A new species of *Pseudodiaptomus* (Crustacea: Copepoda: Calanoida) from the Philippines, with a key to pseudodiaptomids from the Philippines and comments on the status of the genus *Schmackeria*

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Abstract.—Four species of the demersal calanoid copepod genus Pseudodiaptomus were collected from Panay Island, Philippines in September 2003. They represented three species groups (sensu Walter 1986a): P. terazakii, a new species, and P. annandalei (Lobus group), P. bispinosus (Hyalinus group), and P. clevei (Nudus group). The female of the new species differs from its congeners in the possession of 3 pairs of anterolateral spines on the genital double-somite. The male is distinguished by the fifth leg right endopod, which is bifid at its apex, and the left non-bifid endopod. A key to the 14 pseudodiaptomid species known from the Philippines is provided herein. A review of the genus Schmackeria Poppe & Richard (1890) is presented, and all species attributed to this genus are merged into the genus Pseudodiaptomus. Because many new species of Pseudodiaptomus have been described recently, a revised key to the species-groups of Walter (1986a) is presented.

The taxonomy of marine planktonic copepods in southeastern Asia is generally accepted to have been initiated by A. Scott (1909), and subsequently has been elaborated by many copepodologists (e.g., Mulyadi 1997, 1998, 2002a, 2002b; Mulyadi & Ueda 1996; Nishida & Rumengan 2005; Ohtsuka et al. 1998, 1999, 2003; Walter 1984, 1986a; Walter et al. 2002). The species of the demersal calanoid family Pseudodiaptomidae G. O. Sars, 1902 are typically found in coastal environments and are highly diversified in the Indo-Pacific region. A preliminary survey of coastal copepods conducted off Panay Island, Philippines, in September 2003 resulted in the collection of four species of the genus Pseudodiaptomus, one

of which is new to science. Pseudodiaptomus bispinosus (the first record after the original description), P. annandalei, and P. clevei were also collected from this locality. The present study describes the new pseudodiaptomid, with notes on the other three species from Panay Island. The 77 currently recognized species of the genus are presented in Table 1, following an alphabetical arrangement of the species within their designated species groups as established by Walter (1986a).

Materials and Methods

Copepods were collected from three localities (Leganes, Culasi Ajuy, and Iloilo at the International Port, Fort San

Table 1.—List of the 77 species of *Pseudodiaptomus*. Arrangement is alphabetical by species within their assigned species groups and subgroups.

Americanus species group:

(acutus—subgroup)

- 1. P. acutus (F. Dahl, 1894)
- 2. P. cristobalensis Marsh, 1913
- 3. P. galapagensis Grice, 1964
- 4. P. richardi (F. Dahl, 1894)
- 5. P. wrighti Johnson, 1964 (pelagicus—subgroup)
- 6. P. cokeri González & Bowman, 1965
- 7. P. culebrensis Marsh, 1913
- 8. P. euryhalinus Johnson, 1939
- 9. P. longispinosus Walter, 1989
- 10. P. marshi Wright, 1936
- 11. P. panamensis Walter, 1989
- 12. P. pelagicus Herrick, 1884

Burckhardt species group

13. P. burckhardti Sewell, 1932

Hyalinus species group (aurivilli—subgroup)

- 14. P. aurivilli Cleve, 1901
- 15. P. bowmani Walter, 1984
- 16. P. compactus Walter, 1984
- 17. *P. mertoni* Früchtl, 1923 (*trihamatus*—subgroup)
- 18. P. baylyi Walter, 1984
- 19. P. bispinosus Walter, 1984
- 20. P. dauglishi Sewell, 1932
- 21. P. griggae Walter, 1987
- 22. P. incisus Shen & Lee, 1963
- 23. P. occidentalus Walter, 1987
- 24. P. sewelli Walter, 1984
- 25. P. trihamatus Wright, 1937 (syn. P. penicillus Li & Huang, 1984)

Improcerus species group

- 26. P. andamanensis Pillai, 1980
- 27. P. batillipes Brehm, 1954
- 28. P. hessei (Mrázek, 1895)
- 29. P. ornatus (Rose, 1957)
- 30. P. pankajus Madhupratap & Haridas, 1992
- 31. P. pauliani Brehm, 1951
- 32. P. stuhlmanni (Poppe & Mrázek, 1895)
- 33. P. trispinosus Walter, 1986a

Lobus species group

(forbesi—subgroup)

- 34. P. annandalei Sewell, 1919
- 35. P. binghami Sewell, 1912
- 36. P. brehmi Kiefer, 1938
- 37. P. bulbosus (Shen & Tai, 1964)
- 38. P. forbesi (Poppe & Richard, 1890)
- 39. P. inflatus (Shen & Tai, 1964)
- 40. P. inopinus Burckhardt, 1913

Table 1.—Continued.

- 41. P. inopinus gordiodes Brehm, 1952
- 42. P. inopinus saccupodus (Shen & Tai, 1962)
- 43. P. lobipes Gurney, 1907
- 44. P. malayalus Wellershaus, 1969
- 45. P. mixtus Walter, 1994
- 46. P. poplesia (Shen, 1955)
- 47. P. spatulatus (Shen & Tai, 1964)
- 48. *P. terazakii*, new species (*poppei*—subgroup)
- 49. P. poppei Stingelin, 1900
- 50. P. smithi Wright, 1928
- 51. P. tollingerae Sewell, 1919

Ramosus species group

(hickmani—subgroup)

