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DIOGENES PALLESCENS WHITELEGGE, *D. GARDINERI* ALCOCK AND *D. SERENEI* FOREST (DECAPODA: ANOMURA: PAGUROIDEA: DIOGENIDAE): DISTINCT SPECIES OR MORPHOLOGICAL VARIANTS?

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ABSTRACT. - The morphology of the hermit crab species *Diogenes pallescens* Whitelegge, 1897, *D. gardineri* Alcock, 1905, and *D. serenei* Forest, 1956 is reviewed, based on the type series, and supplemental materials. No single character, or suite of characters, has been found that will separate the three taxa. Consequently, it is concluded that morphological variants, rather than distinct species are represented. *Diogenes pallescens* is the senior synonym.

KEY WORDS. – Indo-Pacific, Crustacea, Paguroidea, Diogenidae, *Diogenes,* synonyms.

INTRODUCTION

A survey of the marine biodiversity of the island of Guam, Micronesia, undertaken by faculty and staff of the University of Guam Marine Laboratory, has revealed a wealth of heretofore unknown and/or unreported hermit crabs (e.g. McLaughlin, 2001b, c). Of particular interest was a species observed by divers to be associated with the sea cucumber, *Holothuria (Halodeima) atra* Jaeger, 1833. Nearly all representatives of this hermit crab observed at the Tumon moat site were crawling on the sea cucumbers, with only a few detected on nearby sandy areas. *Holothuria atra* excretes a slimy coating that is quickly embedded with sand grains, and it appeared as though the hermits were feeding on the slime or on detritus associated with the sand grains (G. Paulay, pers. comm.). In the process of attempting to identify this species from the existing literature, it quickly became apparent that three species, *Diogenes pallescens* Whitelegge, 1897, *D. gardineri* Alcock 1905a, and *D. serenei* Forest, 1956, all corresponded well in morphological attributes to the taxon in question. Species of *Diogenes* frequently present problems in identification because of the tendency, in many species, to exhibit sexual dimorphism, as well as marked variation in the shape and armature of the left cheliped (e.g. Forest & Guinot, 1956: 32, Figs. 1-3). This is particularly true of the group of species referred to as the "*gardineri* group" (e.g., Forest, 1956; Lewinsohn, 1969; Ball & Haig, 1972; Morgan, 1987, 1990; Rahayu & Forest, 1995).

Although Whitelegge (1897) described the habits and habitats of the semiterrestrial hermit crabs found on the atoll of Funafuti, he noted only that the seven specimens of his new species, *D. pallescens,* all occupied shells of a single gastropod species. In Alcock's (1905a) description of *D. gardineri* from the Maldives and Minikoi, he remarked on the similarity of his new species with Whitelegge's (1897) *D. pallescens,* particularly in the "remarkable length of the eyestalks and the abbreviated antennal peduncle". Alcock (1905b) repeated his description and comments regarding *D. gardineri,* including the notation again that it was a new species. In describing *D. serenei,* Forest (1956) related it closely to *D. gardineri, D. pallescens,* and *D. senex* Heller, 1865. Based upon Forest's (1956) remarks, Lewinsohn (1969) placed Middle East specimens attributed to *D. senex* by Bouvier (1892), Nobili (1906b), Balss (1927), and Ramadan (1936) in synonymy with *D. gardineri.*

Ball & Haig (1972) corrected some of the inaccuracies in Whitelegge's (1897) description of *D. pallescens,* after examining three of his syntypes. These authors also noted some variations and sexual dimorphism exhibited by their own specimens from

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New Guinea. Ball & Haig (1972) additionally recorded *D. gardineri* and *D. serenei* from New Guinea, including one location where the three species appeared to occur sympatrically. Morgan (1987) reported the occurrence of *D. gardineri* and *D. serenei* in northern Australia, and described a species, *D. biramus* Morgan, 1987, that he attributed to the "*gardineri* group" because of its characteristically short antennal peduncles. In this group, Morgan included, as Forest (1956) had, *D. senex* and added *D. leptocerus* Forest, 1956 and *D. capricorneus* Grant & McCulloch, 1906. Haig & Ball (1988) assigned their new species, *D. viridis* Haig & Ball to the group, as delimited by Morgan (1987). However, McLaughlin & Haig (1996) demonstrated that *D. senex* of most authors was not Heller's (1865) taxon, and the latter was not related to the "*gardineri* group" of species. Of the taxa referred by Lewinsohn (1969) to *D. gardineri,* McLaughlin & Haig (1996) concluded that a more detailed study of Alcock's (1905a, b) species would be required before its true characters could be defined. The composition of the "*gardineri* group" was changed by Rahayu & Forest (1995), who omitted *D. pallescens, D. biramus, D. capricorneus,* and *D. viridis,* but added *D. spinicarpus* Rahayu & Forest, 1995 and *D. timidus* Rahayu & Forest, 1995. However, these authors suggested the probable conspecificity of *D. biramus* and *D. viridis.* Although these latter four or five species all share characters such as short and slender antennal peduncles and antennal flagella that lack paired long setae, other characters serve to distinguish them from the original trio. Rahayu & Forest (1995) also reported both *D. serenei* and *D. pallescens* from four of the same Indonesian localities, with *D. gardineri* also recorded from one of them.

MATERIALS AND METHODS

In addition to the 21 Guam specimens, courtesy of Gustav Paulay, now deposited in the collections of the Florida Museum of Natural History, University of Florida, Gainsville, Florida (FMNH), the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A (USNM), and the author's personal collection (PMcL), it has now been possible to reexamine the seven syntypes of *D. pallescens,* courtesy of the Australian Museum, Sydney, Australia (AM), Alcock's two specimens of *D. gardineri* from the Maldives and three from Minikoi, courtesy of Museum of Zoology, Cambridge University, Cambridge, United Kingdom (MZCU), and the male syntype (indicated by Forest as the lectotype) of *D. serenei,* courtesy of the Muséum national d'Histoire naturelle, Paris, France (MNHN). Supplemental materials examined include two specimens identified as *D. pallescens* and six identified as *D. serenei* by Ball & Haig (1972) from New Guinea, all courtesy of the late Janet Haig, and now part of the collection of the Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM), two specimens of *D. serenei* from Indonesia, reported on by Rahayu & Forest (1995), courtesy of J. Forest, and now part of the author's personal collection, two specimens from Singapore tentatively identified by the author as *D. serenei,* courtesy of the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Republic of Singapore (ZRC), and two of the specimens recorded as *D. gardineri* from the Maldives by Hogarth et al. (1998), now also part of the author's personal collection.

A lectotype has been designated for *D. gardineri,* but not for *D. pallescens.* Of the seven syntypes of the latter species, only one, a small ovigerous female, is complete. As it was entirely retracted into its shell, it is improbable that it was among the specimens upon which Whitelegge (1897: 141, pl. 6, figs. 2, 2a-c) based his description and illustrations, thus not really appropriate as the lectotype. Among the other six, only one detached left and one detached right cheliped remain, and these cannot confidently be associated with any of the larger specimens. Almost all the remaining ambulatory legs similarly are detached. The largest individual (sl = 2.9 mm) and probably Whitelegge's illustrated specimen, is now missing the left anterior portion of the shield and the entire left antennal peduncle and flagellum.

