THE ZOOGEOGRAPHY OF THE GENUS PSEUDODIAPTOMUS (CALANOIDA: PSEUDODIAPTOMIDAE)

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Abstract: Pseudodiaptomids are primarily demersal in habit, found from freshwater to coastal marine waters, and circumglobal in distribution. These calanoids generally migrate into the water column at dusk and remain near or attached to bottom substrates during the day. The 70 species in the genus Pseudodiaptomus are divided into 7 morphologically, though not necessarily geographically, distinct species groups. Morphological variations in the fifth pair of legs of males are used for species determination. About 35 species are present in the eastern Indo-Pacific, 23 in the western Indo-Pacific, 15 in the Americas, 6 in Japanese waters, and 5 species along southern African waters. Allopatry, sympatry, and parapatry are expressed within these species groups.

Recent plankton studies using emergence traps or diver-towed nets near the bottom, have yielded new species and distributional information on several demersal calanoids (Alldredge and King, 1980; Ohlhorst, 1982; Barr, 1984; Walter, 1984). Members of the genus Pseudodiaptomus inhabit fresh to hypersaline waters, in most tropical and temperate coastal areas, and display a pronounced diel migration.

In the genus Pseudodiaptomus, species and species groups can be distinguished primarily by the presence or absence of endopods (Ri) on the right and left male fifth legs (P5), with the female P5 and habitus of both the male and female serving a secondary role in species determination (Walter, unpubl. data). The 70 known species, 39 of which I have examined, may be divided into 7 species groups (Table 1).

Table 1: *Characteristics for Pseudodiaptomus species groups and species subgroups assemblages. IP = Found in Indo-Pacific; A = Found around southern half of Africa; B = Found in North and/or South American waters; F = Reported from freshwater habitats; S = Schmackeria according to Marsh, 1933; U = Specimens deposited at USNM; X = Reported only once in literature; O = Only female reported in the literature; NA = No available or unclear illustrations in the literature.*

	IP	A	B	F	S	U	X	O	NA
1) NUDUS									
1) P. clevei Scott, 1909	+	-	-	-	-	+	-	-	-
2) P. gracilis (Dahl, 1894)	-	-	+	+	-	+	-	-	-
2) AMERICANUS									
A) "acutus-subgroup"									
3) P. acutus (Dahl, 1894)	-	-	+	-	-	+	-	-	-
4) P. acutus leptopus Loeffler, 1963	-	-	+	-	-	-	-	-	-
5) P. galapagensis Grice, 1964	-	-	+	-	-	+	-	-	-
6) P. richardi (Dahl, 1894)	-	-	+	+	-	+	-	-	-
7) P. richardi inequalis (Brian, 1926)	-	-	+	+	-	-	+	-	-
8) P. wrighti Johnson, 1964	-	-	+	-	-	+	+	-	-
B) "pelagicus-subgroup"									
9) P. americanus Wright, 1937	-	-	+	-	-	-	+	-	-
10) P. cokeri González and Bowman, 1965	-	-	+	-	-	+	-	-	-
11) P. coronatus Williams, 1906	-	-	+	-	-	+	-	-	-
12) P. cristobalensis Marsh, 1913	-	-	+	-	-	-	-	-	-

Table 1 (continued)

