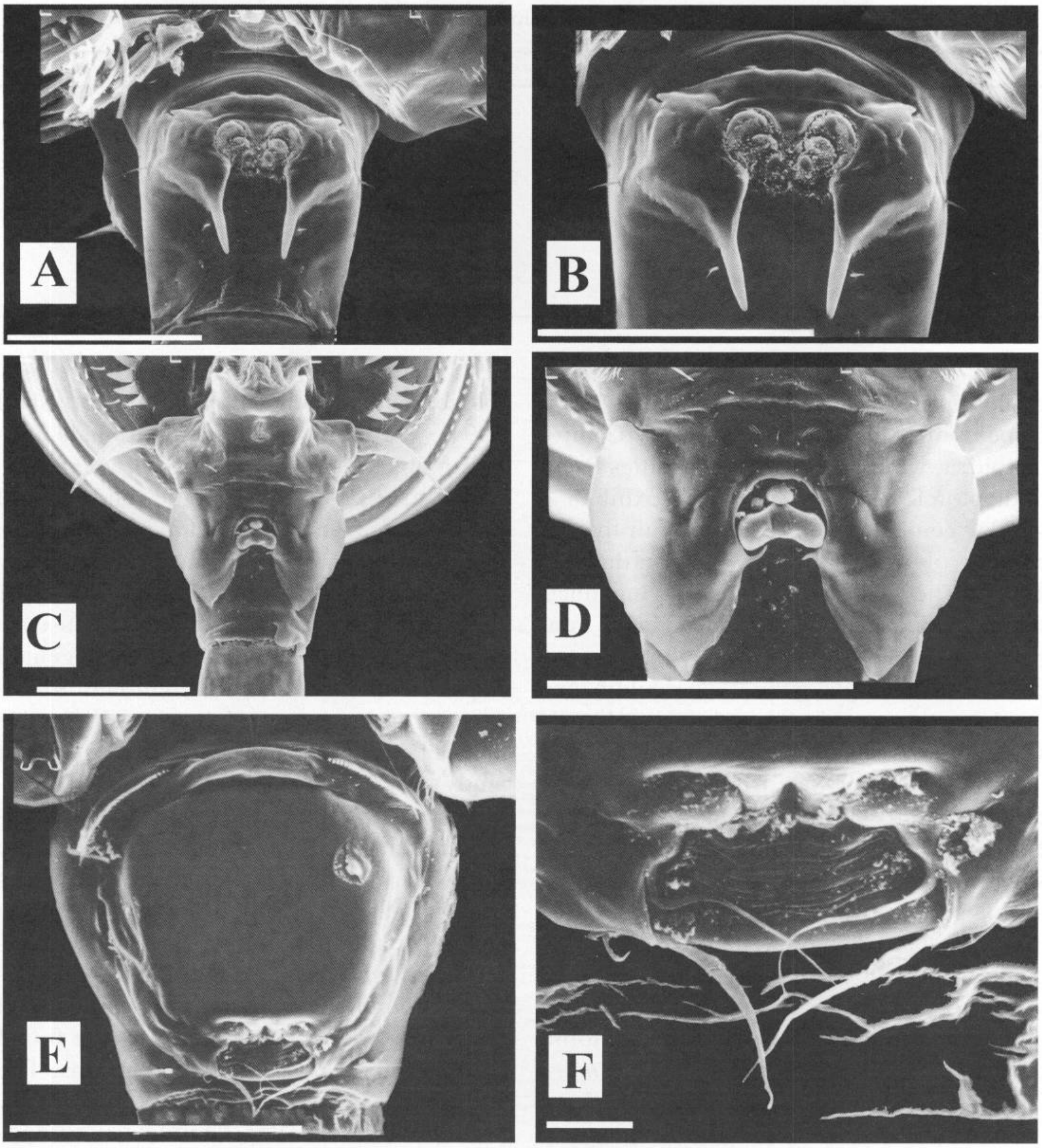

Fig. 9. *Pseudodiaptomus inopinus,* female (A–B). A, Genital double somite, ventral view; B, magnification of same view; *Pseudodiaptomus annandalei,* female (C–D). C, Genital double somite, ventral view; D, magnification of same view; *Pseudodiaptomus clevei,* female (E–F). E, Genital double somite, ventral view; F, magnification of same view. Scale bars: A–F, scale = 0.1 mm.

