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ARE ATLANTIC AND INDO-PACIFIC POPULATIONS OF THE RAFTING CRAB, *PLAGUSIA DEPRESSA* (FABRICIUS), DISTINCT? NEW EVIDENCE FROM LARVAL MORPHOLOGY AND mtDNA

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ABSTRACT. – Crabs of the genus *Plagusia* Latreille, 1804 (Crustacea: Brachyura: Plagusiidae) are well known for their habit of clinging to driftwood or ship hulls and are therefore prone to trans-oceanic transport. One of the consequences of this large dispersal potential seems to be the circumtropical distribution of one species, *Plagusia depressa* (Fabricius, 1775). This species comprises two subspecies, the Atlantic *P. d. depressa* and the Indo-Pacific *P. d. squamosa* (Herbst, 1790) (= *P. d. tuberculata* Lamarck, 1818). There are only subtle differences in adult morphology between these subspecies. For further comparison of the Atlantic and Indo-Pacific populations, we describe the morphology of the first zoeal stage of *P. d. squamosa* and the megalopa of *P. d. depressa* and present sequence data of the mitochondrial 16S rRNA gene. The comparisons of zoeae, megalopae, and mtDNA all provide evidence that the two subspecies of *Plagusia depressa* are clearly distinct. We therefore propose that *Plagusia squamosa* deserves species status, that the adult morphology is conserved, and that the major continents represent barriers for dispersal of this rafting tropical crab.

KEY WORDS. – Subspecies, Zoea, Megalopa, 16S rRNA, Brachyura, Plagusiidae.

INTRODUCTION

Crabs of the genus *Plagusia* can often be seen clinging to drifting debris, buoys, oil platforms, and ship hulls (Alcock, 1900; Rathbun, 1918; Dawson, 1987). This behaviour allows these crabs to distribute over long distances by rafting and makes them prone to anthropogenic introductions (see Garth, 1966; Carlton, 1987). Benech (1978) found a community of *Plagusia dentipes* that was transported on a self-propelled oil drilling platform from Japan to California. Foster & Willan (1979) and Dawson (1987) reported two independent introductions of *Plagusia depressa squamosa* (as *P. depressa tuberculata*) into New Zealand from Japan and Taiwan on an oil platform and long-line float, respectively.

The status of the seven presently recognized species of the genus *Plagusia* was last revised by Dawson (1987). In his listing and morphological key, the species *P. depressa* is subdivided into two subspecies, the Atlantic *P. depressa depressa* (Fabricius, 1775) and the Indo-Pacific *P. d. tuberculata* Lamarck, 1818. Only recently, it was discovered that the latter must be considered a junior synonym of *P. d. squamosa* (Herbst, 1790) (see Schubart & Ng, 2000). A subspecific separation of the morphologically very similar

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Atlantic and Indo-Pacific forms was previously proposed by Alcock (1900) and Rathbun (1918). Laurie (1906) also included *P. immaculata* as a subspecies of *P. depressa*. Some morphological differences have been suggested to distinguish the two geographic forms (see Miers, 1878; Laurie, 1906), but only one seems to be reliable: the shape of the lobe from the coxal joints of the walking legs (dentate in *P. d. depressa* and rounded in *P. d. squamosa*, see Fig. 154 in Rathbun, 1918). However, de Man (1883) and Laurie (1906) pointed out, that even this character does not seem to be completely consistent. Dawson (1987) suggests that the shape of the first male pleopods (rounded lobes vs. subcylindrical) might also allow to distinguish the two subspecies of *P. depressa*, but he preferred to continue referring to *P. d. tuberculata* as a subspecies of *P. depressa*. According to Dawson's (1987) taxonomy, the species *P. depressa* is thus circumtropical, with records from West Africa to eastern America (*P. d. depressa*) and western America to Asia, Oceania and East Africa including the Arabian and Red Sea (*P. d. squamosa*).

The subspecific status of *Plagusia d. squamosa* (as *P. d. tuberculata*) has been always accepted more readily for the western American representatives of this species (see Edmondson, 1959; Garth, 1965; Hendrickx, 1995; Wicksten, 1996) than for the populations from Oceania, Asia and East Africa, where some reports or taxonomical accounts consider *P. squamosa* (as *P. tuberculata*) a distinct species (Hartnoll, 1975; Holthuis, 1977; Vannini & Valmori, 1981; Miyake, 1983; Dai & Yang, 1991; Ng, 1998) and others a subspecies (Montgomery, 1931; Barnard, 1950; Crosnier, 1965; Sakai, 1976; Kensley, 1981; Shiber, 1981; Jones & Morgan, 1994).