	IP	A	B	F	S	U	X	O	NA
13) P. culebrensis Marsh, 1913	-	-	+	-	-	-	-	-	-
14) P. euryhalinus Johnson, 1939	-	-	+	-	-	+	-	-	-
15) P. marshi Wright, 1936	-	-	+	-	-	+	+	-	-
16) P. pelagicus Herrick, 1884	-	-	+	-	-	?	+	-	-
3) BURCKHARDTI									
17) P. burckhardti Sewell, 1932	+	-	-	-	-	+	-	-	-
4) IMPROCERUS									
18) P. adamanensis Pillai, 1980	+	-	-	-	-	-	-	-	-
19) P. batillipes Brehm, 1954	-	+	-	-	-	-	+	-	-
20) P. charteri Grindley, 1963	-	+	-	-	-	-	-	-	-
21) P. hessei (Mrazek, 1894)	-	+	-	-	-	-	-	-	-
22) P. pauliani Brehm, 1951	-	+	-	-	-	-	+	-	-
23) P. stuhlmanni (Poppe and Mrazek, 1895)	-	+	-	-	-	-	+	-	-
24) P. sp. 1	+	-	-	-	-	+	-	-	-
5) LOBUS									
A) "forbesi-subgroup"									
25) P. annandalei Sewell, 1919	+	-	-	+	+	+	-	-	-
26) P. binghami Sewell, 1912	+	-	-	+	+	-	-	-	-
27) P. binghami malayalus Wellershaus, 1969	+	-	-	+	-	+	-	-	-
28) P. brehmi Keifer, 1938	+	-	-	+	-	-	+	-	-
29) P. bulbosus (Shen and Tai, 1964)	+	-	-	+	-	-	+	-	-
30) P. forbesi (Poppe and Richard, 1890)	+	-	-	+	+	-	-	-	-
31) P. inflatus (Shen and Tai, 1964)	+	-	-	+	-	-	+	-	-
32) P. inopinus Burckhardt, 1913	+	-	-	+	+	-	-	-	-
33) P. inopinus saccupodus (Shen and Tai, 1962)	+	-	-	+	-	-	+	-	-
34) P. lobipes Gurney, 1907	+	-	-	+	+	-	-	-	-
35) P. poplesia (Shen, 1955)	+	-	-	+	-	-	-	-	-
36) P. spatulatus (Shen and Tai, 1964)	+	-	-	+	-	-	+	-	-
B) "poppei-subgroup"									
37) P. poppei Stingelin, 1900	+	-	-	+	+	-	+	-	-
38) P. smithi Wright, 1928	+	-	-	+	+	+	+	-	-
39) P. tollingeri Sewell, 1919	+	-	-	+	+	+	-	-	-
6) HYALINUS									
A) "aurivilli-subgroup"									
40) P. aurivilli Cleve, 1901	+	-	-	-	-	+	-	-	-
41) P. bowmani Walter, 1984	+	-	-	-	-	+	-	-	-
42) P. compactus Walter, 1984	+	-	-	-	-	-	-	-	-
43) P. mertoni Fruchtl, 1923	+	-	-	-	-	+	-	-	-
B) "trihamatus-subgroup"									
44) P. baylyi Walter, 1984	+	-	-	-	-	+	-	-	-
45) P. bispinosus Walter, 1984	+	-	-	-	-	+	-	-	-
46) P. incisus Shen and Lee, 1963	+	-	-	-	-	-	+	-	-
47) P. sewelli Walter, 1984	+	-	-	-	-	-	-	-	-
48) P. trihamatus Wright, 1937	+	-	-	-	-	+	-	-	-
49)?P. dauglishi Sewell, 1932	+	-	-	+	-	?	-	-	-
7) RAMOSUS									
A) "serricaudatus-subgroup"									
50) P. ardjuna Brehm, 1953	+	-	-	-	-	-	-	-	-
51) P. sp. 2	+	-	-	-	-	+	-	-	-
52) P. hickmani Sewell, 1912	+	-	-	+	-	-	-	-	-
53) P. sp. Nishida (pers comm)	+	-	-	-	-	+	-	-	-
54) P. jonesi Pillai, 1970	+	-	-	-	-	+	-	-	-
55) P. marinus Sato, 1913	+	-	-	-	-	+	-	-	-
56) p. serricaudatus (T. Scott, 1894)	+	-	-	-	+	+	-	-	-
B) "salinus-subgroup"									
57) P. sp. 3	+	-	-	-	-	+	-	-	-
58) P. colefaxi Bayly, 1966	+	-	-	-	-	+	-	-	-
59) P. cornutus Nicholls, 1944	+	-	-	-	-	+	-	-	-
60) P. sp. 4	+	-	-	-	-	+	-	-	-
61) P. galleti (Rose, 1957)	+	-	-	-	-	+	-	-	-
62) P. nihonkaiensis Hirakawa, 1983	+	-	-	-	-	+	-	-	-
63) P. sp. 5	+	-	-	-	-	+	-	-	-
64) P. salinus (Giesbrecht, 1896)	+	-	-	-	-	-	-	-	-

Table 1 (continued)

	IP	A	B	F	S	U	X	O	NA
8) DUBIOUS UNASSIGNED SPECIES									
65) P. beieri Brehm, 1951 [= ?P. dauglishi]	+	-	-	-	-	-	-	-	+
66) P. bulbiferus (Rose, 1957)	+	-	-	-	-	-	-	+	-
67) P. heterothrix Brehm, 1953	+	-	-	-	-	-	-	-	+
68) P. masoni Sewell, 1932	+	-	-	-	-	-	-	+	-
69) P. nankauriensis Roy, 1977	+	-	-	-	-	-	-	+	-
70) P. ornatus (Rose, 1957)	+	-	-	-	-	+	-	+	-