- 52. P. ardjuna Brehm, 1953
- 53. P. australiensis Walter, 1987
- 54. P. hickmani Sewell, 1912
- 55. P. hypersalinus Walter, 1987
- 56. P. ishigakiensis Nishida, 1985
- 57. P. jonesi Pillai, 1970
- 58. P. marinus Sato, 1913
- 59. P. philippinensis Walter, 1986a
- 60. P. sulawesiensis Nishida & Rumengan, 2005 (serricaudatus—subgroup)
- 61. P. arabicus Walter, 1998
- 62. P. caritus Walter, 1986a
- 63. P. colefaxi Bayly, 1966
- 64. P. cornutus Nicholls, 1944
- 65. P. diadelus Walter, 1986a
- 66. P. galleti (Rose, 1957)
- 67. P. inflexus Walter, 1987
- 68. P. nihonkaiensis Hirakawa, 1983
- 69. P. pacificus Walter, 1986a
- 70. P. salinus (Giesbrecht, 1896)
- 71. P. serricaudatus (T. Scott, 1894)

Nudus species group

- 72. P. clevei A. Scott, 1909
- 73. P. gracilis (F. Dahl, 1894).

Unassigned species (These species were inadequately described or based on only one sex, thus making the species-group determination difficult.)

- 74. *P. bulbiferus* (Rose, 1957) [probably Ramosus group]
- 75. *P. heterothrix* Brehm, 1953 [probably Lobus group]
- 76. *P. masoni* Sewell, 1932 [probably Ramosus
- 77. *P. nankauriensis* Roy, 1977 [probably Hyalinus group]

Pedro) at 10°45′N, 122°30′E along the southeastern coast of Panay Island, Philippines, on September 27, 2003, by means of towing a conical plankton net

(diameter 30 cm, mesh size 0.1 mm) near the surface. Samples were collected at night at Iloilo, and during the day at the other two localities. All samples were fixed by 10% neutralized formalin/seawater immediately after collection. Specimens were dissected and mounted in CMC-10 (Masters Company, Ltd.) or gum-chloral. Copepods were examined with a differential interference contrast microscope (Nikon Optiphoto), and illustrated with the aid of a camera lucida. One adult female of a new species, described below, and four specimens of P. bispinosus were dehydrated in ethanol series, critical-point-dried, ion-sputtered, and observed with a scanning electron microscope (Jeol T-20). Body and appendage terminology follows Huys & Boxshall (1991). Types of the new species are deposited in the National Museum of Natural History, Smithsonian Institution, U.S.A. All measurements were done with a calibrated ocular micrometer and are presented in millimeter(s). Abbreviations used in this work appear primarily in the keys and tables: ae, aesthetasc; Ba, basis; CR, caudal rami; P5, leg 5; Pdg, pedigerous somite; Re, exopod; Ri, endopod; SD, standard deviation; Ur, urosomite(s); USNM, United States National Museum.

Order Calanoida G. O. Sars, 1903 Family Pseudodiaptomidae G. O. Sars, 1902

Genus *Pseudodiaptomus* Herrick, 1884 *Pseudodiaptomus terazakii*, new species Figs. 1–3

Material examined.—Holotype: female (USNM 291494). Allotype: male (USNM 291495). Paratypes: 5 males, 1 female, partly dissected and mounted on glass slides (USNM 291496); 4 females, 5 males, undissected specimens in ethanol (USNM 291497). All collected near the surface off Leganes, Panay Island, Philippines on September 27, 2003 by S. Ohtsuka.

Description.—Female: Body length 1.06— $1.27 \text{ mm} \text{ (mean } \pm SD = 1.20 \pm 0.08,$ N = 6). Prosome and urosome in approximate proportion 1.9:1, with both cephalosome and pedigerous somite 1 and pedigerous somites 4 and 5 completely fused (Fig. 1A, B), the latter ending in rounded posterolateral corners with sparsely distributed spinules anterolaterally, posterolateral margin with row of spinules. Urosome 4-segmented (Fig. 1C), slightly asymmetrical. Genital doublesomite (=urosomite 1) (Figs. 1A–D, 3A, B) swollen anteriorly, with 3 pairs of long spines directed laterally, left posterolateral margin protruding posteriorly, almost covering left side of urosomite 2, right dorsolateral margin with oblique row of spinules. Genital double-somite with ventral paired genital flaps expanded laterally into rounded lamellar lobes, each with posteriorly pointed tip; paired gonopores located beneath flaps, egg-sacs paired. Urosomite 2 relatively small, with spinules along posterodorsal margin, urosomite 3 with incomplete posterior margin spinule row, urosomite 4 (anal somite) slightly asymmetrical. Caudal rami highly asymmetrical, with left ramus longer and thicker than right, fourth caudal spine longer and thicker at base than others. Urosomites and caudal rami with proportions 32:9:13:11:35(left) 30 (right) = 100. Antennule (Fig. 1E) reaching distal end of anal somite, indistinctly 22-segmented, segments 6-7 partly fused and counted separately. Armature elements as follows (segment number = setae + ae): 1 = 1 +ae, 2 = 3 + ae, 3 = 2 + ae, 4 = 3 + ae, 5 =3 + ae, 6 = (1 spiniform element), 7 = 2 +ae, 8 = 1 + (1 spiniform element) + ae, 9= 2 + ae, 10 = 1 (1 spine) + ae, 11-14 = 2+ ae, 15-17 = 2, 18-19 = 1, 20-21 = 2, 22= 7 + ae.