General terminology for the species description follows that of McLaughlin & Clark (1997), and for the fourth pereopods that of McLaughlin (1997). One measurement, shield length (sl), measured from the midpoint of the rostral lobe to the midpoint of the posterior margin of the shield, provides an indication of animal size. Variations in the carpi and chelae of the left chelipeds are illustrated for the two specimens in the *D. gardineri* type series, and the Guam specimen (Fig. 1). For comparative purposes, the shields and cephalic appendages (Fig. 2), left second pereopods (Fig. 3), carpus, propodus and dactyl of the left fourth pereopod (Fig. 4), and telsons (Fig. 5) of the lectotypes of *D. gardineri* and *D. serenei,* syntypes of *D. pallescens,* and the largest of the Guam specimens also have been illustrated.

INITIAL DESCRIPTIONS

Diogenes pallescens was described in considerable detail by Whitelegge (1897: 141, pl. 6, figs. 2, 2a-c). Presumably diagnostic characters included the spinose lateral margins of the shield, the ocular peduncles that were approximately equal to the length of the antennules, but considerably longer than the antennal peduncles, and an intercalary rostriform process that only slightly overreached the apices of the spines of the ocular acicles.

The left cheliped was described and illustrated as having prominent spines on the ventral margin of the merus, and spines on the upper margin and outer face of the carpus. Whitelegge (1897) indicated that the lower margin of the palm and fixed finger were as long as the combined length of the carpus and merus, but he made no mention of the concave configuration illustrated for that margin (Whitelegge, 1897: pl. 6, fig. 2a). The palm reportedly had four prominent spines on the upper margin, granules and two or three small spinules in the upper half of the outer face, and a short, longitudinal row of three or four spines "on the angle". The upper surface of the dactyl was described as being "closely studded with small bead-like granules".

The ambulatory legs reportedly were armed only with a dorsodistal and dorsoproximal spine on each carpus, and a row of six spines on the merus of each second pereopod. The dactyls were described as nearly as long as the combined lengths of the propodi and carpi.

Whitelegge (1897) described the colour of the carapace and ambulatory legs of *D. pallescens* as white, with the larger cheliped having a slight reddish tint, more intense on the merus and carpus.

Alcock's (1905a, b) two specimens of *Diogenes gardineri* from the Maldives are indicated in the Gardiner collection as the syntypes, and it would appear that Alcock (1905a) based his description on the intact male from Mahlos, Maldives, although he did indicate that he had additional material from Minikoi. In his subsequent account (Alcock, 1905b) he referred only collectively to specimens from the Maldives and Minikoi (spelled as Minnikoy). Alcock's (1905a, b) descriptions of *D. gardineri* were not nearly as detailed as Whitelegge's (1897) of *D. pallescens.* Among Alcock's (1905a: 830, b: 73) diagnostic characters, he mentioned the "remarkably long" ocular peduncles that were nearly as long as the antennular peduncles and much longer than the antennal peduncles. The outer surface of the left chela was described as having a "longitudinal finely granulose bulge, or low carina", Alcock reported that the ambulatory legs were provided with setae, but other than a spinule at the dorsodistal margin of each carpus, were smooth. Alcock (1905a, b) made no mention of colour in his description of *D. gardineri.*

Diogenes serenei was described by Forest (1956) from two specimens collected at Baie de Caude, Vietnam. Forest's diagnosis was brief, but very explicit in the characters he felt differentiated his species from Alcock's (1905a, b) *D. gardineri.* In addition to Alcock's description, Forest (1956) used comparative material from Tuamotu, identified by Nobili (1906c) as Alcock's taxon, and deposited in the collections of the Muséum national d'Histoire naturelle. Although there were significant similarities between the two species, including the "bifid" intercalary rostiform process, the antennular peduncles consistently overreached the distal margins of the corneas in specimens of *D. gardineri,* while not reaching the bases of the corneas in *D. serenei.* Forest (1956) also found notable differences in the ambulatory legs of the two species. Firstly, the dactyls were more slender and less recurved in *D. gardineri.* Secondly, although Alcock (1905a, b) had not described a dorsoproximal spine on the carpus of each second pereopod, Forest (1956) detected a minute spinule in his figures (Alcock, 1905a, pl. 68, fig. 1; 1905b, pl. 7, fig. 3); no spine or spinule could be observed on the carpi of the third pair. A similar armature was found on the Tuamotu specimens. In contrast, prominent dorsoproximal spines were present on the carpi of both second and third pereopods of *D. serenei.* Thirdly, Forest (1956) found the ventral margin of the propodus of the left third pereopod weakly serrate in his specimens of *D. gardineri,* but smooth in *D. serenei.*

Forest differentiated *D. serenei* from *D. pallescens* by Whitelegge's (1897, pl. 6, figs. 2, 2b, c) illustrated broad separation of the ocular acicles and more slender propodi of the ambulatory legs of the latter species. However, Ball & Haig (1972: 90) showed that those characters were inaccurately illustrated. No information on colour was provided in the original description of *D. serenei.*

EXAMINATIONS OF TYPE AND SUPPLEMENTAL MATERIAL

Diogenes pallescens Whitelegge, 1897

(Figs. 2A, 3A, 4A, 5A)

Material examined. - Syntypes - 3 males, 4 females (sl = 1.8-2.6 mm) (AM G1402), Funafuti, Ellice Islands, coll. G. Hedley, no date.

Others - 2 males (sl = 1.6, 3.2 mm) (LACM), inside Sek Ialand, New Guinea, coll. E. Ball, 4 Oct.1969.

Remarks. - Contrary to Ball & Haig's (1972) statement that Whitelegge (1897) based his description of *D. pallescens* on the seven specimens in his possession (AM G1402), that is clearly not the case. Three of the seven had never been removed from their shells. Of the four specimens without shells, three were examined by Haig (Ball & Haig, 1972: 91), who pointed out some of the exaggerations depicted in Whitelegge's (1897: pl. 6, figs. 2, 2a-c) illustrations. The additional specimens, two males, one lacking all appendages, and two ovigerous females also have now been examined. Not only do these latter specimens demonstrate the amount of morphological variation inherent in this species, but their characters contradict, in part, the description of *D. pallescens* given by Whitelegge (1897) and the diagnostic characters cited by Forest (1956) and Ball & Haig (1972) to distinguish this taxon from *D. gardineri* and *D. serenei.* These characters include:

1. Shield shapes that range from longer than broad to as broad as long, while armature varies from prominent spines on the lateral margins to only small spinules.
2. In one specimen, the intercalary rostral process is provided with a prominent ventral spine (Fig. 2A).
3. Ocular peduncle length varies from 0.75 the length of shield to equally as long as the shield.
4. The antennular peduncles in two of the four specimens overreach the distal margins of the corneas by approximately half the length of the ultimate peduncular segment, whereas in the other two, the antennular peduncles reach to bases of the corneas in one, and nearly to the distal margins in the other.
5. In the three specimens with ambulatory legs, the length of the propodi of the second pereopods varies from 4.2 to 5.4 times the height, while this ratio of the third pereopods varies from 4.0 to 6.4 times. A check of this ratio in the four second and five third pereopods remaining among the specimens examined by Haig shows a range between 4.8 and 5.5 times in the second, and 4.4 to 6.2 times in the third.
6. Dorsoproximal spines are absent on both right and left carpi of the third pereopods in one specimen, and absent on the right of a second.
7. The number of spines on the ventral margins of the meri of the second pereopods varies from two to five.

