

**A REDESCRIPTION OF *DIOGENES SENEX* HELLER, 1865,
SENSU STRICTO (DECAPODA: ANOMURA: PAGURIDEA:
DIOGENIDAE)**

Patsy A. McLaughlin and Janet Haig

Shannon Point Marine Center, Western Washington University, Anacortes Washington
98221-4042 (PAM); Allan Hancock Foundation, University of Southern California,
University Park, Los Angeles, CA 90089-0371 U.S.A (JH)

ABSTRACT: *Diogenes senex* Heller, 1865 sensu stricto is redescribed from specimens collected in Australia, particularly in and around the type locality of Sydney. A neotype has been designated. Comparisons of this material with other specimens identified as *D. senex* by a number of authors has shown that at present only the Australian material truly represents Heller's taxon.

KEY WORDS: Hermit crab - Diogenidae - *Diogenes senex* - redescription

INTRODUCTION

Diogenes senex Heller, a species first described by Heller (1865) from specimens reportedly collected in Sydney, Australia, has been a source of systematic confusion for more than a century. The species was included in Haswell's (1882) catalog of Australian Stalk and Sessile-eyed Crustacea, but Haswell merely presented a translation of Heller's (1865) original description. In his list of the marine and freshwater invertebrate fauna of Port Jackson, New South Wales, Australia, Whitelegge (1889) noted *D. senex* in shells of *Lampania australis* Quoy and Gaimard, 1834 (= *Velacumantus australis*, cf. Wilson, 1993). Outside Australian waters, *D. senex* was reported from Moçambique by Hilgendorf (1879), from the Suez by Bouvier (1892) and Balss (1927), from Malaysia (Penang) by Lancaster (1902), from Singapore by Nobili (1903), from the Gulf of Oman and Djibouti by Nobili (1906a, b), from the Red Sea by Ramadan (1936), from Durban, South Africa by Barnard (1950), from the Ryukyu Islands, Japan, by Nakasone (1975) and Miyake (1978), and from the Kii Peninsula, Japan by Miyake and Imafuku (1980).

Forest (1956) compared the specimens in the Muséum National d'Histoire Naturelle, Paris (MNHN), from Suez and Djibouti identified as *D. senex* by Bouvier and Nobili, with those from the Gulf of Oman, similarly identified by Nobili, and concluded that the latter author had confounded two species under the name *D. senex*, but he (Forest, 1956) was uncertain which of the two might represent Heller's (1865) taxon. Lewinsohn (1969) called attention to the fact that the reports of *D. senex* from Suez, the Red Sea and Djibouti were founded on very few specimens, and in the case of Ramadan (1936) no specimens at all. Based on Forest's (1956) remarks concerning Bouvier's (1892) and Nobili's (1906b) reports, Lewinsohn (1969) questionably placed the *D. senex* of these authors, as well as those of Balss (1927) and Ramadan (1936) in synonymy with *Diogenes gardineri* Alcock, 1905. As Lewinsohn's (1969) discussion pertained only to *D. gardineri*, he made no comments on the reports of *D. senex* from other localities, except to point out inadequacies in Heller's (1865) original description and cast doubt on the accuracy of Heller's type locality. "That Heller

stated the Type locality - Sydney - is to be reflected upon. The fauna of Sydney can be appreciably better associated with the fauna of the cold waters of Southern Australia than with the tropical-subtropical further northern parts of Australia. On the contrary one notes however, that the locality information in the work of Heller ('Novara'-expedition) are not always accurate and so *D. senex* may have come from another region." (Translation from Lewinsohn, 1969: 46).

We have now had the opportunity to examine four lots of *Diogenes* from New South Wales, Australia, including specimens from Watson Bay, Port Jackson, apparently those reported by Whitelegge (1889) as *D. senex* (Dr. Paul Clark, personal communication), and feel confident that all represent Heller's taxon. Additionally we have found specimens referable to this species from Queensland and Northern Australia. We have compared these specimens with the Paris specimens (MNHN Pg 1514, 1515, 1516) identified by Bouvier and Nobili as *D. senex* from Suez and Djibouti, as well as with specimens in The Natural History Museum, London, (NHM) from the Suez Canal (NHM 1927.11.2.226), Singapore (NHM 1905.10.21.33-36), and East Africa (NHM 1955.3.5.58-60) similarly identified as *D. senex*. Additionally we have examined specimens from Okinawa, Ryukyu Islands (Imafuku collection) questionably referred to *D. senex*. Among these, only the Australian specimens can be considered representative of *D. senex* sensu stricto. As Heller's (1865) type material is believed to be no longer extant (J. Forest, personal communication), we are designating a neotype from Port Jackson, which is in Sydney Harbor.