Leg 5 uniramous (Fig. 1F), slightly asymmetrical, left leg slightly longer than right; coxae and intercoxal sclerite fused to form common base; inner margins of basis expanded medially, with lateral row

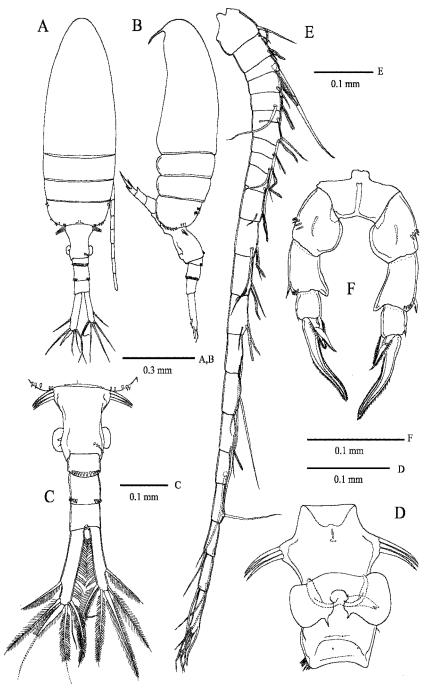


Fig. 1. *Pseudodiaptomus terazakii*, female, holotype. A, Habitus, dorsal view; B, Habitus, left lateral view; C, Prosomal end and urosome, dorsal view; D, Genital double-somite, ventral view; E, Antennule; F, Leg 5, anterior view.

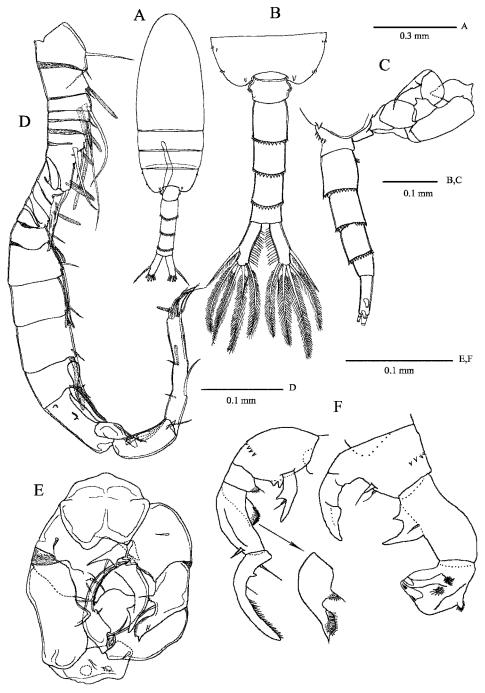
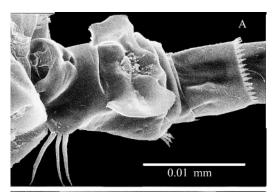


Fig. 2. *Pseudodiaptomus terazakii*, male, paratypes. A, Habitus, dorsal view; B, Prosomal end and urosome, dorsal view; C, Urosome, right lateral view; D, Right antennule; E, Leg 5, posterior view; F, Leg 5, anterior view (arrowed structure, posterior view of the right first exopod).



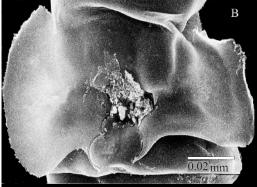


Fig. 3. SEM micrographs of *Pseudodiaptomus terazakii*, female. A, Urosome, ventrolateral view; B, Genital area, showing large expanded genital flaps, ventral view.

of minute spinules at midlength extending onto anterior surface, large seta on posterior surface. Exopods 3-segmented, first exopodal segment distomedial corner produced into triangular expansion, distolateral corner with row of small spinules plus lateral serrate subterminal spine. Second segment medial corner produced distally into large serrate process, distolateral corner with small medially serrate spine. Third segment proximally swollen, with small medial spine, and produced distally into long curved serrate process.

Male: Body length 0.94-1.09 mm (mean $\pm SD = 0.99 \pm 0.04$, N = 10); (Fig. 2A) similar to female, but more slender, prosome to urosome ratio 1.8:1, terminal somite rounded, with pair of minute posterodorsal acute processes and 2 pairs of lateral spinules. Urosome 5-segmented (Fig. 2B, C), almost symmet-

rical. Genital somite (urosomite 1) slightly asymmetrical, moderately produced anterolaterally with lateral spinule row. Urosomites 2–4 with complete spinule rows along posterior margin, urosomite 2 with anteroventral row of spinules. Caudal rami symmetrical. Urosomites and caudal rami with proportions 16:21:17:16:8:22= 100. Right antennule (Fig. 2D) geniculate and indistinctly 20-segmented, with only 2 distal segments after geniculation; armature elements as follows: 1 = 3, 2-3 = 2 +ae, 4 = 1, 5 = 2 + ae, 6 = 1, 7 = 2 + 4 + 4 + 4 = 1(1 spiniform element) + 2ae, 8 = process +ae, 9 = 2 + ae, 10 = 1, 11 = (1 spiniform)element) + ae, 12 = 1 + (1 spiniform)element) + ae, 13-16 = 2 + ae, 17 =process + 1, 18 = 2 processes (proximal and distal processes serrate and naked, respectively), 19 = 1 + (2 processes), 20 =9 + 2ae. Left antennule 22-segmented, armature as in female.

Leg 5 (Fig. 2E, F) heavily chitinized, highly modified, details difficult to observe, because it is typically contracted and held close to body. Coxae and intercoxal sclerite fused to form common base. Right leg exopod 3-segmented, left leg 2-segmented. Posterior view, legs contracted (Fig. 2E). Right leg basis medially expanded, with 2 small knoblike processes, distal to short bifurcated endopod with setule between fork and lateral spinule row. First exopodal segment medially produced, apex acute, margin flared and hirsute, with distal process bearing spinule patch and apical seta (arrowed structure Fig. 2F). Second segment elongate, bearing outer subdistal lateral spine. Third segment medially curved, tapering distally, inner margin setulose along distal half, proximal half with 2 spinules and small knob-like process between them. Left leg massive, with basis and endopod completely fused, forming strong medially curved inner process with terminal triangular knob, medial margin with 2 small processes with terminal setae and lateral spinule row.