2001, Fig. 8A, Fig. 8B, respectively) show that these species have a genital operculum and a single egg-sac. Three species of the Lobus group, *P. inopinus* Burckhardt, 1913, *P. annandalei* Sewell, 1919 (Fig. 9A–B, Fig. 9C–D, respectively), and *P. poplesia* (Shen 1955) (see Soh et al. 2001, Fig. 3A,B) do not have a genital operculum and have paired egg sacs, thus suggesting that the presence or absence of a genital operculum covering the paired gonopores is correlated the number of egg-sacs. In the species (or groups) with a single egg-sac, the genital operculum is present and the paired

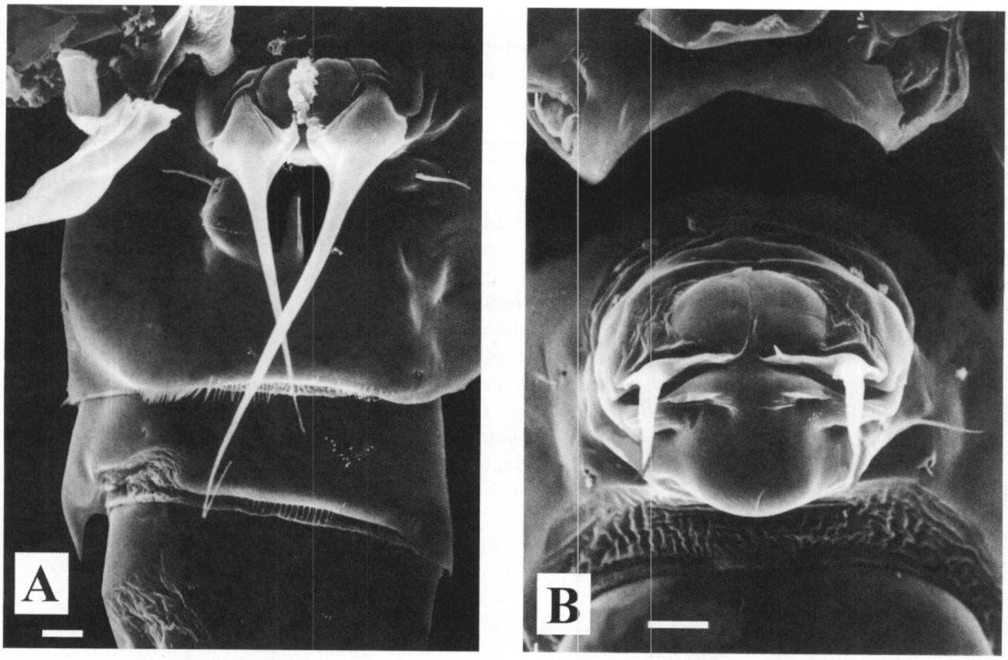

Fig. 10. *Pseudodiaptomus trihamatus,* female A, Genital double somite and second urosomal segemt, ventral view; *Pseudodiaptomus bowmani,* female B, Genital double somite, ventral view. Scale bars: A–B, scale = 0.01 mm.