MATERIALS AND METHODS

Specimens of *D. senex* s.s. have come from the collections of the Allan Hancock Foundation (AHF), University of Southern California, now incorporated into the collections of the Natural History Museum of Los Angeles County (LACM), Los Angeles; the Museums and Art Galleries of the Northern Territories (MNT), Darwin; the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; and the Natural History Museum, London [formerly British Museum (Natural History)]. All specimens have been returned to their institutions of origin except one, which remains in the personal collection of the senior author. One measurement, shield length (SL), as measured from the midpoint of the anterior margin of the carapace directly posterior to the rostriform process to the midpoint of the cervical groove, is given as an indication of specimen size. Measurements were made to the nearest 0.01 mm using an ocular micrometer mounted in a Wild M-5 microscope.

SYSTEMATIC ACCOUNT

Diogenes senex Heller, 1865

Figs. 1-3

Diogenes senex Heller, 1865: 85, pl. 7, fig. 3.--Haswell, 1882: 158.--Whitelegge, 1889: 232.--Alcock, 1905: 166 (in part) (lit).--Barnard, 1950: 446 (in part).--Gordan, 1956: 318 (in part) (lit).

? *Diogenes gardineri*: Morgan, 1987: 175; ? not *Diogenes gardineri* Alcock, 1905.

? Not *Pagurus (Diogenes) senex*: Hilgendorf, 1878: 824.

Not *Diogenes senex*: Bouvier, 1892: 55.--Lanchester, 1902: 366.--Nobili, 1903: 16; 1906a: 78; 1906b: 118.--Balss, 1927: 224.--Ramadan, 1936: 4 (list).--Forest, 1956: 531.--Nakasone, 1975:1, fig. 1.--Miyake, 1978:23 (key).--Miyake and Imafuku, 1980: 3.--Morgan, 1987: 176. Neotype (herein selected). Male (SL = 3.20 mm), Watson Bay, Port Jackson, NHM 1912.11.22.111.

Additional material examined. Northern Australia: Caiman Creek, Port Essington (11°13.7'S, 132° 12.2'E), 1 female, 2 ovigerous females (SL = 1.33 - 1.63 mm), low water, 13 May 1983, MNT. Queensland: Clontarf Beach, 6 males, 4 females (SL = 1.82 - 2.81 mm), 3 May 1973, collector J. Garth, LACM (AHF). New South Wales: Watson Bay, Port Jackson, 1 male, 1 female, (SL = 2.75, 3.08 mm), NHM 1912.11.22.111 (neotype) and 1912.11.22.112-113. Gunnametta Bay, Port Hacking (3405'S, 15110'E) 13 males, 9 females (SL = 1.58 - 4.75 mm), tidal flats, November 1925, USNM 64670, 64690. Jervis Bay, near mouth of Moona Moona Creek, 6 males, 1 female (SL = 2.06 - 4.5 mm), intertidal, 25 May 1980, collector J. Haig, LACM (AHF 2011- 01), PMcL.

REDESCRIPTION

Shield longer than broad; anterior margin concave between rostrum and prominently developed lateral projections; anterolateral margin sloping; posterior margin truncate; dorsal surface with sparse tufts of long setae, scattered spines and transverse spinulose ridges laterally on each side, lateral margins sometimes also with few small spines and long setae. Branchiostegal dorsal margin with row of 4-8 small spines or spinules and few long setae, 1 additional small spine, practically obscured by dense setae, on distal margin of branchiostegite dorsally. Rostrum obsolete to broadly rounded. Lateral projections extending well beyond rostrum, terminating in strong marginal or submarginal spine. Anterolateral margins with 1 to several spines and scattered long setae submarginally. Rostriform process slender, acute, usually not reaching distal margin of inner-most spine of ocular acicles, occasionally equaling or slightly exceeding length of acicular spines. No ventral process or spine, but often few setae.

Ocular peduncles $3/4$ - $4/5$ length of shield, distal margin of cornea usually reaching distal $1/2$ - $1/3$ of ultimate segment of antennular peduncle; antennular peduncle reaching only to base of cornea. Cornea dilated little if at all. Ocular acicles roundly triangular or subrectangular, distal margin with usually 1 or 2 moderately strong and 2-4 much smaller spines, not reaching beyond $1/2$ of lateral margin, occasionally with only 4 or 5 small spines; separated basally by width of rostriform process (approximately $1/4$ basal width of 1 acicle).

