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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 group]
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 mm (mean ± *SD* = 1.20 ± 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 double-somite (=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

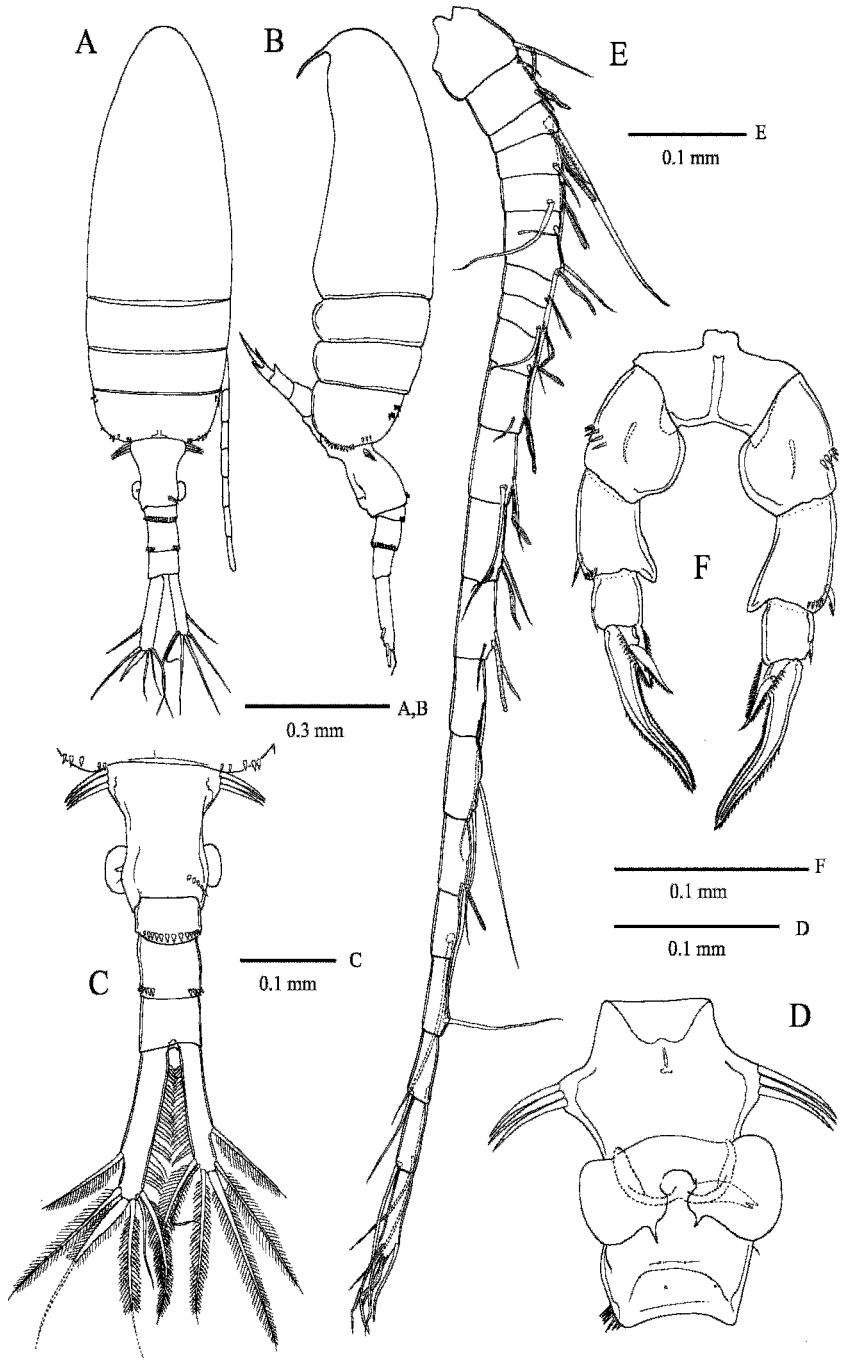

Fig. 1. *Pseudodiaptomus terazakii*, female, holotype. A, Habitus, dorsal view; B, Habitus, left lateral view; C, Prosomal end and urosome, dorsal view; D, Genital double-somite, ventral view; E, Antennule; F, Leg 5, anterior view.