genital flaps, which are expansions of the opercular pad (Cuoc & Defaye, pers. comm.), partially or completely cover the gonopore. The two strings of eggs are released from the gonopores into a single egg-sac within the genital atrium. In contrast, when the paired gonopores are exposed and there is no distinct genital operculum, as in *P. inopinus* and *P. poplesia,* the two strings of eggs are released from the gonopores directly into paired egg-sacs which may be modified. An example of modified egg sacs are those of *P. annandalei* which are lateral in position, as contrast to *P. inopinus* and *P. poplesia* which are ventrolateral. The paired genital flaps of *P. annandalei* are close to each other medially, but laterally they expand beyond the lateral margin of the genital double somite. This arrangement seems to result in two lateral egg-sacs separated by a slit between the somite and the flaps. In addition, the distance between both gonoporal slits may be related to the number of egg sacs in pseudodiaptomids (Cuoc, pers. comm.). The absence of a genital operculum is found also in a monotypic genus *Sulcanus* in the centropagoidean family Sulcalidae (Barthélémy et al. 1998a). So the absence of a genital operculum in some may have evolved convergently within the Centropagoidea.

Zoogeography of Indo-West Pacific species.—Sewell (1956), Grindley (1984), Madhupratap & Haridas (1992) and Walter (1986b) inferred on the basis of the present distribution and the plate tectonics that the ancestors of *Pseudodiaptomus* may have originated in the Cretaceous and spread through the Tethys Sea. In contrast, the cladistic analysis of Ohtsuka & Reid (1998) strongly suggests that another brackish/coastal calanoid genus *Tortanus,* which has almost the same distributional pattern as in *Pseudodiaptomus* (Indo-West Pacific plus western Atlantic, lacking completely in the northeastern Atlantic), could have originated from the Indo-Malayan region after the closure of the Tethys Sea (Miocene). They

Table 3.—Distributional patterns for Indo-West Pacific nominal species of *Pseudodiaptomus.* Type I: wide distribution of the Indo-West Pacific; Type II: confined distribution mainly or restrictedly in the Indian Ocean; Type III: confined distribution mainly or restrictedly in the West Pacific.

Species group	Distributional type	Species
Nudus	Type I	*P. clevei*
Burckhardti	Type I	*P. burckhardti*
Improcerus	Type II	*P. andamanensis, P. batillipes, P. hessei, P. pankajus, P. pauliani, P. stuhlmanni*
	Type III	*P. ornatus*
Lobus	Type I	*P. annandaelei, P. tollingerae*
	Type II	*P. binghami, P. lobipes, P. malayalus*
	Type III	*P. brehmi, P. bulbosus, P. forbesi, P. inflatus, P. inopinus, P. inopinus saccupodus, P. poplesia, P. poppei, P. spatulatus, P. smithi*
Hyalinus	Type I	*P. aurivilli, P. baylyi, P. mertoni*
	Type II	*P. bowmani, P. compactus, P. occidentalis, P. sewelli*
	Type III	*P. bispinosus, P. dauglishi, P. griggae, P. incisus, P. trihamatus*
Ramosus	Type II	*P. ardjuna, P. hickmani, P. hypersalinus, P. jonesi, P. salinus, P. serricaudatus*
	Type III	*P. australiensis, P. caritus, P. colefaxi, P. cornutus, P. diadelus, P. galleti, P. inflexus, P. ishigakiensis, P. marinus*, P. nihonkaiensis, P. pacificus, P. philippinensis*
Unassigned	Type II	*P. heterothrix, P. masoni, P. nankauriensis*
	Type III	*P. bulbiferus*

* The species assigned to *P. marinus* from the Andaman Sea and Mauritius is suggested to be another species.

also noted that, the northwestern Atlantic subgenus *Acutanus* is one of the last offshoots of the five subgenera. Although a strict cladistical analysis has not yet been employed for the members of *Pseudodiaptomus,* apomorphies of the American species group (Walter 1989) such as the absence of a right endopod of male leg 5 and the asymmetry of caudal rami support the idea that the American species could have derived from an Indo-West Pacific ancestor. The ancestor could have been introduced to the western Atlantic via passages in the middle and northern South America before the closure of these passages (Pliocene), as has been proposed for the evolution of *Tortanus* by Ohtsuka & Reid (1998). This scenario can be applicable to the history of one of the pseudodiaptomid species groups, the Nudus group, which is unique in that it is comprised of only two species lacking both right and left endopods on male leg 5, an Indo-West Pacific species, *P. clevei* and a South American species, *P. gracilis* (Dahl, 1894). One-way transoceanic dispersal from the Indo-Malayan to the western Atlantic in the Miocene and Pliocene for non-copepods is also suggested for a pelagic shrimp *Acetes* (van der Spoel 1983).