Antennular peduncles with 1-3 moderately long setae on dorsal margin of ultimate segment; penultimate segment with few scattered setae; basal segment with 1 or 2 very small, acute or nearly blunt spinules at laterodistal margin.

Antennular peduncle with supernumerary segmentation. Fifth segment short, rarely longer than fourth, ventral surface with numerous long setae. Fourth segment with 1, rarely 0 or 2, often prominent, spine(s) or spinule(s) on dorsal surface in distal $1/2$, ventral surface with numerous long setae. Third segment with ventrodistal margin unarmed or rarely with tiny spinule. Second segment with spine on slightly produced dorsolateral distal angle, dorsomesial distal angle usually with spine, occasionally

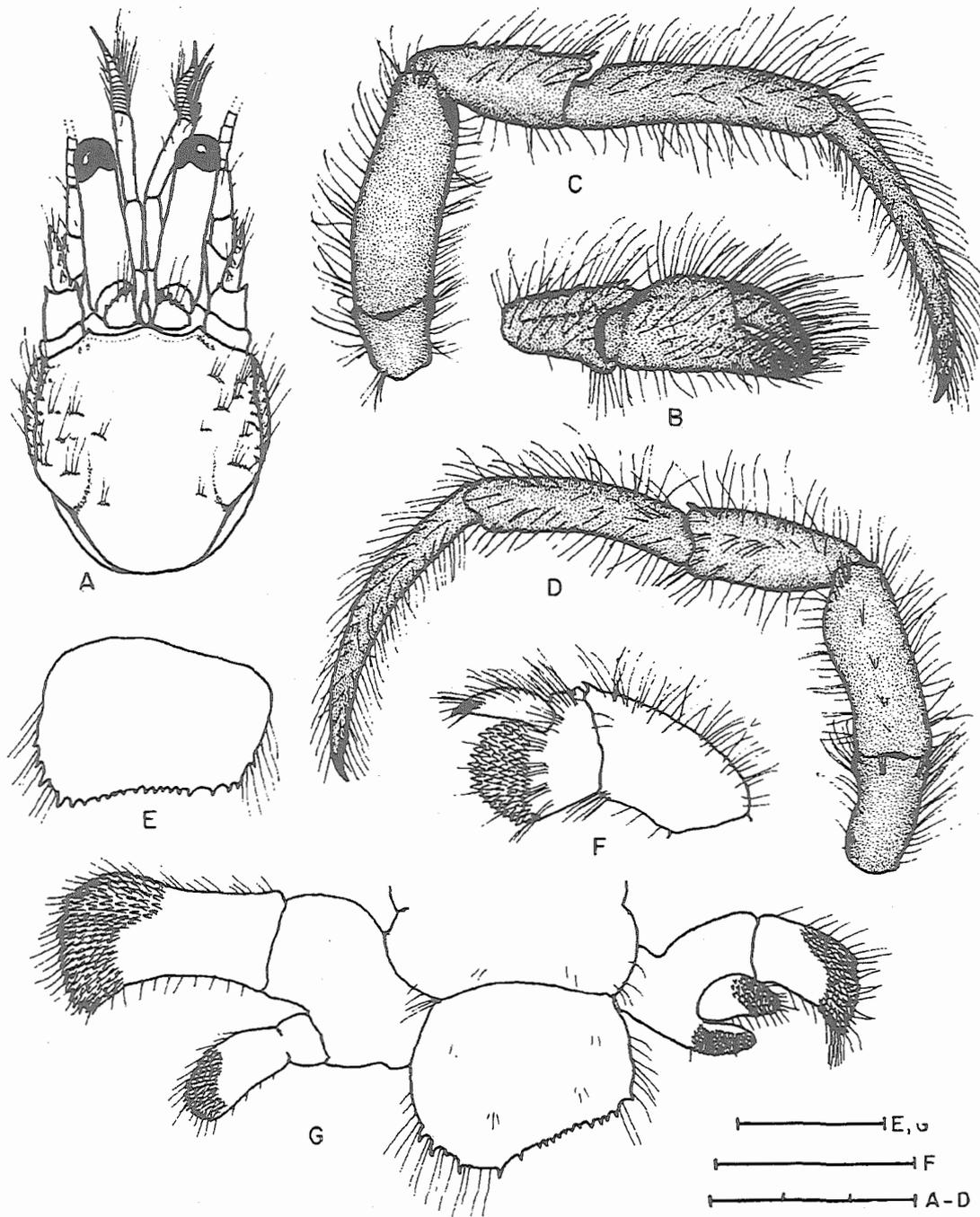


Fig. 1. *Diogenes senex* Heller, sensu stricto, Port Jackson, Sydney. A-E, Neotype; F, G, second male. A, shield and cephalic appendages; B, chela and carpus of right cheliped; C, second right pereopod; D, third left pereopod; E, telson; F, dactyl, propodus and carpus of left fourth pereopod; G, uropods and telson. Scales equal 3.0 mm (A-D) and 1.0 mm (E-G).

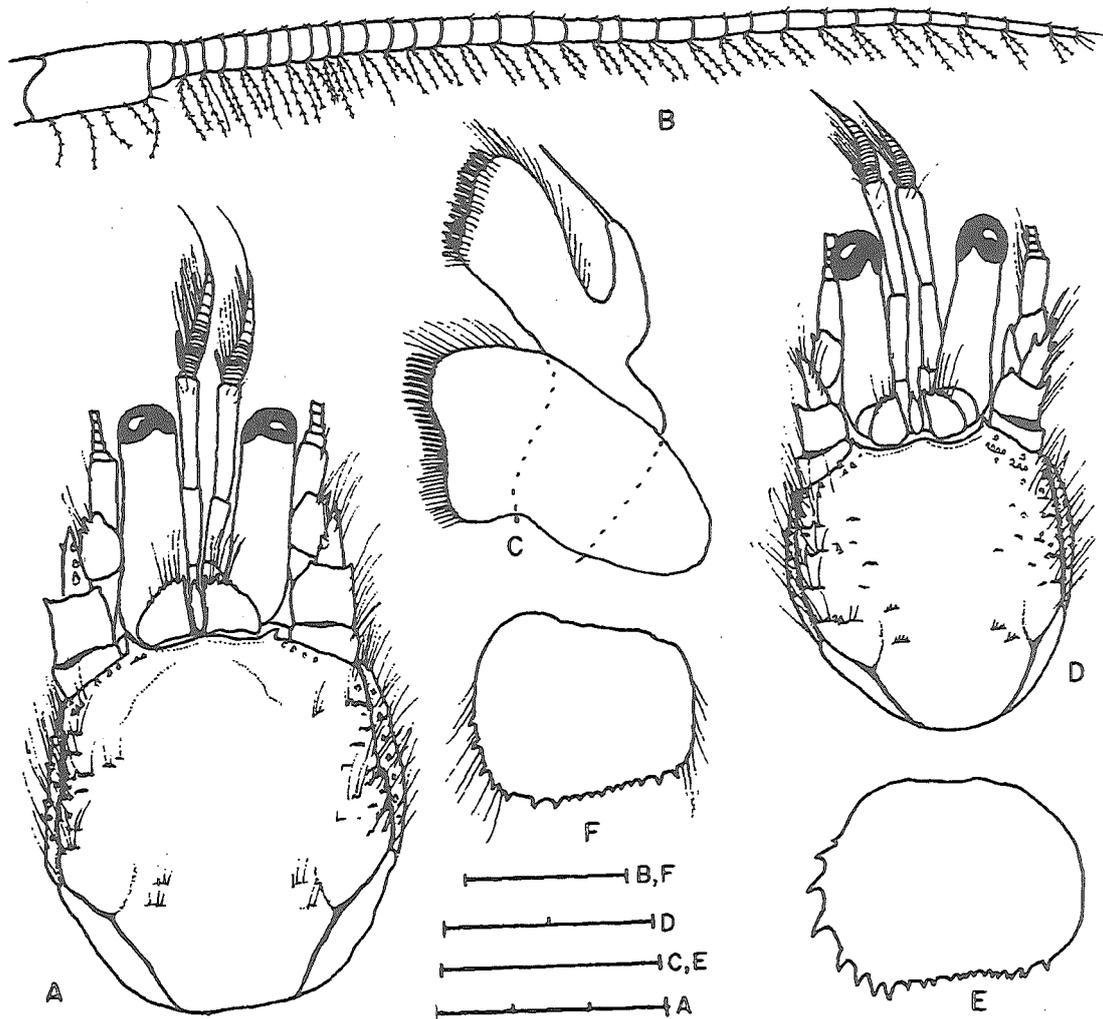


Fig. 2. *Diogenes senex* Heller, sensu stricto. A-C, male, Port Hacking; D, E, male, Queensland; F, male, Jervis Bay. A, shield and cephalic appendages; B, antennal flagellum; C, maxillule; D, shield and cephalic appendages; E, telson; F, telson. Scales equal 3.0 mm (A), 2.0 mm (D), and 1.0 mm (B, C, E, F).