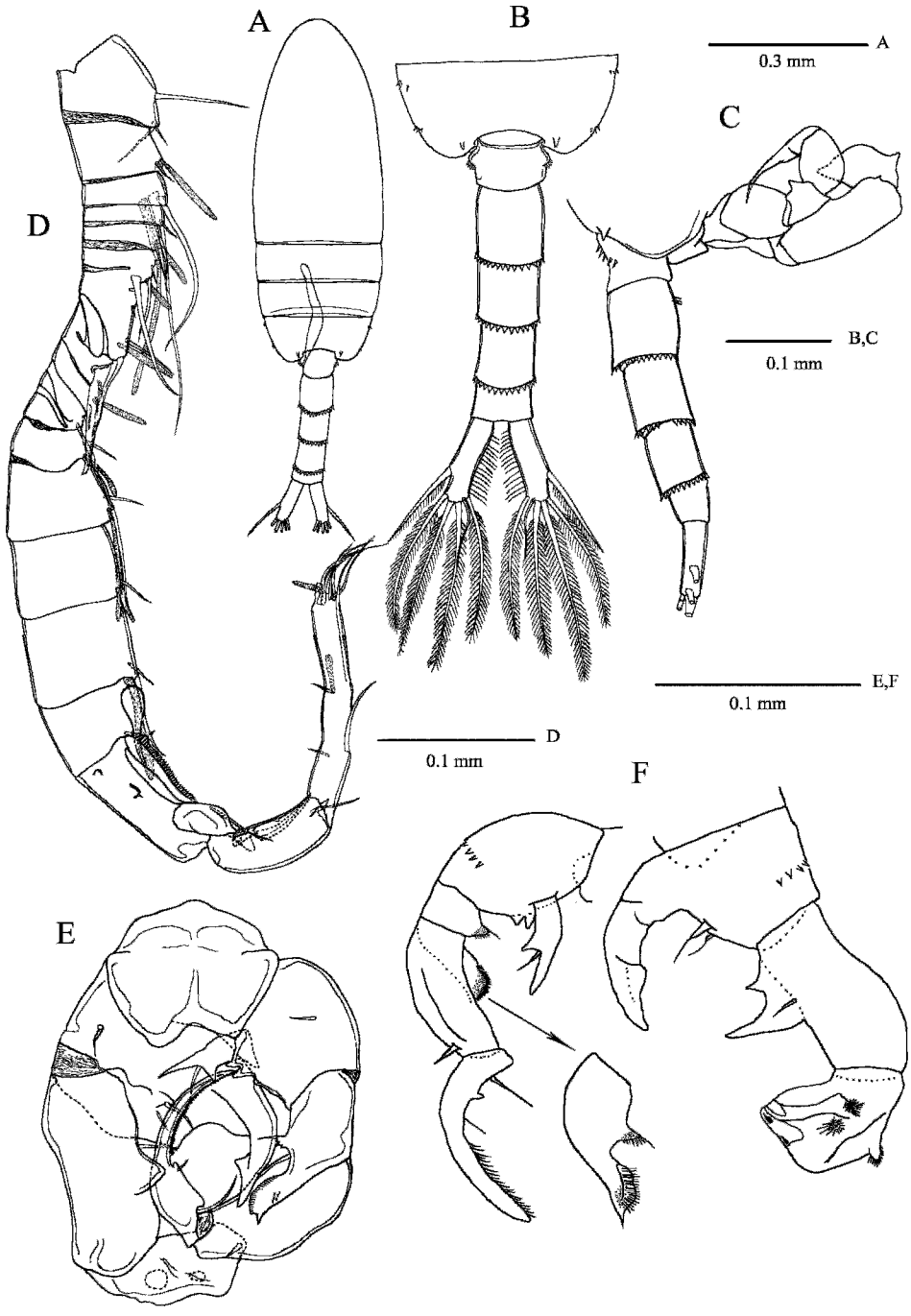

Fig. 2. *Pseudodiaptomus terazakii*, male, paratypes. A, Habitus, dorsal view; B, Prosomal end and urosome, dorsal view; C, Urosome, right lateral view; D, Right antennule; E, Leg 5, posterior view; F, Leg 5, anterior view (arrowed structure, posterior view of the right first exopod).

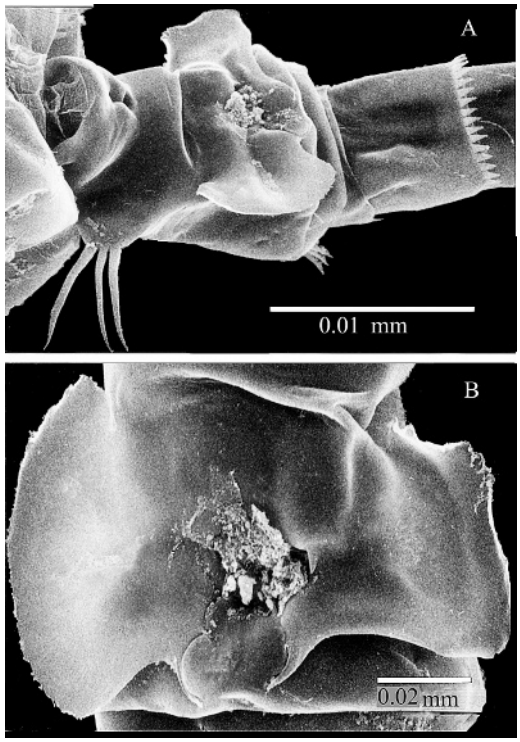

Fig. 3. SEM micrographs of *Pseudodiaptomus terazakii*, female. A, Urosome, ventrolateral view; B, Genital area, showing large expanded genital flaps, ventral view.