Extant species of *Pseudodiaptomus* have a worldwide distribution and include 74 nominal species at present. Among them 58 species have been recorded from the Indo-West Pacific. A recent paper discussed the zoogeography of *Pseudodiaptomus* species occurring in the Gulf of Thailand and the Andaman Sea (Ohtsuka et al. 2000) and introduced three basic types of distribution patterns for the Indo-West Pacific species of *Pseudodiaptomus.* The boundaries for the patterns are based on general geographical concepts: Type I—wide distribution in the Indo-West Pacific; Type II—confined distribution mainly or restrictedly to the Indian Ocean (some species extending to southern Africa); Type III—confined distribution mainly or restrictedly to the West Pacific (Table 3); species synanthropically introduced outside their original habitat are excluded from Table 3 [*P. marinus* in Hawaii, U.S.A. (Jones 1966), *P. marinus* and *P. forbesi* (Poppe & Richard 1890) in California, U.S.A. (Orsi & Walter 1991), *P. inopinus* in Washington and Oregon, U.S.A. (Cordell et al. 1992), and *P. trihamatus* in Brazil (Medeiros et al. 1991)].

Remarkable climatic or hydrological events in East and Southeast Asia such as regressions, upwellings, and inflows of freshwaters during the Pleistocene glacial periods could have caused the speciation of parts of Indo-West Pacific species of *Pseudodiaptomus,* as hypothesized for the speciation mechanisms of a pontellid species group, *Labidocera pectinata* group (Fleminger 1986) and of a *Tortanus* subgenus *Eutortanus* (Ohtsuka et al. 1992, Ohtsuka & Reid 1998). Two possible explanations for the present wide distribution for the Type I group species are: the species may have been broadly distributed throughout the Indo-West Pacific without any subsequent speciation, or their ancestors could have been isolated in either the Indian Ocean or the West Pacific by the events during glacial periods which then caused speciation, and subsequent generations may have rapidly extended their distribution from one side to other of the Indo-West Pacific region. The second possibility would hopefully be disclosed by future cladistic and molecular analyses. The speciation of the present tropical pseudodiaptomids in the Indo-Malayan region (belonging to Types II and III) is primarily ascribed to reduction of eustatic sea level changes around the Indo-Australian region during the glacial periods, which could have acted as a distinct barrier between the Indian and the West Pacific populations (Fleminger 1986). The ancient East China Sea, existed as a huge gulf during the Pleistocene, could also have caused secondary speciation of members of the Lobus species group which fall into the Type III distribution pattern. Vicariance between the Indian and the West Pacific may have occurred within each of the Improcerus, Lobus, Hyalinus and Ramosus groups, because these species groups contain both Types II and III representatives.

Acknowledgments

We express our sincere thanks to the following persons for collection of copepods: Dr. A. D. McKinnon; the staff of the Phuket Marine Biological Center; the captain and crew of TR/V Toyoshio-maru; Dr. H. Y. Soh who kindly provided us with information on the female genital structures of Korean species of *Pseudodiaptomus* and C. Cuoc for personal comments on female genital structures.

Literature Cited

Barthélémy, R. M. 1999. Functional morphology and taxonomic relevance of the female genital structures in Acartiidae (Copepoda: Calanoida).—Journal of the Marine Biological Association of the United Kingdom 79:857–870.

———, C. Cuoc, D. Defaye, M. Brunet, & J. Mazza. 1998a. Female genital structures in several families of Centropagoidea (Copepoda: Calanoida).—Philosophical Transactions of the Royal Society of London (B) 353:721–736.