In order to test whether *Plagusia depressa* sensu lato can indeed be considered a single circumtropical species or consists of more than one species, we searched for additional characters that could potentially separate the two subspecies of *P. depressa*. Therefore, the morphology of the first zoeal stage of *P. d. squamosa* and the megalopa of *P. d. depressa* were described and a 546-basepair region of the mitochondrial 16S rRNA gene was sequenced for several specimens of both subspecies. The comparison of homologous mtDNA sequences, as well as of zoeal and megalopal morphology with previous descriptions of zoeae of *P. d. depressa* by Wilson & Gore (1980) and the megalopa of *P. d. squamosa* by Muraoka (1965) allowed us to shed new light on the biogeography and systematics of these tropical rafting crabs.

MATERIALS AND METHODS

Three megalopae of *Plagusia d. depressa* were collected from different localities in the Caribbean Sea. One was from the calcareous rocks near the Discovery Bay Marine Laboratory (Jamaica), collected in 1992 by Martina Schuh. The other two megalopae were collected off the Bellairs Research Institute (near Holetown, Barbados): one by NBR on 12 July 1996 from the anchor line of a boat (anchored in approximately 10m of water), about 200m offshore; the other one in November 1997 by Steven Searcy 1km offshore from a mooring line anchored in approximately 300m of water. The Jamaican specimen moulted in the lab to the first crab stage. However, the condition of the moult of the megalopa did not allow us to use it for dissections.

Two ovigerous crabs of *Plagusia d. squamosa* were collected near Hengchun (Pingtung county) in Taiwan by HCL on 30 June and 28 July 1999 (in the second case together with *P. immaculata*). Larvae hatched in the laboratory in seawater on 6-7 July and 31 July 1999, respectively. Shortly after hatching and active natatory behaviour was observed, samples of zoea I larvae were fixed in 70% ethanol.

Drawings and measurements were based on two megalopae and 40 zoeae analyzed with a Wild MZ6 and Zeiss compound DIC (Nomarski) microscope, both equipped with a camera lucida. All measurements were made by ocular micrometer. For zoea larvae, rostrodorsal length (rdl) was measured from the tip of the rostral spine to the tip of the dorsal spine, carapace length (cl) from the base of the rostrum to the posterior margin, carapace width (cw) as the distance between the tips of the lateral spines, dorsal spine (ds) from the base to the tip of the dorsal carapace spine, rostral spine (rs) from the base to the tip of the rostral carapace spine, and antenna (ant) from the base to the tip of the antenna. For the megalopae, carapace length (cl) was measured as the distance between the frontal margin and the posterior margin of the carapace, and carapace width (cw) as the greatest distance across the carapace. Semipermanent mounts of whole larvae and dissected appendages were stained using CMC 10 and lignin pink. Parental females and samples of zoea I of *Plagusia d. squamosa* were deposited at the National Taiwan Museum, Taipei under the catalog number TMCD 3273 - 3275. For comparison, we also studied zoea larvae of *P. d. depressa* that were obtained by Wilson & Gore (1980) and deposited in the Smithsonian Institution under the accession number USNM 172313.

Several adult specimens of both subspecies of *Plagusia depressa* were studied (see Table 1 and Schubart & Ng, 2000 for material examined) in order to confirm the consistency of the shape of the coxal lobe of the walking legs as separating character. Genomic DNA of seven specimens of *Plagusia depressa* (see Table 1 for subspecies and localities) was isolated from muscle tissue of walking legs using a phenol-chloroform extraction (Kocher et al., 1989). Selective amplification of a fragment of the mitochondrial large subunit rRNA gene (16S mtDNA) was carried out by polymerase-chain-reaction (PCR) using the primers 16Sar (5'-CGCCTGTTTATCAAAAACAT -3'), 16Sbr (5'-CCGGTCTGAACTCAGATCACGT -3'), and 1472 (5'-AGATAGAAACCAACCTGG -3') (see Schubart et al., 2000a: Tab. 3). PCR products were purified with Microcon 100 ® filters prior to sequencing with the ABI BigDye ® terminator mix in an ABI Prism 310 Genetic Analyzer ®. Sequences were aligned manually with the multisequence editing program ESEE (Cabot & Beckenbach, 1989) and deposited in the genetic database EMBL (see Table 1).

Table 1. Specimens of two subspecies of *Plagusia depressa* (Fabricius, 1775) used for DNA sequencing and population comparisons, with locality of collection, museum catalog number, and genetic database (EMBL) accession number. R: Collection Rudolf Diesel, Starnberg; SMF: Senckenberg Museum, Frankfurt a.M.; ULLZ: University of Louisiana at Lafayette Zoological Collection, Lafayette, ZRC: Zoological Reference Collection, National University of Singapore.