First exopodal segment with proximomedial margin forming small and large triangular processes, spinule inserted at base of processes (small knob absent in one paratype specimen). Second segment with serrate medial process on lateral surface, truncate distally, with 2 circular patches of small setules; distal tip appears to be formed usually by 2 elongate plus 1 sub-triangular heavily chitinized elements (latter element absent in two paratypes). Anterior view, legs separated (Fig. 2F), basis with 3–4 large surface setae.

Etymology.—The species is named in honor of Professor Makoto Terazaki, Ocean Research Institute, University of Tokyo.

Remarks.—Pseudodiaptomus terazakii is easily assignable to the Lobus species group, forbesi—subgroup (Walter 1986a) by the male leg 5 left endopod fused to the basis, forming a large medially curved process, and the female leg 5 first exopodal segment with a triangular process at its distomedial corner. Pseudodiaptomus terazakii shares relevant characters with both P. smithi (poppei—subgroup) and P. annandalei (forbesi—subgroup): female genital double-somite asymmetrical, with anterolateral paired spines and second exopodal segment of male left fifth leg distally truncate, as in P. smithi; and endopod of male right fifth leg distally bifid and left first exopod medially produced with 2 acute processes, as in P. annandalei. However, P. terazakii is readily distinguishable from P. smithi by the following characters: (1) three anterolateral pairs of spines on the female genital double-somite whereas the latter has only one pair; (2) female urosomites 2 and 3 slightly shorter than in P. smithi; and (3) male leg 5 right endopod bifid at its apex and the left endopod simple, whereas in P. smithi the right the endopod is simple and left endopod bifid. The new species can be differentiated from P. annandalei by the presence in the latter of: (1) female genital double-somite with

only one pair of anterolateral spines and no ventral lamellar plates, (2) first exopodal segment of female leg 5 lacking distomedial triangular process, (3) male urosomite 2 with a dorsal spinule patch, and (4) endopodal process on the basis of the male left fifth leg lacking medial knobs, and the first right exopodal segment with a long simple spiniform process.

We noted slight variation of characters in the fifth leg of two paratypic males. The left leg of one lacks the small proximomedial process on the first exopodal segment and an outer process on the second exopodal segment. In the other male, the second exopodal segment of the left leg lacks the small distal chitinized triangular element. Because the remaining characters of the fifth legs of these aberrant paratypes show no additional variations, we suppose that these are intraspecific abnormalities.

Pseudodiaptomus terazakii is a member of the Lobus group. However, if the species-group key presented by Walter (1986a) is used, this species would key down to either the Hyalinus and/or Ramosus groups because of the forked endopod on the male right leg 5. Therefore, we present an emended key to appropriately include this new species.

Distribution.—This species is currently known only from the waters off Panay Island, Philippines.

Pseudodiaptomus bispinosus Walter, 1984 Figs. 4, 5

Pseudodiaptomus bispinosus Walter, 1984: 384–387, fig. 7.

Material examined.—Culasi Ajuy, Panay Island, Philippines, September 27, 2003, 8 females, 16 males; Iloilo (Fort San Pedro), Panay Island, Philippines, September 27, 2003, 1 male; Iloilo (International Port), Panay Island, Philippines, September 27, 2003, 1 male, by S. Ohtsuka.

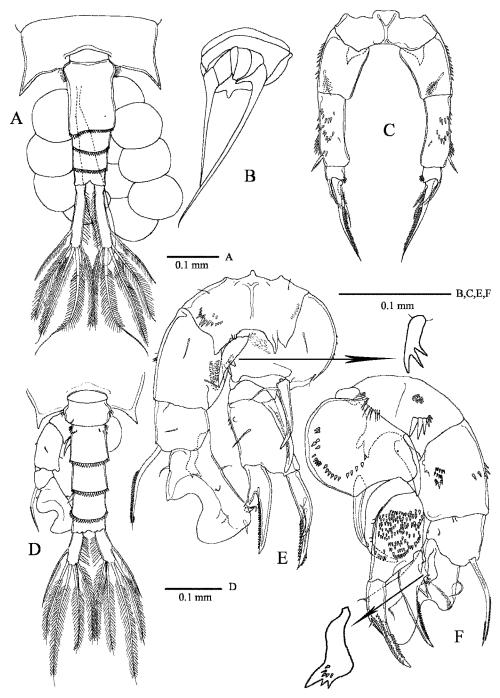


Fig. 4. *Pseudodiaptomus bispinosus*, female (A–C), male (D–F). A, Prosomal end and urosome, with egg sac and dotted line indicating ventrally attached spermatophore, dorsal view; B, Genital area, ventral view; C, Leg 5, anterior view; D, Prosomal end and urosome, dorsal view; E, Leg 5, posterior view (arrowed structure, shows detail of the right tricuspate endopod); F, Leg 5, anterior view (arrowed structure, shows detail of the proximal process on left second exopod).

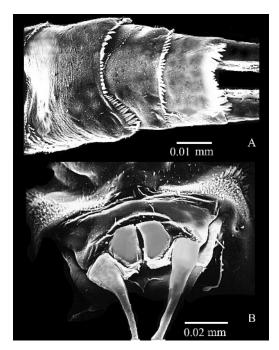


Fig. 5. SEM micrographs of *Pseudodiaptomus bispinosus*, female. A, Urosome, dorsal view of left posterolateral corner of genital double-somite; B, Genital area, ventral view.