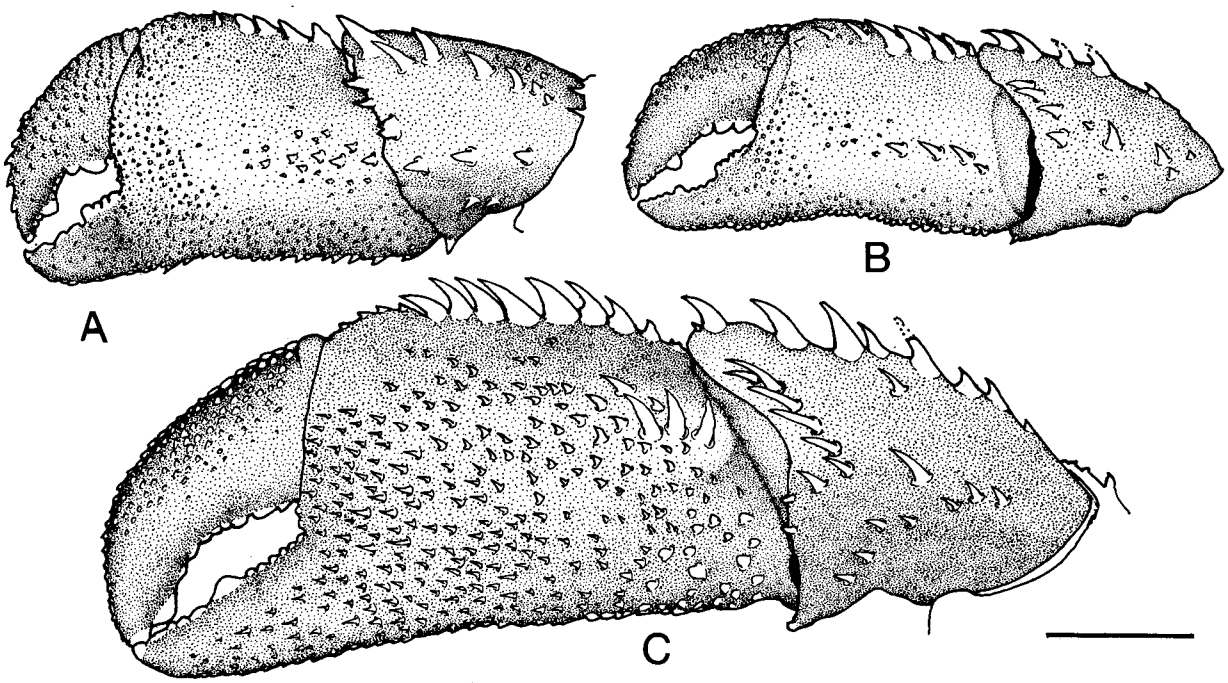

Fig. 1. Chelae and carpi of left cheliped (setae omitted). A, male lectotype (sl = 1.8 mm, MZCU) of *Diogenes gardineri* Alcock, 1905; B, male paralectotype (sl = 1.7 mm, MZCU) of *Diogenes gardineri* Alcock, 1905; C, male (sl = 2.9 mm, USNM 1000219) of *Diogenes pallescens* from Guam. Scale equals 1 mm.

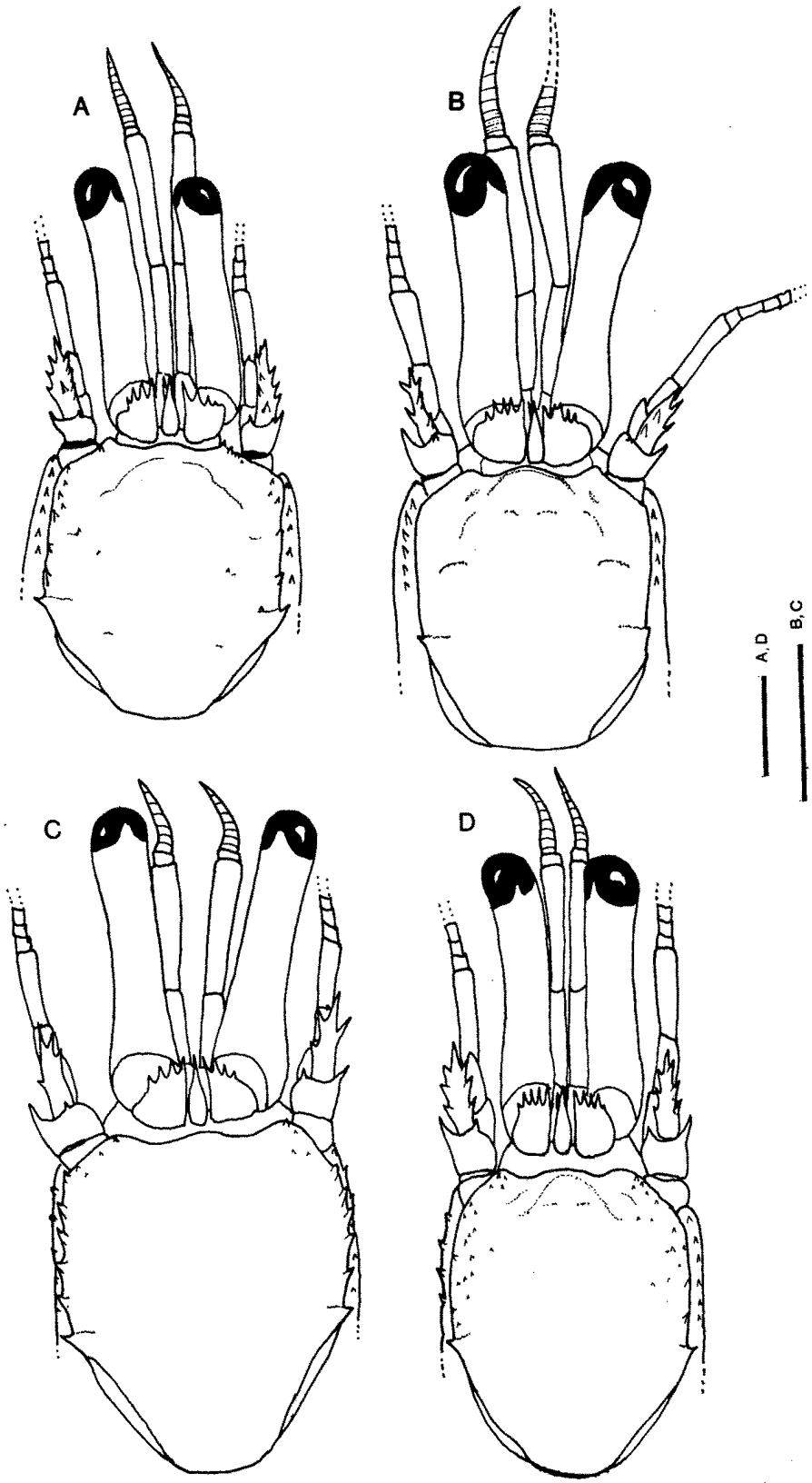

Fig. 2. Shields and cephalic appendages (aesthetascs and setae omitted). A, male syntype (sl = 2.6 mm, AM G1402) of *Diogenes pallescens* Whitelegge, 1897; B, male lectotype (sl = 1.8 mm, MZCU) of *Diogenes gardineri* Alcock, 1905; C, male lectotype (sl = 2.3 mm, MNHN Pg 1502) of *Diogenes serenei* Forest, 1956; D, male (sl = 2.9 mm, USNM 1000219) of *Diogenes pallescens* from Guam. Scales equal 1 mm.