Specimen	*Locality and date of collection*	*catalog #*	*EMBL #*
Plagusia d. depressa	Jamaica: Portland: Christmas River (3/1997)	ULLZ 3813	AJ250649
Plagusia d. depressa	Puerto Rico: Playa Laguna Tortuguero (7/1994)	R-152	AJ311791
Plagusia d. depressa	Barbados: 1km off coast (11/1997)	ULLZ 4311	AJ311792
Plagusia d. depressa	Ivory Coast: beach 10km west of Sassandra (12/1998)	SMF 25976	AJ311793
Plagusia d. squamosa	Hawaii: Oahu: Kewalo (1/2000)	ZRC 2000.0412	AJ311796
Plagusia d. squamosa	Taiwan: Taipei: Keelung market (11/1997)	ZRC 2000.0988	AJ311795
Plagusia d. squamosa	Taiwan: Pingtung: Kenting (2/1999)	SMF 25972	AJ311794

RESULTS

Plagusia depressa squamosa (Herbst, 1790)

Zoea I (Figs. 1, 2)

Dimensions: rdl: 1.66 ± 0.03 mm; cl: 0.68 ± 0.02 mm; cw: 0.70 ± 0.01 mm; ds: 0.71 ± 0.04 mm; rs: 0.40 ± 0.02 mm; ant: 0.21 ± 0.01 mm.

Carapace (Fig. 1A). Globose, smooth and without tubercles, except one posterodorsal humped tubercle and a vertical carina on frontal region. Dorsal and rostral spines long and straight. Lateral spines present and well developed. One pair of posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

Antennule (Fig. 1B). Uniramous. Endopod absent. Exopod unsegmented with 3 aesthetascs (2 long and 1 thin and short) and 2 setae.

Antenna (Fig. 1C). Protopod well developed (approximately 1/3 of rostral spine length) and bearing two rows of spines. Exopod short, with two long terminal setae, the longer reaching almost to the tip of the spinous process.

Mandible. Endopod palp absent.

Maxillule (Fig. 1D). Coxal endite with 6 plumodenticulate setae. Basial endite with 5 setae (1 cuspidate and 3 plumodenticulate). Endopod 2-segmented with 1 plumodenticulate seta on the proximal segment and 1 subterminal and 3 terminal plumodenticulate setae on the distal segment. Exopod absent.

Maxilla (Fig. 1E). Coxal endite bilobed with 5+4 plumodenticulate setae. Basial endite bilobed with 5+4 plumodenticulate setae. Endopod unsegmented, bilobed with 2 and 3 setae of diferent size on the inner and outer lobe respectively. Scaphognathite with 4 plumose marginal setae and a long setose posterior process.

First Maxilliped (Fig. 2A). Basis with 8 medial setae arranged 2,2,2,2. Endopod 5-segmented with 2,2,1,2,5 (1 lateral + 4 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Second Maxilliped (Fig. 2B). Basis with 4 medial setae arranged 1,1,1,1. Endopod 3-segmented with 1,1,5 (2 subterminal + 3 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Third Maxilliped. Absent.

Pereiopods. Absent.

Abdomen (Fig. 2C). Five abdominal somites. Somites 2-5 with one pair of dorsolateral processes and with one pair of posterodorsal setae. Pleopods absent.

Telson (Fig. 2C). Telson bifurcated with 3 pairs of serrulate setae on posterior margin.

Plagusia depressa depressa (Fabricius, 1775)

Megalopa (Figs. 3-5)

Dimensions: cl: 6.08, 5.83 mm; cw: 5.11, 4.96 mm.

Carapace (Fig. 3A). Longer than broad and without spines. Frontal region with two clefts. Tubercles and setation as shown in Fig. 3A.

Antennule (Fig. 3B). Peduncle 3-segmented with 17, 12 and 5 setae, basal segment bulbous. Endopod unsegmented with 6 setae (3 terminal and 3 subterminal). Exopod 3-segmented with 12, 15 and 17 aesthetascs and 2, 2 and 2 setae, respectively.

Antenna (Fig. 3C). Peduncle 3-segmented with 1 long seta and 6 minute simple setae on the proximal segment, and 6 and 1 simple setae on the second and third segment respectively. Flagellum 8-segmented, with 0, 1, 5, 3, 7, 5, 4, 4 setae.

Mandible. Mandibular palp 2-segmented with 0, 20 setae.

Maxillule (Fig. 3D). Coxal endite fringed with 48-49 setae, 6 of them terminal. Basial endite with 29 marginal setae and 8 inner setae. Endopod 2-segmented with 3 long and 1 short setae on the proximal segment and 2+2 setae on distal segment. Five long setae on the protopodal margin.