Description.—Female: Body length 1.15— $1.22 \text{ mm} \text{ (mean } \pm SD = 1.18 \pm 0.03,$ N = 8). Pedigerous somites 4–5 fused (Fig. 4A) with posterolateral prosomal corners produced into sharply pointed, slightly asymmetrical wings. Genital double-somite (Fig. 4A) expanded anterolaterally on both margins, left posterolateral margin protruberant (Fig. 5A); genital operculum terminating in a pair of long processes (Fig. 5B), left process longer than right (Fig. 4B). Urosomites 1-3 with rows of spinules on posterior margin. Single egg sac with 11-15 eggs in ovigerous females. Caudal rami asymmetrical, right ramus slightly longer than left.

Leg 5 uniramous (Fig. 4C), coxae and intercoxal sclerite fused to form common base with distomedial corner produced, basis with expanded proximomedial corner and lateral spinule row, posterior surface with plumose seta. First exopodal segment with distolateral spine and clusters or rows of surface spinules; second segment small,

medially produced into curved process, with slender outer distal seta and medial patch of minute spinules; third segment distally produced with proximomedial seta, and setulose long medial margin.

Male: Body length 0.85–0.98 mm (mean \pm SD= 0.92 \pm 0.03, N = 14). Posterolateral prosomal corners (Fig. 4D) produced into sharply pointed process reaching beyond posterior margin of genital somite. Genital somite laterally swollen at midlength, with spinules; second urosomite longest, with rows of spinules on anterolateral and posteroventral surfaces; third urosomite with ventral rows of spinules, urosomites 2–4 with spinule row on posterior margin.

Leg 5 (Fig. 4E, F) only supplementarily described here, after description by Walter (1984). Coxae and intercoxal sclerite almost completely fused to form common base with spinules on posterior and anterior surfaces. Right leg: basis with proximomedial spinule patch, endopod tricuspate, and large distolateral curved spine with proximal setae; first exopodal segment produced into large curved distolateral process; second segment, distolateral corner with large spine bifurcate at midlength with 2 small surface spinules. Left leg: first exopodal segment with long narrow medially curved serrate spine; second segment, anterior view, apex of proximomedial process with small prominences.

Remarks.—The specimens from Panay Island vary slighty from the original description by Walter (1984) in a few minor characters: (1) female leg 5 basis and second exopodal segments bearing surface spinules, rather than setules; (2) male leg 5 coxae and intercoxal sclerite of male leg 5 almost completely fused, lacking small pair of distomedial protruberances; and (3) right second exopodal segment of male leg 5 with different spinulation pattern. We believe that these differences fall within intraspecific variability. This species is a member of the

Hyalinus group and the *trihamatus* - subgroup of Walter (1986a).

Distribution.—This is the second record of the species, which appears to be endemic to coastal waters of the Philippines.

Pseudodiaptomus annandalei Sewell, 1919

Pseudodiaptomus annandalei Sewell, 1919: 5–7, pl. 10, fig. 9.—1924:787, pl. 44, fig. 2a–c. —Brehm 1934:88–92, figs. 3–4.—1953:306–308, figs. 68–71.—Kasturirangan 1963:39, fig. 35a–d.—Wellershaus 1969:263, figs. 25–26.—Grigg 1972:84–86, figs. 34a–b, 36a–e. —Bayly 1975: table 1.—Pillai 1980:248–250, fig. Ig–j.—Reddy & Radhakrishna 1982:268–270, pl. 6, figs. 1–12.—Goswami 1983:254–257.—Walter 1986a:159–162, fig. 14A–L.—Mulyadi 2002a:9–10, fig. 2.

Pseudodiaptomus nostradamus Brehm, 1933: 137–142, figs. 8–12.—1934:84–92, figs. 5–6.—Kiefer 1938:81–91, figs. 9–17. Pseudodiaptomus dubius Kiefer, 1936: 231–235, figs. 9–12.—1938:86–91, figs. 18–24.

Schmackeria annandalei (Sewell).—Marsh 1933:42–43, pl. 20 fig. 8, pl. 21 fig. 1. Schmackeria dubia (Kiefer).—Shen & Song 1979:77–78, fig. 34a–e.—Chen & Zhang 1965:23, pl. 32, figs. 1–6.

Material examined.—Leganes, 4 females, 4 males; Iloilo, Fort San Pedro and International Port, 2 females, 1 male, Panay Island, Philippines, September 27, 2003 by S. Ohtsuka. Body length, female 1.13-1.46 mm (mean \pm SD=1.33 \pm 0.15, N = 4), male 1.05-1.11 mm (mean \pm SD=1.08 \pm 0.03, N = 4). These specimens do not differ from those described by Walter (1986a, 1987).

Distribution.—This species is broadly distributed in the Indo-West Pacific, from the coasts of India, Philippines, Indonesia, Australia, and China. From the

Philippines it was recorded from Calatagan, Batangas Province, Luzon Island (Walter 1986a), and Panay Island (Golez et al. 2004). Recently, it was found off Taiwan (R. Huys, pers. comm. to S. Ohtsuka, 2004).

Pseudodiaptomus clevei A. Scott, 1909

Pseudodiaptomus clevei A. Scott, 1909: 116–117, pl. 37, figs. 1–8.—Früchtl 1924: 48–49, figs. 29–30.—Sewell 1932:235. —Marsh 1933:31, pl. 6, figs. 1–2.—Mori 1942:553.—Pillai 1980:246, 256, fig. lo–s.—Walter 1986a:139–140, fig. 4A–H.—Ohtsuka et al. 2000:133–137, 144, fig. 4b, c.—Mulyadi 2002a:11–12, fig. 4.