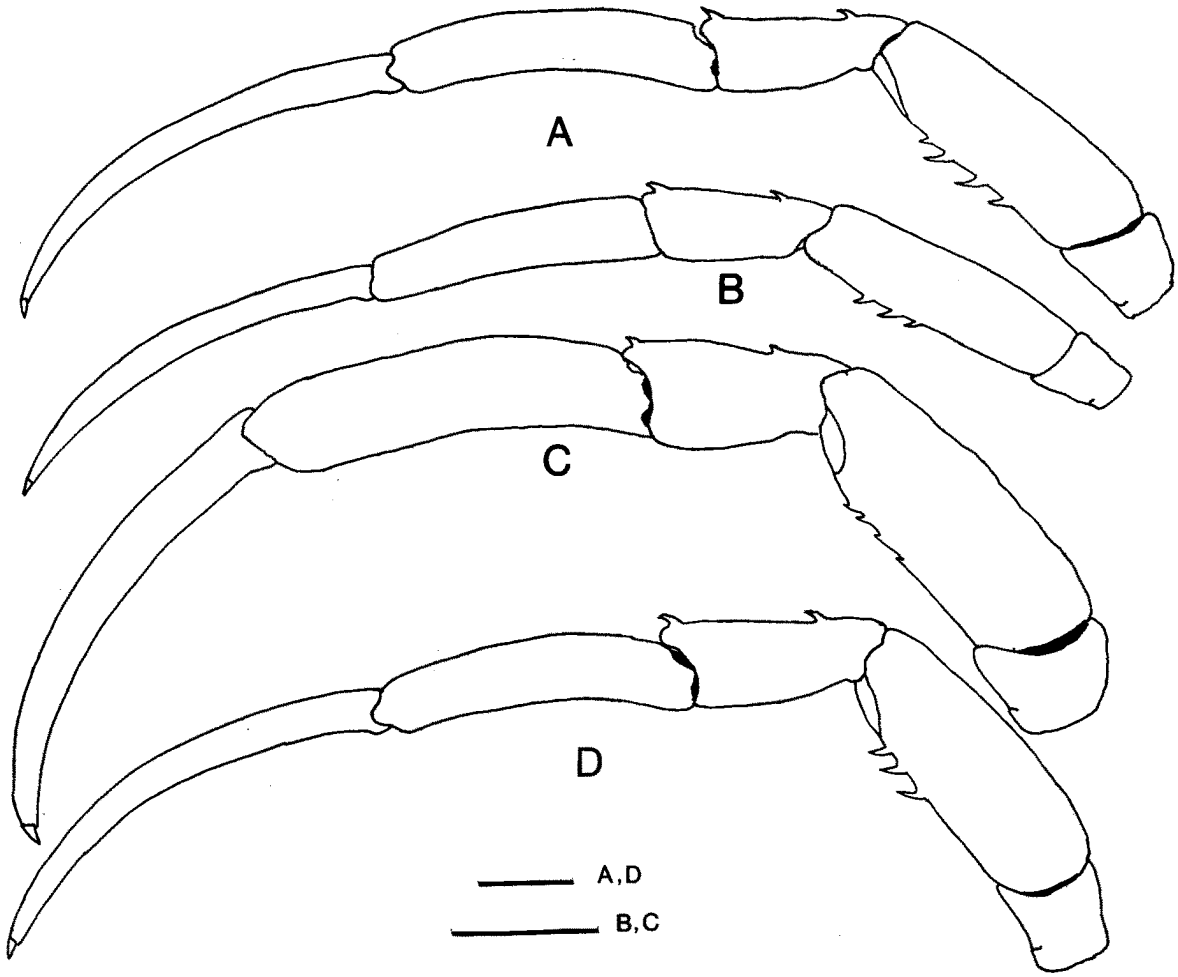

Fig. 3. Left second pereopods (lateral view, setae omitted). A, detached appendage of a syntype (AM G1402) of *Diogenes pallescens* Whitelegge, 1897; B, male lectotype (sl = 1.8 mm, MZCU) of *Diogenes gardineri* Alcock, 1905; C, male lectotype (sl = 2.3 mm, MNHN Pg 1502) of *Diogenes serenei* Forest, 1956; D, male (sl = 2.9 mm, USNM 1000219) of *Diogenes pallescens* from Guam. Scales equal 1 mm.

A character not considered by Whitelegge (1897) or Ball & Haig (1972) is the presence of spines on the dorsodistal margins of the propodi and carpi of the fourth pereopods. These spines are present on those animals where these appendages are still present on the syntypes.

Ball & Haig's (1972) specimens from "Inside Sek Island" consist of two males. The larger is the specimen illustrated (1972: fig. 2a-c); however, the left cheliped is now missing from the vial. Ball & Haig remarked that the antennular peduncles, as illustrated, appeared considerably shorter than they actually were, but did not give a specific length in relation to the ocular peduncles. In this specimen, the antennular peduncles reach slightly beyond the bases of the corneas, whereas in the smaller specimen they reach only to the corneal bases. The ocular peduncles of the larger specimen, as shown in Ball & Haig's (1972: fig. 2a) appear approximately as long as the shield; however, when measured, they are only 0.80 of the shield length. Ball & Haig reported that Whitelegge's (1897: pl. 6, fig. 2b, c) illustrations of the ambulatory legs exaggerated their slenderness. They found (Ball & Haig, 1972: 91) in both Whitelegge's specimens and their own that the ratio of propodal length to height was "about five, rather than six, times longer". In their two specimens from Sek Island, this ratio varies from 4.8 to 5.4 times.

Ball & Haig (1972: 90) described the colour of their Sek Island specimens as: "Carapace, eyescales and rostriform processes mottled greenish brown and white. Eyestalks with pure white background; a broad

brown ring at base; fine lines of brown, in a netted or ringed pattern, over rest of stalk. ... Antennular peduncles with narrow brown rings on a white to transparent background ... Chelipeds mostly brown, fingers white. Walking legs mottled pale brown on a white background; the color tends to be concentrated into broad bands, the most prominent on occurring about midway along the propodus."

Diogenes gardineri Alcock, 1905
(Figs. 1A, B, 2B, 3B, 4B, 5B)

Material examined. - Lectotype - male (sl = 1.8 mm) MZCU), Mahlos, Maldives, coll. S. Gardiner, no date.

Paralectotype. - male (sl = 1.7 mm) (MZCU), same data as lectotype.

Others. - 3 specimens, fragile condition, 2 partially exposed from shells (sl = 1.2, 1.7 mm) (MZCU), Minikoi, no date; 1 female (sl = 1.5 mm) (PMcL), Malé, Maldives, coll. P. Hogarth, Jan.1991; 1 female (sl = 1.4 mm) (PMcL), Vaavu (Felidu) Atoll, Maldives, coll. F. Gherardi, Dec.1993.