———, S. Ohtsuka, & C. Cuoc. 1998b. Description and female genital structures of a new species of the demersal calanoid copepod *Ridgewayia* from southern Japan.—Journal of Natural History 32:1303–1318.

Brehm, V. 1951. *Pseudodiaptomus pauliani* (Crustacea: Copepoda). Der erste Vertreter der Pseudodiaptomiden in der madagassichen Fauna.—Mémoires de l'Institut Scientifique de Madagascar, Série A, 6:419–425.

———. 1954. *Pseudodiaptomus batillipes* spec. nov., ein zweiter *Pseudodiaptomus* aus Madagascar.—Sitzungsberichten der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abt. 1, 163: 604–607.

Burckhardt, G. 1913. Wissenschaftliche Ergebnisse einer Reise um die Erde von M. Pernod und C. Schröter. III. Zooplancton aus ost- und süd-asiatischen Binnengewässern.—Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 34:341–472.

Cordell, J. R., C. A. Morgan, & C. A. Simenstad. 1992. Occurrence of the Asian calanoid copepod *Pseudodiaptomus inopinus* in the zooplankton of the Columbia River Estuary.—Journal of Crustacean Biology 12:260–269.

Cuoc, C., J. Arnaud, M. Brunet, & J. Mazza. 1989.

Structure, ultrastructure et essai d'interprétation fonctionelle de l'appareil génital femelle d'*Hemidiaptomus ingens provinciae* et de *Mixodiaptomus kupelwieseri* (Copepoda, Calanoida). II. L'aire génitale.—Canadian Journal of Zoology 67:2579–2587.

———, D. Defaye, M. Brunet, R. Notonier, & J. Mazza. 1997. Female genital structures of Metridinidae (Copepoda: Calanoida).—Marine Biology 129:651–665.

Dahl, F. 1894. Die Copepodenfauna des unteren Amazonas.—Berichte der Naturforschenden Gesellschaft zu Freiburg i.B. 8:10–23.

Defaye, D., C. Cuoc, & M. Brunet. 2000. Genital structures and spermatophore placement in female Paradiaptominae (Copepoda, Calanoida, Diaptomidae).—Journal of Crustacean Biology 20:245–261.

Dussart, B. H. 1982. Crustacés copépodes des eaux intérieures.—Faune de Madagascar, ORSTOM, Paris 58. Crustacea, 146 pp.

Fleminger, A. 1986. The Pleistocene equatorial barrier between the Indian and Pacific Oceans and a likely cause for Wallace's line. Pp. 84–97 *in* Pierrot-Bults, A. C., S. van der Spoel, G. J. Zahuranec, & R. K. Johnson, eds., Pelagic biogeography. Proceedings of an International Conference, The Netherlands, 28 May–5 June 1985. UNESCO Technical Papers in Marine Science 49:1–295.

Forbes, S. A. 1882. On some Entomostraca of Lake Michigan and adjacent waters.—American Naturalist 16:537–543, 640–650.

Grindley, J. R. 1963. The Pseudodiaptomidae (Copepoda: Calanoida) of southern African waters, including a new species, *Pseudodiaptomus charteri*.—Annals of the South African Museum 46: 373–391.

———. 1984. The zoogeography of the Pseudodiaptomidae.—*in* Vervoort, W., ed., Studies on Copepoda II. Proceedings of the First International Conference on Copepoda, Amsterdam, The Netherlands, 24–28 August 1981. Crustaceana, Supplement 7:217–228.

Herrick, C. L. 1884. Final report on the Crustacea of Minnesota, included in the orders Cladocera and Copepoda, together with a synopsis of the described species in North America, and keys to the known species of the more important genera.—Reports of the Geological and Natural History Survey of Minnesota 12:1–192.