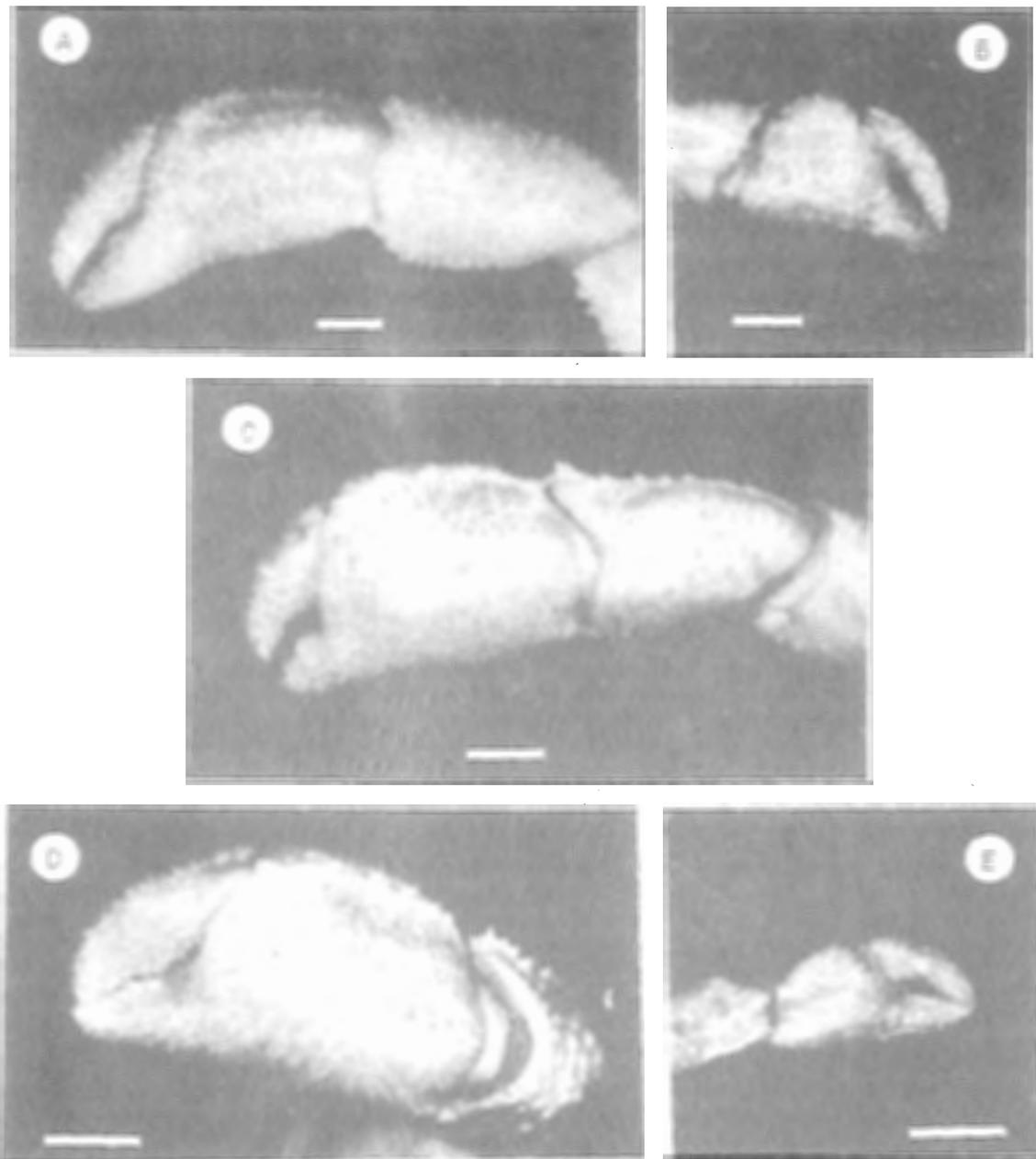


Fig. 3. *Diogenes senex* Heller, sensu stricto. A, B, Port Hacking; C, Port Jackson, Sydney; D, E, Jervis Bay. A, left chela, male USNM 64670; B, right chela, male, USNM 64690; C, left cheliped, male neotype NHM 1912.11.22.111; D, left chela, male, LACM; E, right chela, male, LACM. Scales equal 1.0 mm