Remarks. - Alcock's (1905a) Maldive specimens consist of two males. Only the larger male is complete, although the right cheliped is detached. This specimen is herein designated the lectotype. The second male lacks the right cheliped, left second and right third pereopods. In the lectotype, the shield has only a single small spine on each lateral margin in the posterior half. The shield of the paralectotype is armed with a few lateral spinules; spines on the branchiostegites vary from three to six in the two specimens. In the lectotype, the ocular peduncles are slightly longer than the shield; the intercalary rostral process has a prominent ventral spine; the antennular peduncles reach only to the distal margin of the cornea of the slightly longer left peduncle; the carpi of the second pereopods each has a well developed dorsodistal and dorsoproximal spine; the carpi of the third pereopods each has only a dorsodistal spine; the propodal length varies from 4.4 to 5.5 the height. The paralectotype differs in having ocular peduncles that are only 0.85 the length of the shield; a laterally bifid intercalary rostral process but no ventral spine; antennular peduncles that overreach the distal margins of the corneas by slightly more than 0.35 the length of the ultimate peduncular segments; a right second pereopod with only a dorsodistal spine, and a third left pereopod with both a small dorsodistal and dorsoproximal spine. In both the lectotype and paralectotype, the meri of the second pereopods each has two or three prominent spines on the ventral margin. Dorsodistal spines are present on the propodi and carpi of the fourth pereopods in both specimens.

The sample from Minikoi includes three fragile specimens. Two remain partially in their shells, but with shields exposed sufficiently to permit measurement. The third specimen, and only one with a left cheliped is entirely withdrawn into its shell. It is doubtful that any of these specimens were taken into account in Alcock's (1905a) description, and are not considered syntypes. Because of their conditions, no attempt has been made to extract any from their shells to sex them. The intercalary rostral process is laterally bifid in the larger of the two measured specimens, and simple in the second; no ventral spine can be detected on either. The ocular peduncles are shorter than the shield in both specimens, whereas the antennular peduncles overreach the distal margins of the corneas by 0.25-0.35 the length of the ultimate peduncular segments. Small dorsoproximal spines are present on the carpi of the second pereopods, but not on the third. The ventral margin of the merus of each of the each second pereopods is armed with one or two spines. Only the smaller measured specimen has a right cheliped, and the armature of the carpus and chela is weak.

Two of the specimens of *D. gardineri* from the Maldives that were reported on by Hogarth et al. (1998) have also been reexamined. The larger, a non-ovigerous female, has ocular peduncles nearly as long as the shield, whereas the ocular peduncles of the smaller, ovigerous female are only 0.75 the length of the shield. In both specimens the shield is armed with prominent lateral spines. No ventral spine on the intercalary rostriform process can be detected on either specimen, and in both the antennular peduncles, while overreaching the bases of the corneas, do not overreach the distal margins. Each carpus of both second and third pereopods is armed with a dorsodistal and dorsoproximal spine in the non-ovigerous female, but only the carpi of the second pereopods of the ovigerous female have both spines. The ventral margins of the meri of the second pereopods in both specimens are armed with two to five spines.

Colouration in *D. gardineri* was reported by Morgan (1987) for specimens from Port Essington, Northern Territories. However, McLaughlin & Haig (1996) indicated that Morgan's (1987) specimens identified as *D. gardineri* might possibly represent the true *D. senex,* since these authors had examined specimens from the Port Essington area that actually were referable to Heller's (1865) taxon.

Diogenes serenei Forest, 1956
(Figs. 2C, 3C, 4C, 5C)

Material examined. - lectotype - male (sl = 2.3 mm) (MNHN Pg 1502), Baie de Cauda, Vietnam, coll. R. Serène, 11 Sep.1953.

Others. - 1 male, 1 female (sl = 2.0, 2.4 mm) (PMcL) Seram, Indonesia, coll. D.L. Rahayu, date not given; 1 male (sl = 2.6 mm) (ZRC 1993.858), 1 female (1.2 mm) (ZRC 1993.859), Palau Semakau, Singapore, 26 Apr.1993; 2 females (sl = 1.8, 2.3 mm) (LACM), lagoon 56 km north of Maiwara, New Guinea, coll. E. Ball, 19 Oct.1969; 3 males, 1 female (sl = 1.2-1.7 mm) (LACM), Port Moresby, New Guinea, coll. E. Ball, 17 Dec.1969.

Remarks. - Forest (1956) based his description on both the male lectotype and female paralectotype. Only the lectotype has been reexamined. In his differentiation of *D. serenei* from *D. pallescens,* Forest remarked that the length of the propodi of the third pereopods was less than four times the height, considerably less than the ratio illustrated by Whitelegge (1897, pl. 6, fig. 2c). The length of single third pereopod (left) of the lectotype is 3.3 times the height. The lengths of the propodi of the second pereopods are 4.2 and 5.0 times the height. The meri of the second pereopods have two small spines (right) and four (left) on the ventral margins. In the two specimens from Indonesia, reported as *D. serenei* by Rahayu & Forest (1995), the ventral margins of the meri of the second pereopods of the male have one and two small spines on the right and left respectively, whereas no spine is present on the only second pereopod of the female. The propodal lengths for the third pereopods vary from 3.9 to 6.2 times the height, and for the second pereopods from 4.3 to 4.7 times. In all three specimens the intercalary rostriform process has a prominent ventral spine; the antennular peduncles reach only to the bases of the corneas (lectotype) or slightly beyond (Indonesian specimens), but not to the distal corneal margins. In the lectotype, only the propodus and carpus of the right fourth pereopod each has a dorsodistal spine; the spine on carpus of the left may have been broken off, as only a minute protuberance is visible now. Dorsodistal spines are present on both segments of the Indonesian specimens.

The two females from Ball & Haig's (1972) lagoon station north of Maiwara, and the three males and one female from Port Moresby, New Guinea also have been reexamined. Ball & Haig reported that all of these specimens had a ventral spine present on the intercalary rostriform process. However, no ventral spine can be detected now on the ovigerous female from the lagoon station or on the female and smallest male from Port Moresby. It is probable that these have been broken off. In all six specimens, the antennular peduncles do not reach the distal margins of the corneas. The number of spines on the ventral margins of the second pereopods varies from one to five. Ball & Haig also reported one specimen attributed to *D. gardineri* from the same lagoon station, but it has not been reexamined. The antennular peduncles of this specimen reportedly barely reached the "ends of the eyestalks" (Ball & Haig, 1972: 91); however, the ventral spine of the rostriform process was noted as absent.

Two specimens, a male and female, from Singapore have also been examined. Both specimens have the characteristic ventral spine on the rostriform process. Although the antennular peduncles reach only to the bases of the corneas of the male, they slightly overreach the distal corneal margins of the female. The carpi of the second and third pereopods all are armed with distinct dorsodistal and dorsoproximal spines. The ventral margins of the meri of the second pereopods of the male have three spines (right) and two (left), whereas three spinules are present on the ventral margin of the left second pereopod of the smaller female; the merus of the right is unarmed.

Of colouration in *D. serenei,* Morgan (1987) reported that the shield was cream, spotted and mottled with brown. The ocular peduncles were cream or white with brown mottling and a brown band near the distal end. The antennular and antennal peduncles were cream with some brown mottling and both had dark brown bands at the distal ends of the ultimate segments. The chelipeds were mottled cream and brown. The ambulatory legs were mottled cream and brown, with a darker brown band often middorsally and dorsomesially on meri, carpi, and propodi, and proximally on the dactyls.