Hirakawa, K. 1983. A new species of *Pseudodiaptomus* (Copepoda: Calanoida) from the coast of Niigata, the Japan Sea.—Bulletin of Plankton Society of Japan 30:65–69.

Huys, R., & G. A. Boxshall. 1991. Copepod Evolution.—Ray Society, London 159, 468 pp.

Kritschagin, N. A. 1873. Materialy dlya fauny sostochnogo berega Chernago Morya. (Contributions to the knowledge of fauna of the eastern shore of the Black Sea: Copepoda)—Zapiski Kiivs'kogo Tovaristva Prirodoznavtsiv 3:370–429.

Jones, E. C. 1966. A new record of *Pseudodiaptomus marinus* Sato (Copepoda: Calanoida) from brackish waters of Hawaii.—Crustaceana 10: 316–317.

Labbé, A. 1927. Notes préliminaires sur les copépodes de la faune française (suite).—Bulletin de la Société Zoologique de France 52:434–445.

Madhupratap, M., & P. Haridas. 1978. *Archidiaptomus aroorus,* a new genus and new species of Copepoda (Calanoida, Pseudodiaptomidae) from Cochin Backwater, India.—Crustaceana 35: 253–258.

———. 1992. New species of *Pseudodiaptomus* (Copepoda: Calanoida) from the salt pans of the Gulf of Kutch, India and a comment on its speciation.—Journal of Plankton Research 14:555–562.

Medeiros, G. F., C. E. F. Rocha, & M. L. Silva. 1991. A note on the occurrence of *Pseudodiaptomus trihamatus* Wright, 1937 (Crustacea: Copepoda) in Natal, Brazil.—Boletim do Departamento de Oceanografia e Limnologia, Centro de Biociências, Universidade Federal Rio Grande Norte 8: 113.

Nishida, S. 1985. Pelagic copepods from Kabira Bay, Ishigaki Island, southwestern Japan, with the description of a new species of the genus *Pseudodiaptomus*.—Publications of the Seto Marine Biological Laboratory 30:125–144.

Ohtsuka, S., G. A. Boxshall, & H. S. J. Roe. 1994. Phylogenetic relationship between arietellid genera (Copepoda: Calanoida), with the establishment of three new genera.—Bulletin of The Natural History Museum, London, Zoology 60: 105–172.

———, S. Putchakarn, K. Pinkaew, & S. Chullasorn. 2000. Taxonomy and feeding ecology of demersal calanoid copepods collected from Thailand. Pp.133–147 *in* M. N. Saadon et al., eds., Proceedings of the Tenth JSPS Joint Seminar on Marine and Fishery Science, 496 pp.

———, & J. W. Reid. 1998. Phylogeny and zoogeography of the planktonic copepod genus *Tortanus* (Calanoida: Tortanidae), with establishment of a new subgenus and descriptions of two new species.—Journal of Crustacean Biology 18:774–807.

———, Y. H. Yoon, & Y. Endo. 1992. Taxonomic studies on brackish copepods in Korean waters. 1. Redescription of *Tortanus dextrilobatus* Chen and Zhang, 1965 from Korean waters, with remarks on zoogeography of the subgenus *Eutor-*

tanus.—Journal of the Oceanological Society of Korea 27:112–122.

Orsi, J. J., & T. C. Walter. 1991. *Pseudodiaptomus forbesi* and *P. marinus* (Copepoda: Calanoida), the latest copepod immigrants to California's Sacramento-San Joaquin Estuary. Pp. 553–562 *in* S. I. Uye, S. Nishida, & J. S. Ho, eds., Proceedings of the Fourth International Conference on Copepoda. Bulletin of Plankton Society of Japan, Special Volume: 645 pp.

Pillai, P. P. 1980. A review of the calanoid copepod family Pseudodiaptomidae with remarks on the taxonomy and distribution of the species from the Indian Ocean.—Journal of the Marine Biological Association of India 18:242–265.