Maxilla (Fig. 3E). Coxal endite not bilobed with 38 setae. Basial endite bilobed with 19 setae on the inner lobe and 26 setae on the outer lobe. Endopod unsegmented with 2 simple setae on the inner margin and 11 plumodenticulate setae on the outer margin. Scaphognathite with 111 marginal plumose setae and 13 inner simple setae arranged 5, 1, 7.

First maxilliped (Fig. 4A). Coxal endite with 24 setae. Basial endite with 40 setae. Endopod unsegmented with 1 setae near the base and 25 terminal setae. Exopod 2-segmented with 7 setae on proximal segment and 5 setae on distal segment. Epipodite with triangular shape with 58 long setae.

Second maxilliped (Fig. 4B). Coxa and basis not differentiated. Ischium slightly differentiated and unarmed. Merus, carpus, propodus and dactylus with 6, 4, 13 and 10 setae respectively. Exopod 2-segmented with 11 setae on proximal segment and 5 on distal segment. Epipodite with 57 setae.

Third maxilliped (Fig. 4C). Coxa and basis not differentiated. Endopod 5-segmented with 44, 28, 30, 19 and 13 setae. Exopod unsegmented, reduced, not exceeding length of merus, with 11 setae. Long epipodite with 79 setae.

Pereiopods (Figs. 5B-F). All segments well differentiated and smooth, only chelipeds with segments armed with setae. Dactyli of second to fifth pereiopods armed with 5 strong denticles on the inner margin.

Abdomen (Figs. 3F,G). Six somites. First somite mediodorsally fringed with a row a minute setae. Rest of setation as shown in Fig. 3F-G.

Pleopods (Figs. 3H, 5A). Biramous (except uropods), present on second to sixth somites. Endopod of first to fourth pairs with 9 terminal cincinnuli. Exopod of first to fourth pairs unsegmented with 48, 40, 42 and 36 plumose setae respectively. Protopod of the uropod with 5 plumose setae, exopod unsegmented with 30 plumose setae.

Telson (Figs. 3G, H). Broader than long, posterior margin rounded. Five pairs of mediodorsal setae. Each lateral margin with 6 setae and posterior margin with 4+4 setae.

The genetic comparison of six specimens of *Plagusia depressa* revealed that 16S mtDNA sequences of four *P. d. depressa* differed consistently in 28 out of the 546 positions (17 transitions, 9 transversions, 2 indels) from three

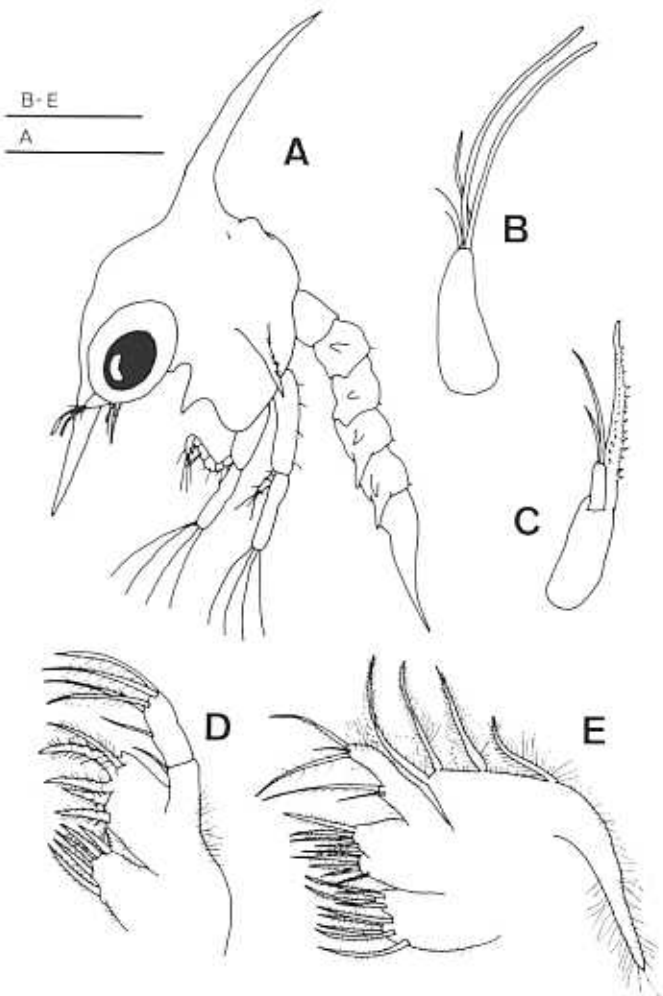

Fig. 1. *Plagusia depressa squamosa* (Herbst, 1790), zoea I. A, lateral view; B, antennule; C, antenna; D, maxillule; E, maxilla. Scale bars A = 0.5 mm, B-E = 0.1 mm.