Material examined.—One female, Iloilo (International Port), Panay Island, Philippines, September 27, 2003 by S. Ohtsuka. Body length.—Female 1.77 mm. This specimen does not differ from those described by Walter (1986a, 1987).

Distribution.—This species has a restricted distribution in the tropical regions of the Indo-West Pacific: Indonesia, the Andaman Sea, Thailand, and the Philippines. From the Philippines it was previously recorded from Padre Burgos, Quezon Province (Walter, 1986a).

Pseudodiaptomus trihamatus Wright, 1937

Pseudodiaptomus trihamatus Wright, 1937: 155–157, pl. 1, fig.1. [male only].—Walter 1984:380–383, figs.5a–i. —Oka, Saisho, & Hirota 1991:86, fig.4a–d.

Mazellina galleti Rose, 1957:235–240, figs.1–3, [female only = *P. trihamatus*] *Pseudodiaptomus penicillus* Li & Huang, 1984:386–390, figs. 12–18.

Remarks.—This species was not found during this study, but has been reported from the Philippines (Walter 1984). We did not examine the specimens of Li & Huang. Nonetheless, we propose the synonymy of *P. penicillus* with *P. trihamatus*, as the former is identical in

appearance and description to the latter and the authors made no reference to the existence of *P. trihamatus*.

Key to the 14 Species of *Pseudodiaptomus* known from the Philippines

Fourteen pseudodiaptomid species, including the new species P. terazakii, have been recorded from the Philippines (Walter 1986a, 1987; Walter et al. 2002; present study). Walter (1984, 1986a, 1987) recognized seven species groups in Pseudodiaptomus, with the following species groups represented by the Philippine species: Nudus group (P. clevei); Improcerus group (P. ornatus, P. trispinosus); Lobus group (P. annandalei, P. brehmi, P. smithi, P. terazakii); Hyalinus group (P. aurivilli, P. bispinosus, P. trihamatus); Ramosus group (P. philippinensis, P. caritus, P. diadelus, P. galleti). The following keys are for each sex and include only those species of Pseudodiaptomus currently known from the Philippines. Only the female of P. trispinosus is known, because the male of this species was re-assigned as the male of P. ornatus (Walter et al. 2002). Abbreviations are used in this key for convenience.

Female

1.	Pediger 5 posterior corners expanded distolaterally
	Pediger 5 posterior corners rounded,
_	not expanded distolaterally 11
2.	
	nences at distomedial corner P. clevei
	P5 Ba without acute prominences at
	distomedial corner 3
3.	P5 Re3 about twice as long as medial
	margin of Re2 4
	P5 Re3 equal or subequal to medial
	margin of Re2 6
4.	
	tion dorsally; P5 Ba with proximo-
	medial corner rounded P. aurivilli
	Ur 1 with dorsal process or pro-
	jection; P5 Ba with proximomedial
	corner pointed 5
5.	Ur1 left posterodorsal margin with 2
	pointed processes P. trihamatus

Url left posterodorsal margin with-

out pointed processes . . . P. bispinosus

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6.	P5 right Ba with bluntly produced
	distomedial process
	P5 right Ba without distomedial
_	process
7.	P5 Ba with distomedial process reach-
	ing midlength of Rel P. ornatus
	P5 Ba with distomedial process
	reaching at most one-fourth length
	of Re1 P. trispinosus
8.	Pediger 5 asymmetrical, with left
	posterior corner larger and more
	laterally directed P. caritus
	Pediger 5 symmetrical 9
9.	P5 Ba with 2-3 distolateral spinu-
	les P. philippinensis
	P5 Ba without distolateral spinules 10
10.	. Url with spinules on left and right
	margins P. diadelus
	Url with spinules on right margin
11	only
11.	Url with 1 or 3 pairs of lateral
	spines anteriorly 12
12	.Url with 3 pairs of lateral spines
12.	anteriorly P. terazakii
	Url with 1 pair of lateral spines
	anteriorly
12	Ur and CR asymmetrical; P5 Re 1
13.	with triangular process near distome-
	dial corner P. smithi
	Ur and CR symmetrical; P5 Re1
	without distomedial process
	P. annandalei
Ma	ale
1	D5 14 4 14 4 0 D1 D 7 1
1.	P5 without right or left Ri P. clevei

2.	Pediger 5 rounded 3
	Pediger 5 distally pointed 7
3.	P5 with left Ri large, elongate,
	medially curved and fused to Ba 4
	P5 with left Ri simple, separated
	from Ba P. ornatus
4.	P5 with left Ri simple 5
	P5 with left Ri bifid P. smithi
5.	P5 with left Re1 produced medially,
	with 2 pointed processes 6
	P5 with left Re1 lacking medial
	pointed processes P. brehmi
6.	P5 right Rel distolateral process

slender and simple P. annandalei

P5 with right and/or left Ri 2

	P5 right Re1 distolateral process
	thickened and hirsute P. terazakii
7.	P5 without left Ri 8
	P5 with left Ri 10
8.	P5 with left Re2 hyaline margin
	convexly curved P. aurivilli
	P5 with left Re2 hyaline margin
	incised 9
9.	P5 right Ri with 3 processes, distal
	process longest; distomedial corner of
	left Ba produced into large acute
	process P. trihamatus
	P5 right Ri with 3 processes, all
	equal in length; distomedial corner of
	left Ba produced into small rounded
	process P. bispinosus
10.	P5 with outer spine on right Re1
	bifid at tip P. philippinensis
	P5 with outer spine on right Re1
	simple at tip
11.	P5 with left Ri small, reaching at
	most distal end of Rel P. galleti
	P5 with left Ri large, reaching well
	beyond distal end of Rel 12
12.	P5 with right Ri widely bifurcated
	distally P. diadelus
	P5 with right Ri narrowly bifurcated
	proximally P. caritus