Fifty species have been reported from the Indo-Pacific region (Figure 1), most of them collected from coastal brackish water to marine habitats (coral reefs, coral rubbles, grassbeds, river mouths, mud embayments, fishponds, and mangroves). Several Indo-Chinese species (particularly of the Lobus group) occur in predominantly freshwater habitats (rivers, inland lakes and reservoirs); most species in this group were assigned by Marsh (1933), who had no Indo-Pacific material to examine, to the genus Schmackeria Poppe and Richard, 1890. I concur with Wright (1936), Vervoort (1965), and Pillai (1980) that Schmackeria is a synonym of Pseudodiaptomus. Some species display a distinctly euryhaline character such as two American species (P. coronatus and P. euryhalinus) and two African species (P. charteri and P. hessei), the latter pair being pioneer species that quickly establish dense populations after estuarine flooding (Wooldridge and Melville-Smith, 1979).

Fourteen species (Americanus group) are endemic to both coasts of North and South America, with all species lacking a right Ri on the male P5. Herrick (1884) described P. pelagicus, the type-species of the genus, from brackish waters of the Mississippi Sound. Unfortunately, no material was deposited and this species has not been reported again. However P. coronatus Williams, 1906, which has strong morphological affinities to P. pelagicus, has been regularly reported from these waters. I have examined pseudodiaptomids from Maine, Massachusetts, Virginia, North and South Carolina, Florida, Louisiana, Texas and Mexico and have found only P. coronatus. I consider P. coronatus a synonym of P. pelagicus because of the close morphological similarities of both species (particularly the male P5), the presence of only 1 species on the Atlantic coast and Gulf of Mexico, and the fact that Williams (1906) made no reference to Herrick's work. Only two species, P. euryhalinus and P. wrighti have been reported from the west coast of North America. The former is unique among pseudodiaptomids in that the female has only 2 instead of the typical 3-4 urosomal segments. Since the reviews of Marsh (1933) and Wright (1936), four new Central-South American species have been reported. After examining most of the known species from North America south to Argentina and Ecuador, I have divided the Americanus species group into 2 subgroups (Table 1), with members of both assemblages present in both Atlantic and Pacific coastal waters. In his review of Argentinian copepods, Ringuelet (1958) synonymized P. richardi emancipans Brehm, 1957 with P. richardi inequalis. The only other American pseudodiaptomid known is P. gracilis (Nudus group) reported from the lower Amazon basin. This species is unique among the American species in that it lacks both a left and right Ri on the male P5 and possesses lateral head hooks. A possible allopatric counterpart to P. gracilis is the marine Indo-Pacific P. clevei, however, the latter lacks lateral head hooks.

Along the coast of western and southern Africa are found P. hessei, P. charteri, and P. stuhlmanni of the Improcerus species group. Another species, P. serricaudatus of the Ramosus group also co-occurs in this region, but extends around north to the Red Sea. Other reports of P. serricaudatus (Mori, 1942; Vervoort, 1965; Wellershaus, 1969) from Indian waters east to the Palau Islands gives this species the most extensive geographical range among pseudodiaptomids. Pseudodiaptomus salinus was originally