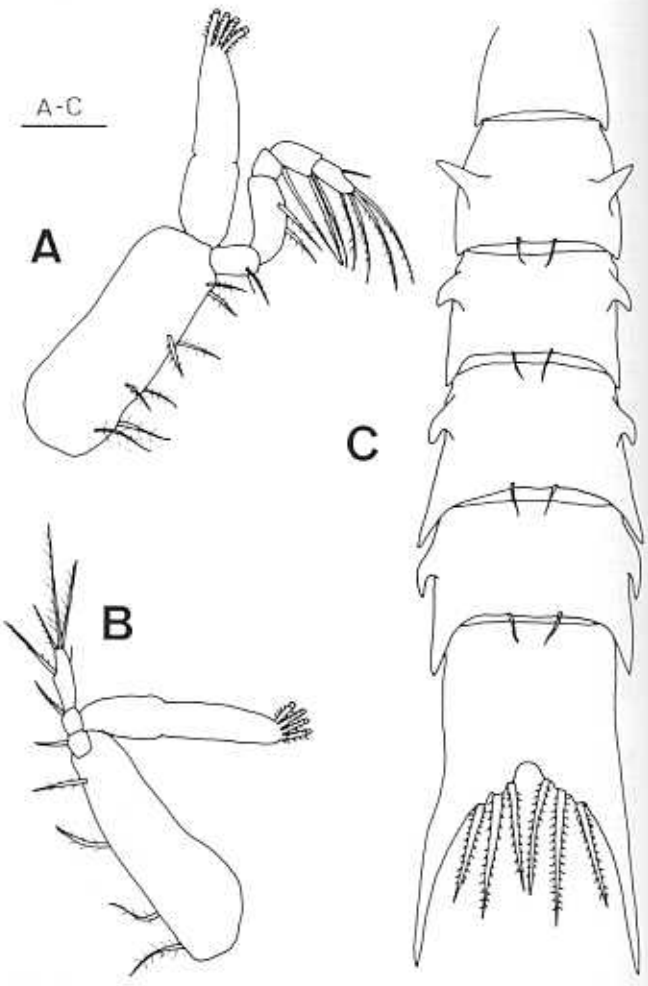

Fig. 2. *Plagusia depressa squamosa* (Herbst, 1790), zoea I. A, first maxilliped; B, second maxilliped; C, abdomen, dorsal view. Scale bar = 0.1 mm.