Haig & Ball (1988) reported a slightly different pattern for D. serenei. While the shield was still described as mottled brown and white, a dark brown spot was reported near each lateral margin. The ocular peduncles reportedly had light brown mottling proximally, white distally and a dark brown ring in the white area. The antennular peduncles had a transparent background, and both basal and terminal segments were marked by a subdistal and distal dark brown band respectively. The antennal peduncles were white with a dark, subdistal band on the terminal segment. The chelipeds were described as mottled black, white and brown, while the ambulatory legs were mottled brown and white, with a black spot on the dorsal margin of each merus and carpus.

Guam specimens
(Figs. 1C, 2D, 3D, 4D, 5D)

Material examined. - 2 males, 5 females (sl = 1.1-2.9 mm) (USNM 1000219), 1 male, 2 females (1.8-2.1 mm) (FMNH), 3 males, 6 females (sl = 1.0, 2.0 mm) (PMcL), Tumon moat, Guam, coll. G. Paulay, 5 Aug. 2000; 1 male, 1 female (1.9, 2.5 mm) (FMNH), Agat Bay, Guam, coll. L. Kirkendale, 23 Feb.2000.

Remarks. - The specimens associated with the holothurian are represented by 19 specimens, six males and 13 females, the majority, ovigerous. Shield length:width ratios vary from approximately as broad as long, to considerably longer than broad, but only in the largest female are the spines on the lateral surfaces of the shield prominently developed. Branchiostegial spines vary in both size and number, but five moderately small spines is most common. In all specimens the ventral spine of the intercalary rostral process is developed, but occasionally not eminently. In the majority of specimens, the antennular peduncles overreach the proximal corneal margins, but do not extend beyond the distal margins. However, in two males and three females, the antennular peduncles overreach the distal margins of the corneas by 0.10 to 0.25 the length of the ultimate peduncular segment. The ventral spines on the meri of the second pereopods are always present, but vary from two or three prominent spines to a row of four or five quite small spines. Both dorsodistal and dorsoproximal spines are always present on the carpi of the second pereopods, although occasionally the proximal spine is quite small. Development of the proximal spine on the carpi of the third pereopods is variable. It may be well developed, present on one carpus but not the other, completely lacking or represented by only a small protuberance. Absence of the spine is observed most frequently on small specimens. In four of the females, the propodus of the left third pereopod is armed with a row of tiny spinules. This latter character was reported by Forest (1956) for Tuamotu specimens of *D. gardineri.* Ratios of propodal length vary from 4.0 to 5.0 times the length for the second pereopods and 4.2 to 6.0 times for the third. Dorsodistal spines are present on the propodi and carpi of the fourth pereopods in the majority of specimens, but occasionally one spine will be missing from one or the other segment on one of pereopods. While uniramous pleopods are typical of the genus, and seen in all the type materials, one small male specimen from this Guam sample has a biramous left third pleopod, suggesting immaturity (cf. Rahayu & Forest, 1995: 411).

Two additional specimens, 1 male and an ovigerous female have been collected intertidally from under rocks in Agat Bay. Both specimens have dorsodistal and dorsoproximal spines on the carpi of the second and third pereopods, and from two to four spines on the ventral margins of the meri of the second pereopods. The male agrees well with most of the characters and with the color patterns of the specimen described and illustrated by Ball & Haig (1972: fig. 2a). Exceptions include smaller carapace spines, and longer ocular peduncles that slightly exceed the length of the shield of the Guam specimen. However, the ovigerous female differs appreciably. The ocular peduncles are only 0.75 the length of the shield; the intercalary rostral process has not only a laterally bifid terminal spine, but a prominent ventral spine as well; the antennular peduncles reach the distal margin of the longer left ocular peduncle; and the ventral margin of the left third pereopod has a row of tiny spinules.

Colouration of the Guam material shows some variation between the two photographed specimens collected at Tumon moat, in association with the holothurians, and the photographed one of the two collected at Agat Bay. For specimens from both areas, the shield is white or cream with streaks or patches of tan or brown. The ocular peduncles are white or cream, with or without a brown band distally in the Tumon moat specimens, and the antennular peduncles are cream or white, with one distal and/or one proximal dark band on the ultimate segment. In contrast, the ocular peduncles of the Agat Bay specimen are cream and have thin brown lines forming irregular bands, similar to those illustrated by Ball & Haig (1972: fig. 2a) for their *D. pallescens,* while the antennular peduncles have subdistal and proximal bands on all three segments. However, while the reticulations on the ocular peduncles remain in preservative on the photographed specimen, no hint of such a pattern is seen on the second specimen. The chelipeds are white or cream with brown or tan patches or mottling in the specimens from both areas. The ambulatory legs are generally white or cream, but each segment has at least one dark band: dactyls each with a dark band at the proximal margin; propodi each with a dark median and proximal band; carpi each with a median dark band overlaid dorsally by a dark (Tumon moat) or red (Agat Bay) patch; meri each with a subdistal and subproximal dark band.

CONCLUSIONS

As is apparent from the reexaminations of the type materials of *Diogenes pallescens, D. gardineri,* and *D. serenei,* there is no single character, or suite of characters that will separate one species from another. The Guam populations and supplemental materials of the three species further support this conclusion. The variation in the number and prominence of spines on the left cheliped (Figs. 1A-C), as pointed out by Forest (1956: 530) and Lewinsohn (1969: 45), renders these characters of no diagnostic significance; however the pattern of the spines is comparable among all three taxa. Similarly, cheliped shape is subject to variation that does not appear to be influenced by sex. The relative length of the antennular peduncles in relation to that of the ocular peduncles (Figs. 2A-D) has been found, at least for this trio, not to be as constant or diagnostic as heretofore believed. The presence of a ventral or otherwise bifid spine on the intercalary rostriform process must also be considered variable. Similarly, the prominence, as well as the presence or absence of a dorsoproximal spine on the carpi of one or both pair of the ambulatory legs is not a specific difference. Neither can the length to height ratio of the propodi of the ambulatory legs be considered diagnostic. This is also true of the length of the ambulatory dactyls, although this has not been used to distinguish among the species of present concern. Colouration similarly varies within and among populations.

Despite the morphological variations exhibited, there are, however, characters that do unite all three. Most important is the shape and armature of the telson (Figs. 4E-G). Additional, although not necessarily mutually exclusive characters include the presence of one to five ventrolateral spines on the second segment of the antennal peduncle, the armature of the antennal acicle, the presence of a dorsodistal spine on the