unarmed or with only tiny spinule. First segment often with small spine or spinule on ventrodistal margin, less frequently unarmed. Antennal acicle not forked, rarely reaching to proximal margin of ultimate peduncular segment; with simple or bifid tip, mesial margin with 2-4 spines and several long setae, lateral margin with 0-2 spines. Antennal flagellum quite short, barely reaching distal margin of carpus of left cheliped; ventral margin of each article with pair of long setae provided with auxiliary setules.

Maxillule with 1 long stiff bristle on weakly developed internal endopodal lobe, external lobe absent.

Left cheliped with usually short dactyl and fixed finger; dactyl approximately as long as upper margin of palm, but curved ventrally, upper surface with row of acute spines or smaller spinulose tubercles, supplemental 1 or 2 similar rows of spines or tubercles and additional scattered spinules or tubercles on upper outer surface; entire outer face with rather long, moderately dense setae. Cutting edges of both dactyl and fixed finger with several small calcareous teeth; no appreciable hiatus. Lower margin of palm and fixed finger rounded, nearly straight to noticeably sinuous, with irregular single or nearly double row of moderately small spines or spinulose tubercles, outer surface of fixed finger with scattered spinules or small tuberculate spines and long setae; outer surface of palm strongly convex, with very distinctly produced midline providing triangular appearance, upper margin somewhat flattened or rounded and with 1 to several irregular rows of small spines or spinulose tubercles, upper outer surface usually with 1 longitudinal row of spines or spinules and occasionally also additional scattered spinules or granules, prominently produced midline armed with irregular single to triple row of spines or spinulose tubercles extending at least half length of palm, and sometimes to articulation of dactyl and fixed finger, strongest in proximal 1/3, lower outer surface with numerous scattered small spines or spinulose tubercles and long setae. Inner surfaces of palm, fixed finger and dactyl with numerous long setae and sometimes also scattered spinules or spinulose protuberances on palm. Carpus only slightly less setose than palm, outer face convex; upper margin with slightly raised row of single spines proximally, sometimes becoming almost double row distally, upper outer surface spinose or tuberculate, frequently with distinct longitudinal row of spines, distal margin with 3-5 acute spines, lower outer surface and lower margin spinose or tuberculate; inner and lower surfaces often with tubercles, spinules or low protuberances and long setae. Merus triangular, dorsal margin with single to triple row of acute or blunt spines, lateral face often with short, transverse rows of spinulose tubercles in dorsal half, scattered spinulose tubercles ventrally; ventrolateral margin with row of small spines, ventral surface tuberculate or with transverse rows of small spines or spinules; mesial face often with few low tubercles dorsally, distal margin with small spines or spinules in ventral 1/3. Right cheliped usually reaching slightly beyond distal margin of carpus of left; dactyl and fixed finger commonly with distinct hiatus; long setae on outer, upper and lower surfaces often virtually obscuring all armature. Dactyl with row of small spines or spinules on upper margin and outer face; fixed finger with few spinules. Outer face and lower margin of palm with scattered spines, spinules or small tubercles, upper margin rounded, unarmed or weakly spinulose. Carpus with long setae on all surfaces; upper surface somewhat flattened, usually with row of small spines, spinules, or small

spinulose tubercles on both inner and outer margins, and commonly 1 stronger spine at each distal angle, outer face usually with scattered spinules or tubercles; inner face unarmed. Merus triangular; dorsal margin and lateral face with long setae arising from low, sometimes spinulose protuberances, 1 small spine on dorsodistal margin; ventrolateral margin with 1 or 2 small spines or spinules distally; mesial face with few low protuberances, ventromesial margin unarmed, ventral surface often with scattered small spinules or spinulose protuberances.