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 ± *SD* = 0.99 ± 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 symmetrical. 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 + (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 knob-like 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.

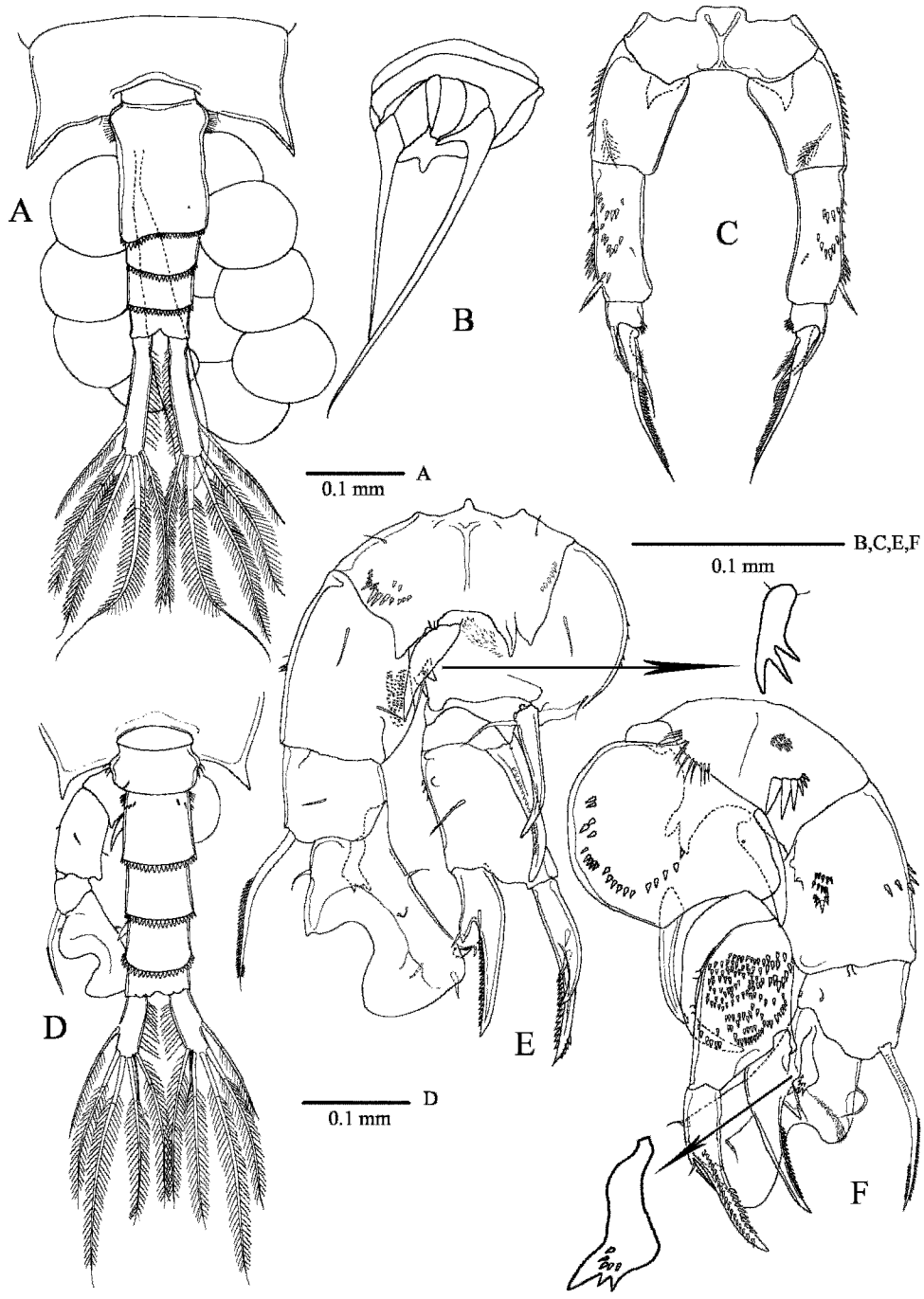

Fig. 4. *Pseudodiaptomus bispinosus*, female (A–C), male (D–F). A, Prosomal end and urosome, with egg sac and dotted line indicating ventrally attached spermatophore, dorsal view; B, Genital area, ventral view; C, Leg 5, anterior view; D, Prosomal end and urosome, dorsal view; E, Leg 5, posterior view (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).