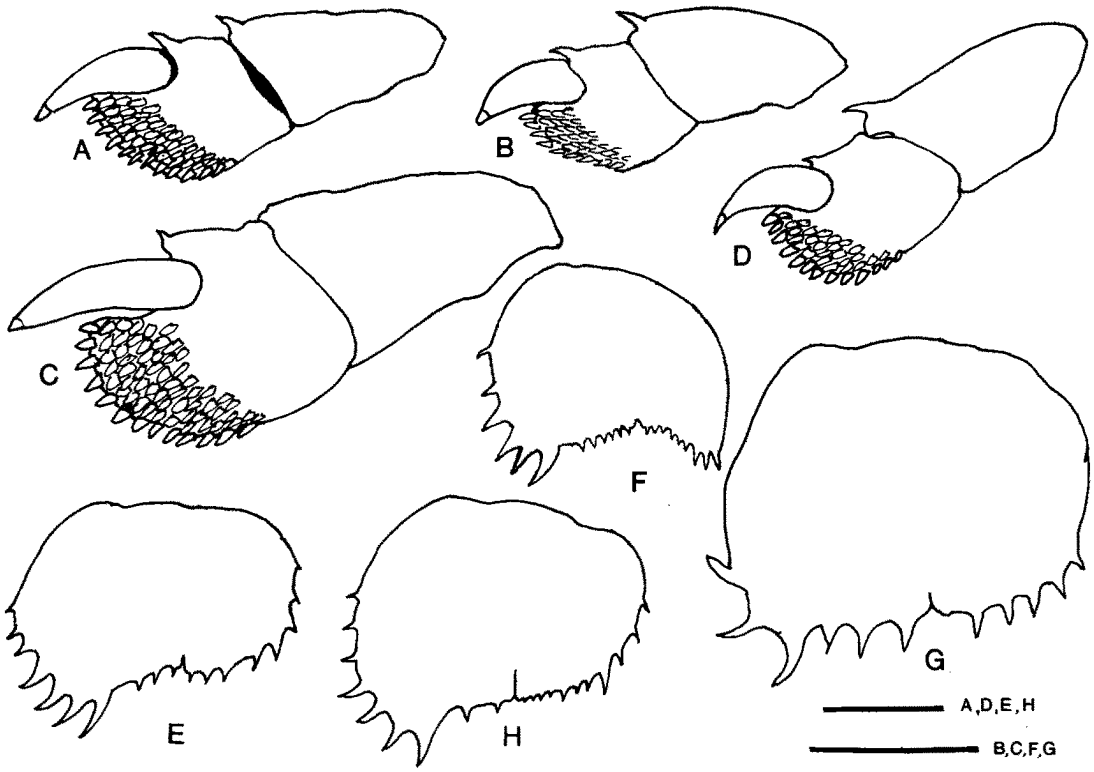

Fig. 4. Dactyls, propodi and carpi of left fourth pereopods (lateral view, setae omitted), A-D; telsons (dorsal view, setae omitted), E-H. A, male syntype (sl = 2.6 mm, AM G1402) of *Diogenes pallescens* Whitelegge, 1897; B, male lectotype (sl = 1.8 mm, MZCU) of *Diogenes gardineri* Alcock, 1905; C, male lectotype (sl = 2.3 mm, MNHN Pg 1502) of *Diogenes serenei* Forest, 1956; D, male (sl = 2.9 mm, USNM 1000219) of *Diogenes pallescens* from Guam; F, male syntype (sl = 2.6 mm, AM G1402) of *Diogenes pallescens* Whitelegge, 1897; B, male lectotype (sl = 1.8 mm, MZCU) of *Diogenes gardineri* Alcock, 1905; G, male lectotype (sl = 2.3 mm, MNHN Pg 1502) of *Diogenes serenei* Forest, 1956; H, male (sl = 2.9 mm, USNM 1000219) of *Diogenes pallescens* from Guam. Scales equal 0.5 mm.

merus of the third maxilliped, one or more spines on the ventral margins of the meri of the second pereopods (Figs. 3A-D), and the presence of a dorsodistal spine on each carpus and propodus of the fourth pereopods (Figs. 4A-D). In view of the character overlap seen among the type series, and the range of variation observed in the Guam populations, it must be concluded that *D. gardineri* and *D. serenei* are junior subjective synonyms of *D. pallescens.*

TAXONOMY

Diogenes pallescens Whitelegge, 1897

Diogenes pallescens Whitelegge, 1897: 141, pl. 6, Figs. 2, 2a-c; Alcock, 1905a: 830; 1905b:74; Forest, 1956: 531; Lewinsohn, 1969: 46;Ball & Haig, 1972: 89, Fig. 2; Morgan, 1987: 176; Rahayu, 1994: 83; 1996: 435; 2000: 391; Rahayu & Forest, 1995: 413.

Diogenes gardineri Alcock, 1905a: 830, Pl. 68, Fig. 1; 1905b: 73, Pl. 7, Fig. 3; Nobili, 1907: 366; Forest, 1956: 530, Fig. 16; Lewinsohn, 1969: 45; Ball & Haig, 1972: 91; Nakasone, 1975: 3; Gherardi & McLaughlin, 1994: 643; Wang, 1994: 568; McLaughlin & Haig, 1996: 123; Rahayu & Forest, 1995: 410; McLaughlin & Clark, 1997: 33; Hogarth et al., 1998: 161; Rahayu, 2000: 390.

? Pagurus (Diogenes) senex: Hilgendorf, 1879: 824.

Diogenes senex: Bouvier, 1892: 55; Nobili, 1906a: 78; 1906b: 118; Balss, 1927: 224; Ramadan, 1936: 4 (list). Not *Diogenes senex* Heller, 1865.

? *Diogenes senex*: Nobili, 1903: 16. Not *Diogenes senex* Heller, 1865.

Diogenes serenei Forest, 1956: 530, Figs. 12-15; Lewinsohn, 1969: 45; Ball & Haig, 1972: 91; Nakasone, 1975: 3; Morgan, 1987: 176; 1989: 402; 1990: 19; Haig & Ball, 1988: 168; Gherardi & McLaughlin, 1994: 643; Rahayu 1994: 83; 2000: 391; McLaughlin & Haig, 1996: 123; Rahayu & Forest, 1995: 412; Rahayu and Komai, 2000: 29; McLaughlin: 2001a (in press).

Not *Diogenes gardineri:* Morgan, 1987: 175; 1990: 18. ? = *Diogenes senex* Heller, 1865.

Not *Diogenes gardineri:* Naiyanetr, 1998: 48 (list) = *Diogenes tumidus* Rahayu & Forest, 1995.

Redescription. - Shield as broad as long or longer than broad; anterior margin between rostral lobe and lateral projections straight or weakly concave; anterolateral margins sloping; posterior margin truncate; dorsal surface frequently with spines or spinules anteriorly and laterally, usually 1 more prominent spine on each lateral margin in posterior half. Rostrum obsolete. Lateral projections roundly triangular, unarmed or with 1 or more marginal spinules. Dorsal margin of branchiostegite with 3-8 spinules or small to prominent spines.

Ocular peduncles sometimes somewhat asymmetrical, 0.70 to approximately equaling length of shield, occasionally slightly longer, becoming longer and more slender with increasing animal size; corneas only weakly dilated if at all. Ocular acicles subrectangular, anterior margin usually with 2-6 strong spines, occasionally worn down or broken off, and often 1 or more smaller spines laterally; separated basally by width of intercalary pro-cess. Intercalary rostral process well developed, reaching to or slightly beyond tips of acicular spines, occasionally terminally bifid, and often with prominent ventral spine.

Antennular peduncles, when fully extended, usually reaching at least to bases of corneas, often to distal corneal margins, and not infrequently considerably beyond. Ultimate and penultimate segments glabrous. First segment usually with 1 or 2 small spines on ventrolateral distal margin.