Species-group Variation in Morphology and Revised Group Key

We have examined more than 75% of the known species of Pseudodiaptomus. It is obvious that extensive variation in body shape and/or the fusion of somites and segments in certain appendages (i.e., antennules and leg 5) occurs within the genus (Table 2). Among the 77 currently recognized species, the mouthparts and swimming legs are almost identical in shape, segmentation, spination, and/or spinulation patterns. The female genital double-somite is of particular interest (Soh et al. 2001, Walter et al. 2002), especially regarding the ventral genital flaps and egg sac number. Antennule segmentation has 3 basic patterns within this genus, with segments 6-7 partly fused and counted separately. In the first pattern, the antennules are 21-segmented in the female and in the left male antennule, with segments 4-5 fused; the right male antennule consists of 20 segments, with 2 of the segments distal from the geniculation (Hyalinus species group). In the second pattern, the antennules are 22-segmented in the female and left male antennule, with segments 4–5 separate; the right male antennule consists of 20 segments, with 2 segments distal after the geniculation (Lobus species group). In the third antennule pattern, the antennules have 22 segments in the female and left male antennule, with segments 4-5 separate; a modified barbed setae is present on the antepenultimate segment (except in the Americanus and Nudus species groups), whereas the right male antennule is typically 21-segmented, with 3 segments distal after the geniculation (Americanus, Burckhardt, Improcerus, Nudus, and Ramosus species groups). The Nudus group is unique in consisting of only two species, P. clevei (from the Pacific) and P. gracilis (from Brazil), and possessess a right male antennule 20-segmented pattern (rather than 21 segments); both species have segments 2-3 fused. Previous reports of antennule segmentation were incorrectly stated for some species groups by Walter (1986a, 1987, 1989) and Walter et al. (2002), but are correct in the above described patterns for the species groups.

The leg 5 in females is typically symmetrical and of limited value to separate species. Exceptions are noted for two species groups: the Improcerus group, in which the basis may have a distinct distomedial rounded processes; and the Nudus group, in which *P. clevei* has a unique pair of sharp spine-like medial protrusions on the basis.

The male leg 5 typically provides the most reliable morphological character(s) used for species determination and species group placement. The presence and/or absence of the left and/or right endopods easily indicates to which group a species belongs. The Lobus group is characterized by the fusion of the large left endopod to the basis, which is typically curved and can be simple or branched, whereas the right endopod is small, of variable shape, and may appear partly fused to the basis in some species. Rather than discuss each of the speciesgroup characteristics of the male leg 5, because each group is unique in terms of the presence and/or absence of an endopod

Table 2.—Salinity preference, geographical distribution and morphological characters for the species groups of Pseudodiaptomus. Additional abbreviations and symbols used in this table: A = Africa; EM = estuarine-marine; FEM = freshwater-marine; IP = Indo-Pacific region; M = marine; NW = New World;! = species introduced into a new geographic region; S = separate; F = fused; * = possesses dorsal spines; ± = some species with or without dorsal spines; P = pointed; R = Ш antepenultimate segment with modified barbed seta; VS = variably shaped; SB = simple or branched; SYM = symmetrical; ASYM = asymmetrical; @ = Ba in P. rounded; L = lacks dorsal spines; + = partly fused in P. aurivilli; % = paired egg sac in P. paulini; △ male right/male left & female antennule segmentation; ▲ clevei with paired printed process; • Ba with distomedial processes; • Ba proximomedially swollen; ■ Rel with produced medial process.

				Species group			
Character	Nudus	Burckhardt	Improcerus	Ramosus	Americanus	Hyalinus	Lobus
Salinity	EM	M	M	M	EM	M	FEM
Geographical Distribution	NW,IP	IP	IP,A	IP	NW	IP,NW,!	IP, NW,!
Cephalon/Pdg1	S	S	S	S	S	Ц	Ц
Pdg4-5	*, F, P (<i>P. clevei</i>)	*,F,P	±,F,P or R	\pm ,F,P or R	L,S,P or R	±,F,P,+	±,F,R
	L,S,R (P. gracilis)						
Egg Sac	single	single	single,%	single	paired	single	paired
Antennule△	21/22 (clevei)	21/22▲	21/22▲	21/22▲	21/22	20/21	20/22
	20/22 (gracilis)						
Male P5 left Ri	lacking	rudimentary	NS	simple	NS	lacking	F, large,SB
Male P5 right Ri	lacking	rudimentary	rudimentary	branched	lacking	SB	△S, small,VS
Female P5	SYM,@	SYM	ASYM,	SYM	SYM	SYM,	SYM,
Female Ur segment no.	4	4	4	4	2–4	4	4

on the right and/or left leg 5, we refer the reader to Table 2.

This key to the species groups and subgroups of *Pseudodiaptomus* is revised from the original presented by Walter (1986a). The key is based primarily on the male fifth leg, because female characters are not consistent among and within species groups. >=(greater than or equal to); <=(less than or equal to).