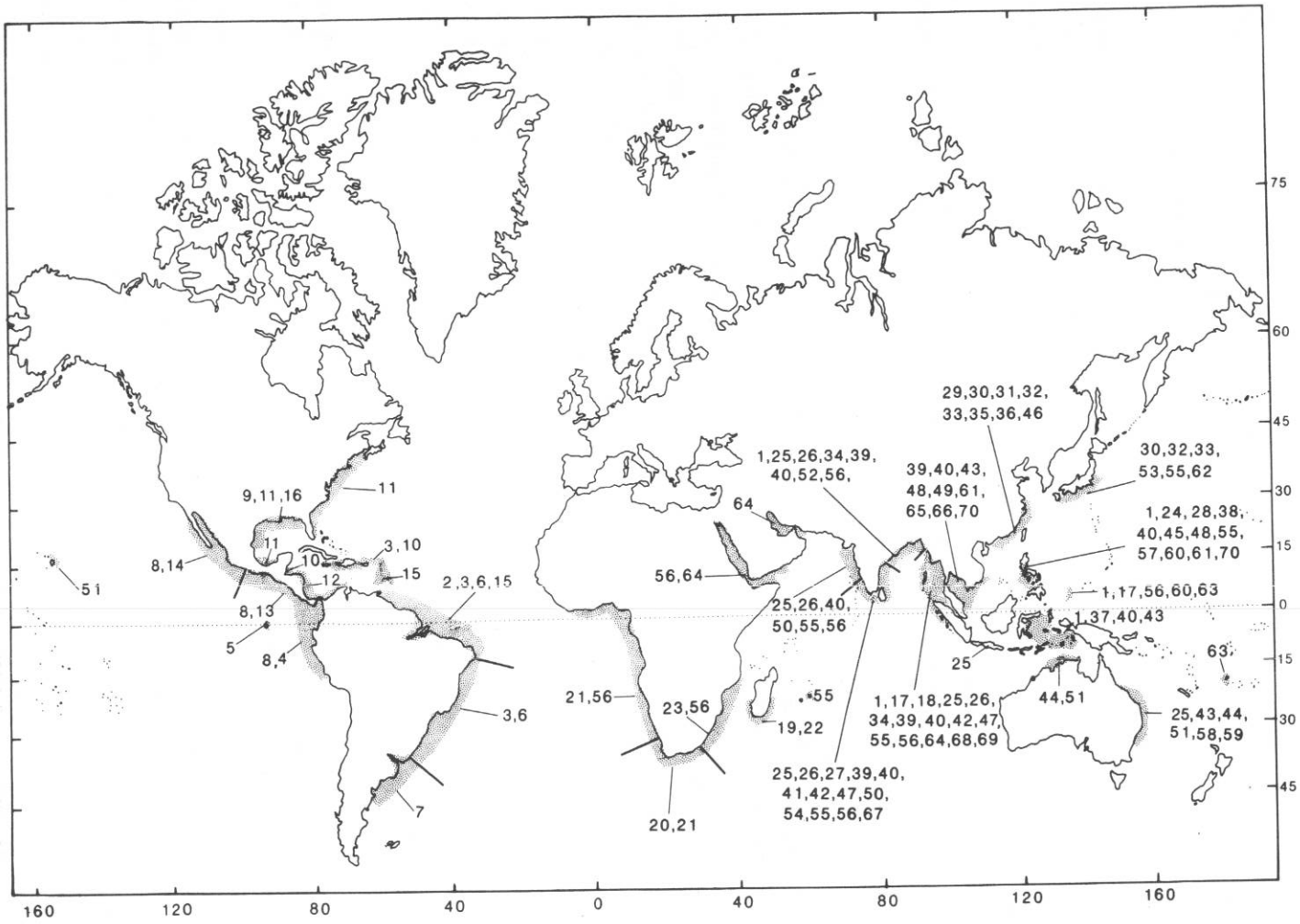

Figure 1. *Worldwide distribution of species in the genus* Pseudodiaptomus. *The numbers refer to species listed in Table 1.*

described from the Red Sea and Arabian Sea area; recently, I have observed it from samples taken in the Persian Gulf. Around the island of Madagascar two poorly known species P. pauliani and P. batillipes have been reported but once in the literature.

In the west Indo-Pacific region 16 species of Pseudodiaptomus, representing 3 species groups (Table 1), are reported from the coastal waters of India. Previous reports of P. mertoni from Indian waters are actually misidentifications of the species P. bowmani, P. sewelli, and P. compactus (Walter, 1984), with P. mertoni restricted to the southern half of the east Indo-Pacific region. The surrounding waters of the Nicobar-Andaman Island chain appear to be the crossroads to the east Indo-Pacific with 15 species known representing 6 species groups.

Along the coastal areas of Malaysia, Thailand, and Viet Nam (east Indo-Pacific region), there occur 3 species groups including 9 species, of which 3 species are common to the Nicobar-Andaman Island vicinity. Further north, a unique assemblage of morphologically distinct species is recorded from China. All but one of these species, P. incisus of the Hyalinus group, were collected from freshwater habitats and are of the Lobus group. From Japan, the northern-most reported area for pseudodiaptomids, 6 species have been reported from 2 species groups. At present there are 12 species, representing 5 species groups, known from the Philippines with ten of these species being marine and collected by emergence plankton traps from one locale (Walter et al., 1982; Walter, 1984; Walter, unpubl. data). The other 2 species were reported from inland lakes on the islands of Luzon and Mindoro. Further east, 5 species (P. burckhardti, P. clevei, P. serricaudatus, P. sp. 4, P. sp. 5) are known from the Palau Islands (Mori, 1942; Walter, unpubl. data). Since P. clevei and P. sp. 4 co-occur in Philippine waters, the other Palau species may eventually be found in these waters. The coastal areas of Papua New Guinea, Aru Archipelago, and the north-eastern coasts of Australia are home to 9 species from 4 species groups.