Ambulatory legs generally similar. Dactyls long, approximately 1/3 longer than propodi, slightly twisted, and distinctly curved ventrally, and with numerous long stiff setae on all surfaces. Propodi 1 1/2 to twice length of carpi, all surfaces with long setae, most numerous dorsally and ventrally. Carpi only slightly shorter than meri, second usually with 1 strong spine at dorsodistal margin and 1-5 small spines usually in proximal half to 2/3; third with dorsodistal spine and usually 1 spine in proximal 1/2, infrequently unarmed; both pairs with long setae particularly dorsally and ventrally. Meri with numerous setae, particularly dorsally and ventrally; third sometimes, and second rarely, with small blister-like protuberances on ventral margins. Sternite of third pereopods with anterior lobe subsemicircular to roundly rectangular, often obscured by long setae.

Males with 4 unpaired uniramous pleopods. Uropods asymmetrical; protopod of right produced ventrally into prominent lobe and provided with rasp of corneous scales; endopods and exopods with well developed, circular or ovate rasps of corneous scales covering 1/2-2/3 of dorsal surfaces. Telson with slightly asymmetrical posterior lobes, median cleft usually indistinct or absent; terminal margins with row of very small spines or spinules, becoming appreciably larger on left and extending at least half length of left lateral margin, occasionally 1 or 2 spines also extending onto right lateral margin.

VARIATION

Among the 46 specimens of *D. senex* examined, considerable variation was observed in the strength and number of spines and/or spinulose tubercles on the left cheliped, as reflected in the description. Most commonly the outer face of the left chela presented a somewhat circular or ovate appearance (Figs. 3C, D); however, in two instances the chela was elongate and relatively slender. In these latter specimens the spines were strong (Fig. 3A), but less numerous than in the more typically shaped chelae. Size, rather than sex, appeared to exert the most influence the strength of the armature in the typical chelae. In larger specimens (SL>2.5 mm), spinulose tubercles covered nearly the entire the outer surfaces of the palm and fixed finger. In small individuals (SL≤2.0 mm), acute spines were most commonly present, but were fewer in number.

Variations were also seen in the length of the rostriform process, and in the number and strength of the spines of the ocular acicles. Generally the rostriform process was slightly shorter than the longest acicular spine. In two moderately small specimens, the rostriform process exceeded the spine length, while in one somewhat larger specimen, the rostriform process was equally as long as the acicular spines of the right side, but slightly shorter than those of the left. Typically the anterior margin of the ocular acicle bore 1 or 2 moderately large spines at the inner angle, followed laterally

by 2-4 appreciably smaller spines; however, in a few individuals, all of the spines were of approximately equal size.

AFFINITIES

Diogenes senex is grouped among those species of *Diogenes* having a well developed, but slender, simple rostriform process, and chelipeds with long, dense or moderately dense setae, i.e., *D. gardineri* Alcock, 1905; *D. penicillatus*, Stimpson, 1858, *D. lanarius* Yap-Chiongco (in Estampador 1937), and those species heretofore erroneously identified as *D. senex*. *Diogenes senex* s.s. is immediately distinguishable from *D. gardineri* and the *D. senex* of Bouvier (1892), Nobili (1906a, b), and Forest (1956) by the presence in the former species of long setae on the ventral surfaces of the penultimate and ultimate segments of the antennal peduncle and the long pairs of setae arising ventrally from each article of the antennal flagellum. In the latter taxa, the antennal segments are sparsely, if at all setose; the setation of the articles of the antennal flagellum consist of 1-4 long and/or short, unpaired setae. *Diogenes senex* presumably can be distinguished from *D. penicillatus* by the shortness of the antennal peduncles in the former species, and by the distinctly different armature of the left chelae in the two species. From *D. lanarius*, *D. senex* appears distinguishable by the presence of spines and tubercles on the right cheliped, and by the shorter antennal peduncles. However, we have not personally examined Stimpson's (1858) or Yap-Chiongco's (1937) species.

DISCUSSION

As previously indicated, the ostensibly cosmopolitan distribution of *D. senex* has been the result of misidentifications by a number of carcinologists. Heller's (1865) original description was lacking in many pertinent details, and clearly could have applied to one of several species of *Diogenes*. In the synonymy given here for *D. senex* s.s., the citations by Alcock (1905), Barnard (1950); and Gordan (1956) have been cited as "in part", as these authors were referencing both the true *D. senex* of Heller (1865), Haswell (1882), and Whitelegge (1889), and the misidentified taxa of other authors.