Antennal peduncles reaching to approximately midlength of ocular peduncles, occasionally slightly shorter or longer, but not reaching to bases of corneas; with supernumerary segmentation. Fifth segment usually with 1-3 long setae on dorsodistal margin, few short setae on dorsal surface. Fourth segment usually, but not always, with small spine at dorsodistal margin. Third segment unarmed or with small ventrodistal spine. Second segment with dorsolateral distal angle usually strongly produced and terminating in prominent simple or occasionally bifid spine, dorsomesial distal angle also with prominent spine, 1-5 spines ventrolaterally. First segment unarmed. Antennal acicle usually not reaching to distal apex of fourth peduncular segment, terminating in simple or bifid spine, with 1-4 spines on both mesial and lateral margins, 1 or 2 spines occasionally also on dorsal surface. Antennal flagella moderately to very short, articles each with 2-4 moderate to long, and often 1-4 shorter setae.

Maxillule with endopod lacking external lobe. Third maxilliped with small to prominent spine on dorsodistal margin of merus.

Left cheliped with abundant but not dense covering of long simple setae on chela. Dactyl varying in length from approximately equal to 0.35 shorter than upper margin of palm; cutting edge with row of small and usually 1-3 larger calcareous teeth; terminating in small calcareous claw, often slightly overlapped by fixed finger; outer surface convex, with partial covering of small granules, tubercles or spinules; upper margin with single or double row of small spines, tubercles or granules, becoming more acute distally; inner surface unarmed. Fixed finger with

outer surface usually somewhat flattened, armed with scattered small, blunt or sharp spines; lower margin usually with row of low tubercles or small, acute or subacute spines, and sometimes forming weak curve with lower, similarly armed margin of palm, occasionally with much stronger, acute spines on palm; cutting edge of fixed finger with row of calcareous teeth; terminating in calcareous claw. Palm with outer surface convex, armed with scattered blunt or acute spines, occasionally only tubercles, at least in lower 0.25-0.40, with somewhat irregular, single or double, short row of stronger, sometimes very prominent spines beginning near midpoint of proximal margin, rarely reaching midlength of palm; upper half of outer surface nearly smooth to weakly armed with small tubercles or spinules; upper margin with 3 to several strong, subacute or acute, often curved spines; often much smaller near distal margin; inner surface unarmed. Carpus approximately equal to or very slightly shorter than palm; upper margin with row of several strong spines interspersed with long, simple setae; lower outer face convex, and with slightly oblique row of 3 to several, often widely-spaced spines, additional row of spines on or adjacent to distal margin; inner surface unarmed. Merus triangular; dorsal margin with row of spinules or small spines and sparse long setae; ventromesial margin usually with 2-4 spines in distal half; ventrolateral margin most frequently with row of strong spines, occasionally only spinules proximally. Ischium unarmed.

Right cheliped appreciably smaller than left; frequently with prominent hiatus between dactyl and fixed finger. Dactyl approximately equal to slightly longer than palm; upper margin with single or double row of small spines, tubercles or granules, dorsal surface with few spinules partially obscured by long setae. Palm with 2-5 prominent spines and long, simple setae on upper margin, outer face flattened or weakly convex, usually 1 or 2 rows of small spines, spinules or granules in midline and additional 1 or 2 rows in lower half and extending onto fixed finger but partially concealed by long, simple setae; inner surfaces of dactyl, fixed finger and palm with long setae, most numerous on dactyl and fixed finger. Carpus with long setae and 2-6 very prominent spines on upper margin, outer surface with row of prominent spines approximately in midline; inner and lower surfaces with scattered setae. Merus triangular; dorsal margin with 1 or 2 to row of spines or spinules and long setae; ventromesial margin usually with 2 or 3 spines in distal half and often few additional spinules or tubercles proximally; ventrolateral margin with 1-4 spines distally and often few additional spinules, tubercles, or granules proximally. Ischium unarmed.

Ambulatory legs with dactyls 0.25-0.65 longer than propodi, unarmed but with numerous long, simple setae projecting from all surfaces. Propodi with length varying from 3.3 to 6.0 times maximum dorso-ventral height; surfaces usually unarmed, but occasionally ventral surface of left third pereopod with row of tiny spinules, dorsal and ventral surfaces particularly with scattered long, simple and weakly plumose setae. Carpi all with dorsodistal spine, usually 1 additional spine on dorsal surface in proximal half of each second pereopod, third with proximal margin, unarmed, with tiny proximal spinule or well developed spine; dorsal and ventral surfaces with long, simple and weakly plumose setae. Meri with long , simple and weakly plumose setae on dorsal and ventral surfaces, ventral margins of second pereopods with 1-5 usually prom nt spines, occasionally with row of very small spines, and rarely unarmed, lateral faces occasionally with few spinules or granules in ventral half; third unarmed. Ischia unarmed, but with long dorsal and ventral, simple and plumose setae. Fourth pereopods each usually with prominent spine at dorsodistal margin of propodus and carpus.

Male pleopods typically uniramous. Female with paired gonopores; unpaired left pleopods 2-4 well developed, biramous; pleopod 5 uniramous. Telson with median cleft distinct; terminal margins each with row of centrally moderate to small spines, larger spines laterally and extending onto lateral margins.

Remarks. - Lewinsohn's (1969) presumption that specimens identified by Bouvier (1892) and Nobili (1906b), Balss (1927) and Ramadan (1936) as *D. senex,* actually were referable to *D. gardineri,* was confirmed for the specimens from Djibouti and Suez, by McLaughlin & Clark (1997). These latter authors also demonstrated the occurrence of "*D. gardineri*" in East Africa. Although Hilgendorf's (1879) specimen from Moçambique, identified as *"Pagurus (Diogenes) senex",* has not been reexamined, it is quite probable that it too is *D. "gardineri",* as suggested by Nakasone (1975).

As noted by McLaughlin & Haig (1996), Nobili's (1903) description of a species from Singapore that he attributed to *D. senex,* could have applied to several species of *Diogenes.* That *D. pallescens* occurs in Singaporean waters was confirmed by Rahayu (1996), and present material from the Raffles Museum of Biodiversity Research (identified as *D. serenei).* However, another species from Singapore, *D. inglei* McLaughlin & Clark, 1997, was described by those authors as a species similar to, but distinct from *D. "gardineri".*

Neither Morgan's (1987) nor Haig & Ball's (1988) descriptions of colouration in *D. serenei* make any mention of stripes on the ocular peduncles. Morgan's (1987: 176) colour notes of his Port Essington specimens attributed to *D. gardineri,* particularly his reference to "...two faint grey-green dorsal stripes" on the ocular peduncles, would give credence to McLaughlin & Haig's (1996) suggestion that his specimens might instead represent *D. senex.* However, the living colour has not been described for *D. senex,* and the possibility that another *Diogenes* species with morphology similar to *D. pallescens* cannot be ruled out. Morgan (1990) stated that his specimens of *D. gardineri* from the Kimberley region exhibited colouration similar to that of the Northern Territories animals, thus are not Alcock's (1905a) taxon.

Naiyanetr (1998) listed *Diogenes gardineri* among hermits found in Thailand. His record was based upon information contained in the unpublished master's thesis of Pitagsalee (1980: 84, figs. 48, 49). One of Pitagsalee's specimens was subsequently reexamined (McLaughlin, 2001a) and found to represent *Diogenes timidus* Rahayu & Forest, 1995.

Distribution. - Red Sea, Persian Gulf, East Africa, Indian Ocean, Andaman Sea, northern Australia, New Guinea, Indonesia, Singapore, Funafuti, Vietnam, Tuamotu Archipelago, Guam; intertidal to 42 m.

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