Poppe, S. A., & J. Richard. 1890. Description du *Schmackeria forbesi* n. gen. et sp., Calanide nouveau recueilli par M. Schmacker dans les eaux douces des environs de Shanghai.—Mémoires de la Société Zoologique de France 3: 396–403.

Reddy, Y. R., & Y. Radhakrishna. 1982. Redescription and/or remarks on four species of *Pseudodiaptomus* Herrick (Copepoda: Calanoida) from South India.—Hydrobiologia 87:255–271.

Richard, J. 1888. Entomostráces nouveaux ou peu connus.—Bulletin de la Société Zoologique de France 13:43–48.

Rose, M. 1957. Description de Copépodes nouveaux du plankton marin de Nha-Trang (Viet-Nam).—Bulletin du Museum National d'Hisoire Naturelle, Paris (2) 29:235–245.

Sars, G. O. 1902. An Account of the Crustacea of Norway, Copepoda Calanoida, Parts VII & VIII, 4.—Bergen Museum Pp. 73–96.

Sato, C. 1913. Free-swimming Copepoda. (1.)—Hokkaido Fisheries Research Laboratory, Investigation Reports 1:1–82.

Scott, A. 1909. The Copepoda of the Siboga Expedition. Part I. Free-swimming, littoral and semiparasitic Copepoda.—Siboga Expeditie, Monograph, Leiden 29a:1–323.

Scott, T. 1894. Report on Entomostraca from the Gulf of Guinea, collected by John Rattray, B.Sc.—Transactions of the Linnean Society of London, Zoology, Series 2, 6:1–161.

Sewell, R. B. S. 1919. A preliminary note on some new species of Copepoda.—Records of the Indian Museum, Calcutta 16:1–18.

———. 1956. The continental drift theory and the distribution of the Copepoda.—Proceedings of the Linnean Society of London 166:149–177.

Shen, C. J. 1955. On some marine crustaceans from the coastal water of Fenghsien, Kiangsu Province.—Acta Zoologica Sinica 7:75–100.

Soh, H. Y., H. L. Suh, O. H. Yu, & S. Ohtsuka. 2001. The first record of two demersal calanoid copepods *Pseudodiaptomus poplesia* and *P. nihonkaiensis* in Korea, with remarks on morphology of the genital operculum.—Hydrobiologia 448:203–215.

Spoel, S. van der. 1983. Pattern in plankton distribution and the relation to speciation: the dawn of pelagic biogeography. Pp. 291–334 *in* R. W. Sims, J. H. Price, & P. E. S. Whalley, eds., Evolution, Time and Space: the Emergence of the Biosphere. Academic Press, London, Special Volume 23:1–492.

Walter, T. C. 1984. New species of *Pseudodiaptomus* from the Indo-Pacific, with a clarification of *P. aurivilli* and *P. mertoni* (Crustacea: Copepoda: Calanoida).—Proceedings of the Biological Society of Washington 97:369–391.

———. 1986a. New and poorly known Indo-Pacific species of *Pseudodiaptomus* (Copepoda: Calanoida), with a key to the species groups.—Journal of Plankton Research 8:129–168.

———. 1986b. The zoogeography of the genus *Pseudodiaptomus* (Calanoida: Pseudodiaptomidae).—Pp. 502–508 *in* G. Schriever, H. K. Schminke, & C. T. Shih, eds., Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13–17 August, 1984. Syllogeus 58:1–662.

———. 1987. Review of the taxonomy and distribution of the demersal copepod genus *Pseudodiaptomus* (Calanoida: Pseudodiaptomidae) from southern Indo-West Pacific waters.—Australian Journal of Marine and Freshwater Research 38:363–396.

———. 1989. Review of the New World species of *Pseudodiaptomus* (Copepoda: Calanoida), with a key to the species.—Bulletin of Marine Science 45:590–628.

Wright, S. 1937. Two new species of *Pseudodiaptomus.*—Anais da Academia Brasileira de Ciências 9:155–162.