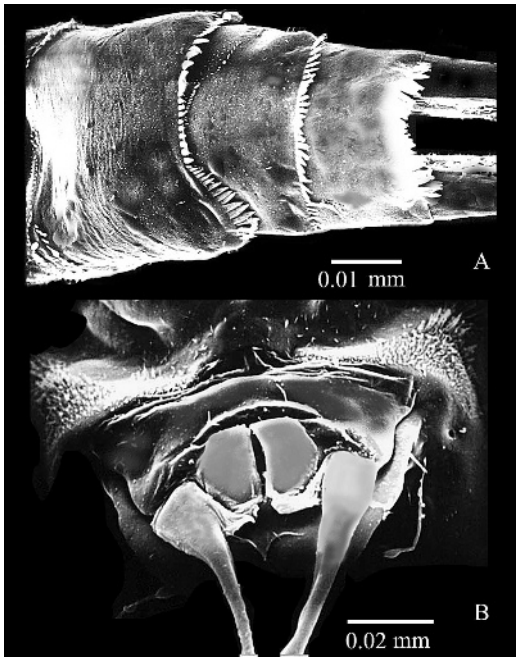

Fig. 5. SEM micrographs of *Pseudodiaptomus bispinosus*, female. A, Urosome, dorsal view of left posterolateral corner of genital double-somite; B, Genital area, ventral view.

Description.—Female: Body length 1.15–1.22 mm (mean ± *SD* = 1.18 ± 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 ± *SD*= 0.92 ± 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 ± *SD* = 1.33 ± 0.15, N = 4), male 1.05–1.11 mm (mean ± *SD*= 1.08 ± 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 2
   Pediger 5 posterior corners rounded, not expanded distolaterally 11
2. P5 Ba produced into 2 acute prominences 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. Ur1 without specialized ornamentation dorsally; P5 Ba with proximomedial corner rounded ... *P. aurivilli*
   Ur 1 with dorsal process or projection; P5 Ba with proximomedial corner pointed 5
5. Ur1 left posterodorsal margin with 2 pointed processes ..... *P. trihamatus*
   Ur1 left posterodorsal margin without pointed processes ... *P. bispinosus*
6. P5 right Ba with bluntly produced distomedial process 7
   P5 right Ba without distomedial process 8
7. P5 Ba with distomedial process reaching midlength of Re1 ..... *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 spinules ..... *P. philippinensis*
   P5 Ba without distolateral spinules 10
10. Ur1 with spinules on left and right margins ..... *P. diadelus*
    Ur1 with spinules on right margin only ..... *P. galleti*
11. Ur1 without lateral spines .... *P. brehmi*
    Ur1 with 1 or 3 pairs of lateral spines anteriorly 12
12. Ur1 with 3 pairs of lateral spines anteriorly ..... *P. terazakii*
    Ur1 with 1 pair of lateral spines anteriorly 13
13. Ur and CR asymmetrical; P5 Re 1 with triangular process near distomedial corner ..... *P. smithi*
    Ur and CR symmetrical; P5 Re1 without distomedial process. . . . . *P. annandalei*

Male

1. P5 without right or left Ri ... *P. clevei*
   P5 with right and/or left Ri 2
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 Re1 distolateral process slender and simple ..... *P. annandalei*

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
11. P5 with left Ri small, reaching at most distal end of Re1 ..... *P. galleti*
    P5 with left Ri large, reaching well beyond distal end of Re1 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 species-group 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 = rounded; L = lacks dorsal spines; + = partly fused in *P. aurivilli*; % = paired egg sac in *P. paulini*; △ male right/male left & female antennule segmentation; ▲ = antepenultimate segment with modified barbed seta; VS = variably shaped; SB = simple or branched; SYM = symmetrical; ASYM = asymmetrical; @ = Ba in *P. clevei* with paired pointed process; ● = Ba with distomedial processes; ◆ = Ba proximomedially swollen; ■ = Re1 with produced medial process.

Character	Species group						
	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	F	F
Pdg4–5	*,F,P (*P. clevei*) L,S,R (*P. gracilis*)	*,F,P	±,F,P or R	±,F,P or R	L,S,P or R	±,F,P,+	±,F,R
Egg Sac	single	single	single,%	single	paired	single	paired
Antennule△	21/22 (*clevei*) 20/22 (*gracilis*)	21/22▲	21/22▲	21/22▲	21/22	20/21	20/22
Male P5 left Ri	lacking	rudimentary	VS	simple	VS	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).

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. Male right Ri rudimentary or small and simple, left Ri fused or separate 4
   Male right Ri large and/or branched, left Ri never fused 6
4. Male left Ri rudimentary .... Burckhardt
   Male left Ri large and variably shaped 5
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 covering 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. ..... .*aurivilli*—subgroup
   (b) Male left Re2 incised, hyaline ..... .*trihamatus*—subgroup
   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 have considered *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 only three characters particular to *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, inflata, 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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