Hilgendorf's (1879) *Pagurus (Diogenes) senex* from Moçambique, is most probably not Heller's (1865) species. Although his (Hilgendorf, 1879) description was brief, and lacking in numerous essential specifics, he described the carpus of the left cheliped as having a six-toothed upper margin and second downwardly directed row of six teeth; the upper margin of the palm was reported to be a toothed crest. The carpus of *D. senex* s.s. has a row of numerous, moderately small to small, spines on the upper margin; when a second row of spines is present on the outer surface, it is composed of a number of relatively small spines forming a generally longitudinal row. The upper surface of the palm is not crested, even in the most prominently spinose specimens. Nakasone (1975) was of the opinion that Hilgendorf's (1879) species might be referable to either *D. gardineri* or *D. serenei* Forest, 1956.

Judging from the reported absence of a rostriform process and the dense setation of the chelae and ambulatory legs, Lanchester's (1902) *D. senex* from Penang is most probably a species referable to the *Troglopagurus* group of *Diogenes* (see Forest,

1952).

Nobili's (1903) description of *D. senex* from Singapore, like so many of the older descriptions, could apply to a host of species of *Diogenes*. Nobili made no mention of rostriform presence, length, or armature; of ocular, antennular or antennal peduncular length; or armature of the ambulatory legs. The four specimens of *Diogenes senex* sensu lato, that we examined from Singapore (NHM 1905.10.21.33-36) clearly are not Heller's taxon, but their identity has yet to be determined.

As noted in the introduction, Lewinsohn (1969) questionably included the *D. senex* of Bouvier (1892), Nobili (1906b), Balss (1927), and Ramadan (1936) in with specimens he (Lewinsohn, 1969) identified as *D. gardineri*. At least the Paris specimens (MNHN Pg 1514, 1515, 1516) from Suez and Djibouti, and the London specimen (NHM 1927.11.2.226) from the Suez Canal agree relatively well with specimens from Bombay, India presented to the Natural History Museum, as *D. gardineri* (NHM 1958.6.23.12-13) by Dr. K. Sankolli, and presumably identified by him. Whether these specimens, as well as those of Lewinsohn (1969) actually represent Alcock's (1905) species from the Maldives, must await a more detailed study of the latter taxon.

Nakasone (1975) provided a rather detailed description of a species of *Diogenes* that he believed to represent Heller's (1865) taxon, and in many respects, his description could apply to *D. senex* s.s. However, the shield of his species was described and illustrated as entirely unarmed; the rostriform process distinctly exceeded the ocular acicles which had only 3 spines; the antennal peduncles reached to the bases of the corneae; and the antennal acicle reached well beyond the proximal margin of the ultimate peduncular segment. None of these characters apply to *D. senex*. Unfortunately, Nakasone (1975) did not describe the setation of the antennal flagellum, the armature of the right cheliped, nor the structure and armature of the telson. Miyake's (1978) reference to *D. senex* was made only in his key to the Japanese species, with an indication that it occurred in the Ryukyu Islands; it was probably based on Nakasone's (1975) report. We have examined two specimens from this area, and while the antennal peduncles are considerably shorter than the ocular peduncles, the length of antennular peduncles is nearly equal to the distal margins of the corneae, and the general structure and armature of the left cheliped resemble that of *D. senex* s.s., these specimens do not belong to this species. In our Okinawa specimens, the rostriform process overreaches the prominent, slender, inner-most spines of the ocular acicles; the right palm and carpus each is armed on the upper surface by two or three strong spines; the telson has a median cleft and fewer, but stronger, spines on the terminal margins. More significantly, the antennal flagellum is sparsely provided with long, albeit sometimes paired, setae; however these arise laterally and/or dorsolaterally, and frequently are accompanied by 1 or more additional long or short setae. Like the other non-Australian specimens, these Ryukyu specimens cannot confidently be placed in a well defined species of *Diogenes* at this time. We have not examined the specimen reported by Miyake and Imafuku (1980) from the Kii Islands; however given the islands location in the Mie Prefecture of Japan, it is also probable that this specimen is not *D. senex* s.s. Morgan (1987) identified specimens from Port Essington, Northern Territories as *D. gardineri*, and

in his discussion compared these with other Indo-West Pacific species, including *D. senex* sensu Forest (1956). We have not had the opportunity to review Morgan's (1987) Port Essington *D. gardineri*; however, having now examined specimens clearly identifiable as *D. senex* s.s. from that locale, Morgan's identification must be considered suspect. He did not describe the setation of the antennal flagella of his specimens, a character which would immediately distinguish the two taxa.

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