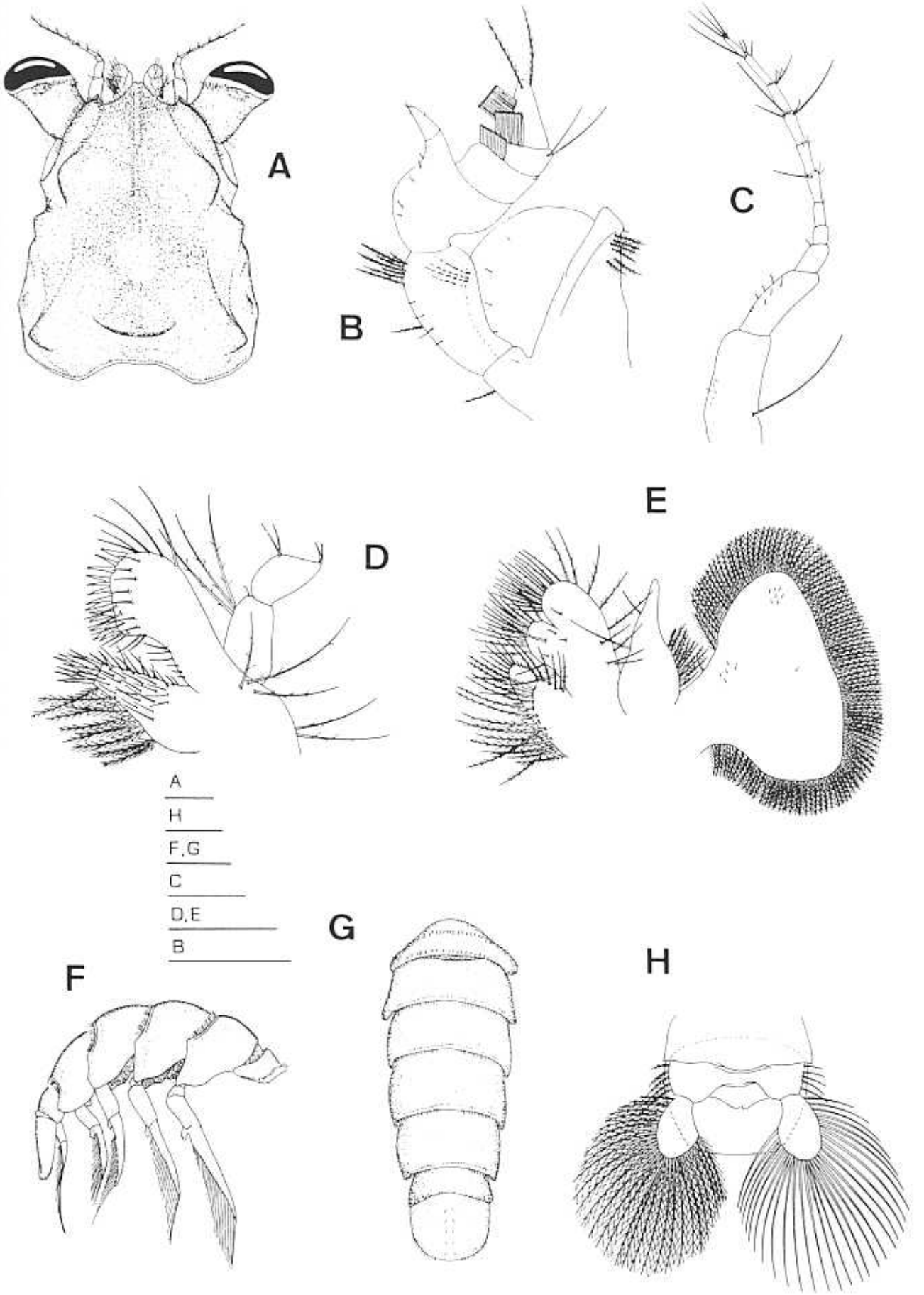

Fig. 3. *Plagusia depressa depressa* (Fabricius, 1775), megalopa. A, carapace, dorsal view; B, antennule; C, antenna; D, maxillule; E, maxilla; F, abdomen, lateral view; G, abdomen, dorsal view; H, telson and uropods, ventral view. Scale bars A, F, G = 1 mm, B-E = 0.2 mm.