Previous attempts to divide the genus (Sewell, 1924; Marsh, 1933; Pillai, 1980) into distinct assemblages have not been entirely successful. The euryhaline nature of pseudodiaptominds led Sewell (1958) to place species into 3 groups based on salinity tolerances (fresh, brackish, and/or marine waters). Members of the Lobus group are predominantely freshwater in habit, but occasionally some are reported from the marine environment. The other groups are recorded from brackish to marine waters and only occasionally enter freshwater habitats, with the Hyalinus and Ramosus groups dominated by marine forms. The present arrangement of species groups and subgroups, based primarily on sexually modified structures on the male P5, appears valid for the genus as a whole, as all species with known males can be assigned to one of the groups.

Although faunal centers of planktonic taxa are difficult to determine, the Indo-Malayan region appears to be the center of speciation for Pseudodiaptomus. The areas of greatest diversity, with 5 and 6 species groups respectively, are the Philippine and Nicobar-Andaman Archipelagos. The co-occurrence of as many as 10 sympatric species of a genus from one locale, such as those collected by the author from the Philippines, is not regularly reported for calanoids. Species diversity declines with increasing distance from the faunal center, appearing lowest along the African and Arabian coastlines. This reduction in diversity may in part be the result of undercollecting. Species previously thought to range from Japan to Australia are separable into series of closely related species (Walter, unpubl. data). Further studies of demersal zooplankton should produce new records and species, allowing better elucidation of phylogenetic relationships and zoogeographical distribution of pseudodiaptomids.

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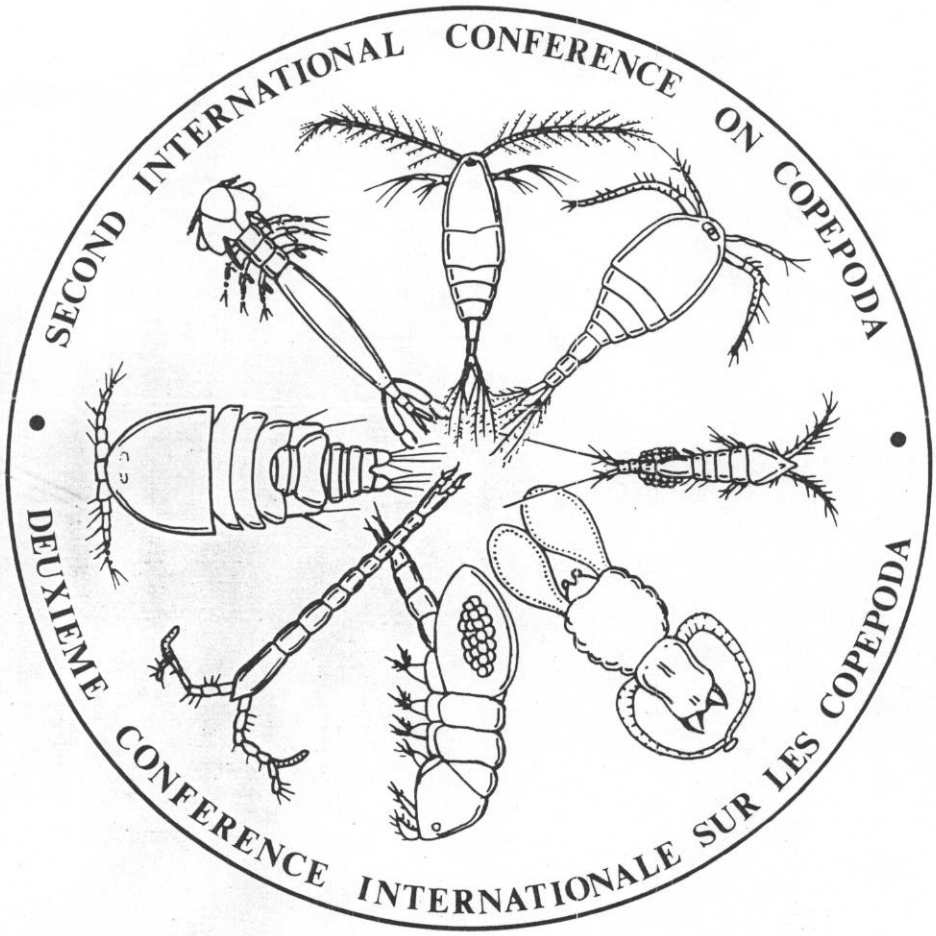

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