Male Ra with right Ri absent

1.	Male Ba with right Ri absent 2
	Male Ba with right Ri present 3
2.	Male left Ri absent Nudus
	Male left Ri small and digitiform
	Americanus
	(a) Male left Re2 rounded
	acutus —subgroup
	(b) Male left Re2 spatulate
	pelagicus—subgroup
3.	
٥.	and simple, left Ri fused or separate 4
	Male right Ri large and/or branched,
	left Ri never fused
4.	Male left Ri rudimentary
4.	
	Burckhardt
	Male left Ri large and variably
_	shaped
5.	Male left Ri simple, large, and variably
	spatulate; Female P5 Ba usually with
	small, bluntly triangular process at
	distomedial corners; cephalon & Pdg1
	separate Improcerus
	Male left Ri large process fused to
	Ba; Female P5 Re 1 with small
	triangular process and hyaline cover-
	ing at distomedial corners; cephalon
	& Pdg1 fused Lobus
	(a) Male left Ri apex hook-like and
	simple forbesi—subgroup
	(b) Male left Ri apex hook-like and
	bifid poppei—subgroup
6.	Male left Ri absent; Female P5 Re3
	>= Re2 Hyalinus
	(a) Male left Re2 convexly curved,
	hyaline
	(b) Male left Re2 incised, hyaline
	Male left Ri present, variable in size;
	Female P5 Re3 <= length of
	Re2 Ramosus
	(a) Male right Rel, distolateral spine
	bifid hickmani—subgroup

(b) Male right Rel, distolateral spine not bifid. serricaudatus—subgroup

Schmackeria: a junior synonym of Pseudodiaptomus

The genus Pseudodiaptomus was established by Herrick (1884) when he described P. pelagicus from the Gulf of Mexico. The establishment of this genus got off to a difficult start, because Herrick did not provide any illustration of the species and it was published in little known publication, The Reports of the Geological and Natural History Survey of Minnesota. An illustration of the species was finally published by Herrick (1887) in another, not widely available publication, the Memoirs of the Denison Scientific Association, University of Denison, where Herrick taught. Herrick's illustrations and description were incomplete. Three years later, Poppe & Richard (1890) described the new genus and species Schmackeria forbesi from Shanghai, China. In that paper they made no reference to Herrick's genus Pseudodiaptomus. Within the next 10 years, seven additional species were described and assigned to different genera: Weismanella acuta Dahl, 1894, W. gracilis Dahl, 1894, and W. richardi Dahl, 1894, from South America; S. hessei Mrázek, 1895 from the Congo; Heterocalanus serricaudatus T. Scott, 1894 from the Gulf of Guinea; S. stuhlmanni Poppe & Mrázek, 1895 from Mozambique; and S. salina Giesbrecht, 1896 from the Red Sea. Poppe & Mrázek (1895) synonymized Weismannella with Schmackeria, recognizing Dahl's species as belonging to Schmackeria even though they were from different oceans. None of these authors made reference to Pseudodiaptomus, and we speculate here that they were unaware of Herrick's articles.

Since 1900, an additional 80 species have been described as *Pseudodiaptomus* or *Schmackeria*, and a number of these have already been synonymized. Currently, we recognize 77 species, including *P*.

terazakii, in the genus Pseudodiaptomus. Boxshall & Halsey (2004), Razouls (1995), Walter (1984, 1986a,b, 1987, 1989), and Walter et al. (2002) concluded that the genera Mazellina, Schmackeria, and Weismanella, and the species Heterocalanus serricaudatus are junior synonyms of Pseudodiaptomus. The species reported as Schmackeria are the 17 members of the Lobus species group. These species typically occur in estuarine and freshwater habitats, though several species are found in fully marine habitats. Most species of this group are known from the waters around China, Japan, and Korea, and some are found throughout the Indo-West-Pacific. Within the last two decades, species of the Lobus species group have been reported as introduced into the eastern Pacific, along the coasts of Oregon and California, mainly via ship ballast water, by Orsi & Walter (1991), Cordell et al. (1992), and Cordell & Morrison (1996).

Some authors considered have Schmackeria and Pseudodiaptomus as separate genera (Marsh 1933; Shen & Song 1979; Dussart & Defaye 1983, 2001, 2002; Borutzky et al. 1991). The publication by Borutzky et al. (1991) is a revision of an old manuscript by Borutzky that was not published until 15 years after his death, by the co-authors Stepanova and Kos. They separated the genera based on three characters particular Schmackeria: (1) last thoracic somite with roundish outer corners, (2) male fifth leg, left basis with long distal outgrowth(s) on inner margin, outgrowth(s) not separated from the segment, endopodite absent. (We believe this means fused, based on the Russian transliteration), and (3) female leg 5 first exopodal segment with pointed outer distal corner (Borutzky et al. probably meant the distomedial corner). Dussart & Defaye (2002), supporting the use of Schmackeria by Borutzky et al. (1991), included the following eight species as members of the genus Schmackeria— bulbosa, forbesi, in-flata, inopina, inopina gordiodes, inopina saccupoda, poplesia, and spatulata. Surprisingly, they did not include the other nine species of the Lobus species group—annandalei, binghami, brehmi, lobipes, malayalus, mixtus, poppei, smithi, and tollingerae—in their account of Schmackeria.

From the data presented in Table 2, it is clear that maintaining the genus Schmackeria is not valid, based on the following considerations: (1) the rounded fifth pedigerous somite is present in the Americanus, Lobus, and Nudus groups, and several species in the Ramosus group; therefore, this character of Pseudodiaptomus is shared with Schmackeria, and is not exclusive to the latter genus as suggested by Borutzky et al. (1991). (2) the female fifth leg with a distomedial processes on the exopodal segment 1 is indeed a character unique to the Lobus group (i.e., Schmackeria). However, the presence of processes is not unique among females in Pseudodiaptomus; members of the Hyalinus, Improcerus and Nudus groups all have different processes and/ or protrusions on their basis segment. (3) although the fusion of the endopod with the basis of the male left fifth leg is unique among the Lobus species group, it is only a variation of endopodal shape, size, and presence within the genus Pseudodiaptomus. Therefore, we conclude that the genus Schmackeria is a junior synonym of Pseudodiaptomus, because Pseudodiaptomus was described in 1884 and has priority over Schmackeria according to the ICZN rules.

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