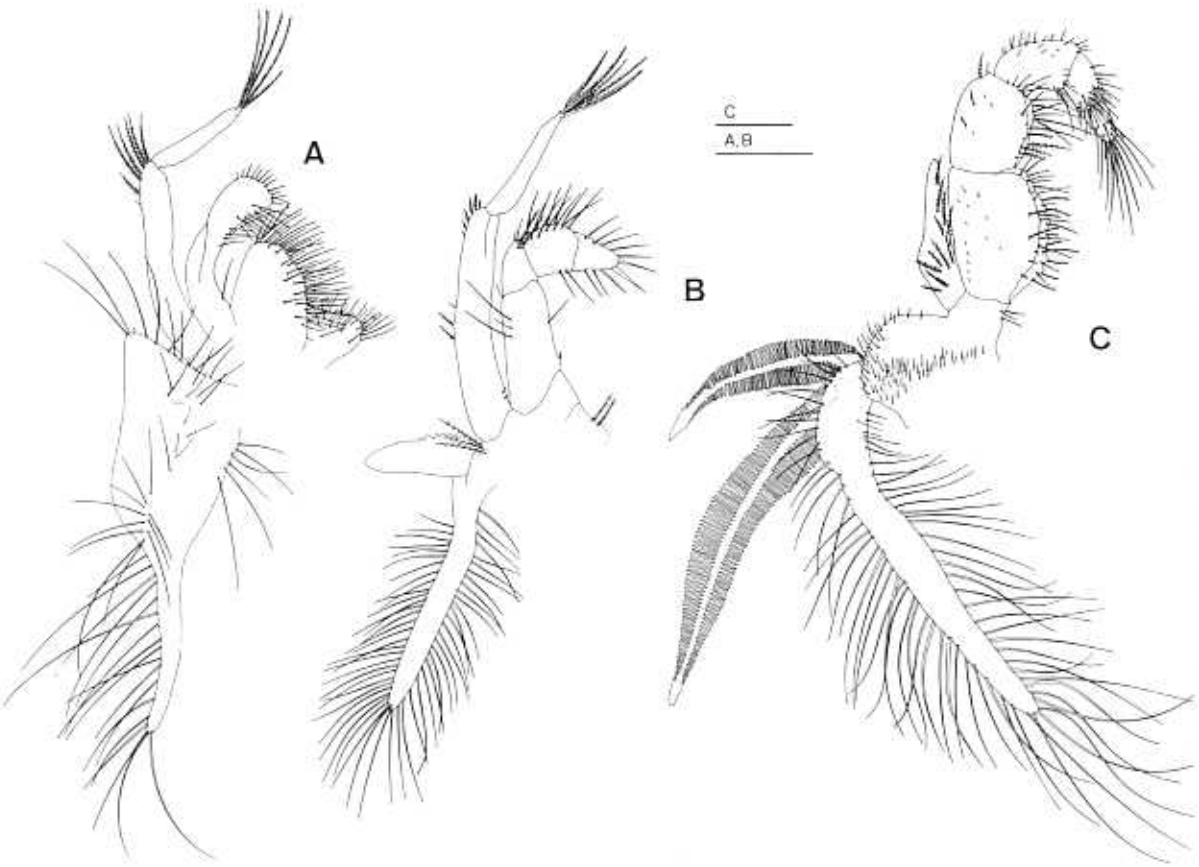

Fig. 4. *Plagusia depressa depressa* (Fabricius, 1775), megalopa. A, first maxilliped; B, second maxilliped; C, third maxilliped. Scale bars = 0.5 mm.

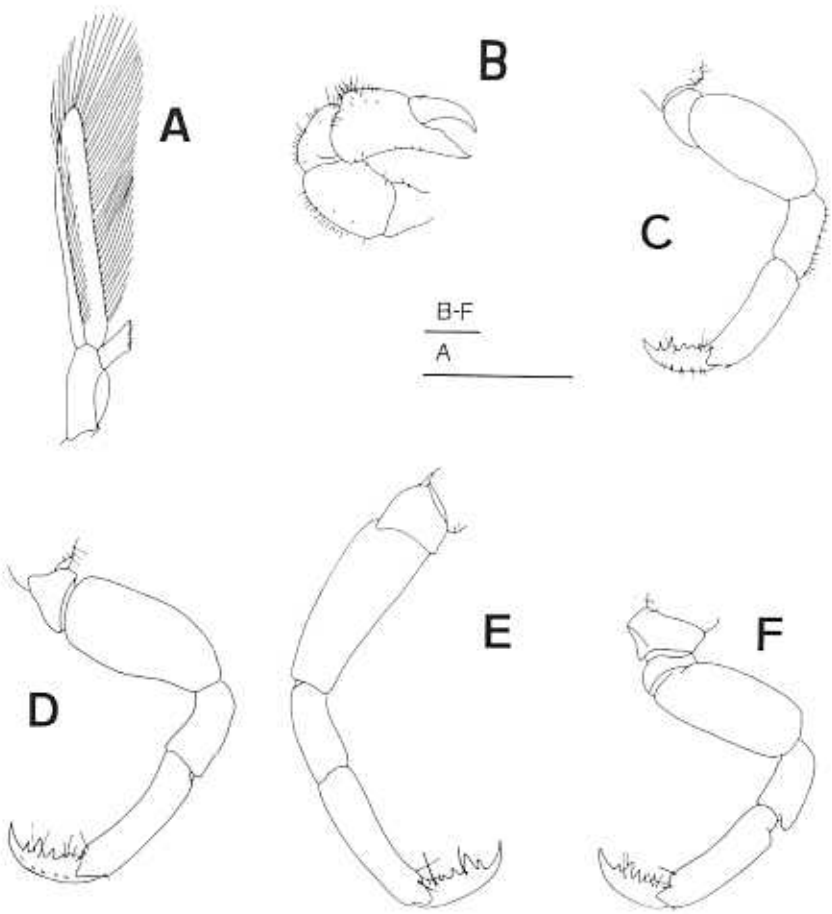

Fig. 5. *Plagusia depressa depressa* (Fabricius, 1775), megalopa. A, second pleopod; B-F, pereiopods 1-5. Scale bars = 1 mm.

specimens of *P. d. squamosa*. On the other hand, variation within *Plagusia d. depressa* (including African and American specimens) never exceeded 5 and within *Plagusia d. squamosa* (including Hawaiian and East Asian specimens) never exceeded 3 out of 546 positions (Table 4).

DISCUSSION

Zoeal morphology. – Re-analysis of first stage zoea larvae of *P. d. depressa* and description of the same stage of *P. d. squamosa* allowed us to determine some morphological differences between these two subspecies (Table 2). The brief description of a prezoeal stage of *P. d. squamosa* by Rajabai (1961) could not be included in this comparison, because it lacks a detailed description of the setation. The presence of a pair of posterodorsal setae on the carapace, and of four setae on the scaphognathite of the maxilla is identical in both subspecies (as well as in all other zoeae I of Grapsoidea), but was incompletely described by Wilson and Gore (1980). These authors also failed to describe three short terminal spines on the exopod of the antenna of *P. d. depressa* zoeae, which could not be distinguished in *P. d. squamosa* (Table 2). The longest terminal seta on the antennal exopod of *P. d. depressa* is longer than shown in Wilson & Gore's drawings (1980: Fig. 2E), reaching almost to the tip of the protopod. More notable and important differences are the chaetotaxy of the antennule and the endopod of the second maxilliped. The antennule of *P. d. squamosa* exhibits one seta more than that of *P. d. depressa*. These kind of differences are often observed between zoeae of congeneric species (e.g. Guerao et al., 1999). Most remarkable is the 1,1,5 setation of the endopod of the second maxilliped. In the Grapsoidea, the setation of this segment is normally constant through development and only differs between major groups that recently have been assigned the rank of families (Cuesta, 1999; Schubart et al., 2000b). In the case of the Plagusiidae, the setation of the endopod of the second maxilliped is normally 1,1,6 and not 1,1,5 (Cuesta & Schubart, 1997; Cuesta, 1999; unpublished results for *P. speciosa*). So far, this character has not been found to vary between species of the same genus. At present, the studied zoeae I larvae of *P. d. squamosa* from Taiwan must therefore be considered an exception within the family Plagusiidae.

Megalopal morphology. – Morphological differences between megalopae of *P. d. squamosa* and *P. d. depressa* are listed in Table 3. One important difference is the number

Table 2. Morphological differences between first zoeal stages of *P. d. depressa* and *P. d. squamosa*. Abbreviations: a, aesthetases; s, setae.

Zoea I	*P. d. depressa* after Wilson & Gore 1980	*P. d. depressa* after present study *of USNM 172313*	*P. d. squamosa* after present study
Antennule	3a, 1s	3a, 1s	3a, 2s
Antenna, exopod	No terminal spines	3 terminal minute spines	No terminal spines
Maxilla, scaphognatite (s)	3	4	4
Maxilliped 2, endopod (s)	1, 1, 6	1, 1, 6	1, 1, 5

Table 3. Morphological differences between megalopal stages of *P. d. depressa* and *P. d. squamosa*. Abbreviations: s, setae; ps, plumose setae; ci, cincinnuli.

Megalopa	*P. d. depressa* after present study	*P. d. squamosa* after Muraoka 1965
Antennule		
Exopod (s)	2, 2, 2	2, 1, 3
Antenna		
Flagellum (s)	0, 1, 5, 3, 7, 5, 4, 4	0, 0, 3, 2, 3, 1, 2, 3
Mandible		
Palp (s)	0, 20	0, 1, 20-30
Maxillule		
Endopod (s)	4, 4	0, 2
Maxilla		
Scaphognatite inner surface (s)	5, 1, 7	4, 5, 6
Maxilliped 3		
Exopod (s)	11	6-7
Pleopod 1-4		
Protopod (ps)	0	1-2
Endopod (ci)	9	8-9
Exopod (ps)	36-48	34-49
Uropod		
Protopod (ps)	5	9
Exopod (ps)	30	27

Table 4. Number of genetic differences (v = transversion, s = transition, i = indel) between 7 haplotypes of *Plagusia d. depressa* (Fabricius, 1775) and *P. d. squamosa* (Herbst, 1790) from 546 basepairs of 16S mtDNA.

	subspecies	Jamaica	Puerto Rico	Barbados	Hawaii	Pingtung	Taipei
Ivory Coast	*depressa*	1s	3s	1s/1i	18s/9v/3i	18s/10v/3i	19s/10v/3i
Jamaica	*depressa*		2s	2s/1i	17s/9v/3i	17s/10v/3i	18s/10v/3i
Puerto Rico	*depressa*		—	4s/1i	18s/9v/3i	18s/10v/3i	19s/10v/3i
Barbados	*depressa*			—	19s/9v/2i	19s/10v/2i	20s/10v/2i
Hawaii	*squamosa*				—	1v	1s/1v
Taiwan, Pingtung	*squamosa*					—	1s
Taiwan, Taipei	*squamosa*						—

of segments of the antennal flagellum: eight in *P. d. depressa*, and nine in *P. d. squamosa* (according to the description of Muraoka, 1965). It would be more likely that there are eight segments in both subspecies (see also González-Gordillo et al., 2000 for *P. dentipes*) and that the last segment of the peduncle has been counted as the first one of the flagellum in *P. d. squamosa*. However, even if there would be only eight segments, the setation pattern would be clearly different (see Table 3). The chaetotaxy of the mouthparts cannot be compared with the necessary detail, because Muraoka's (1965) illustrations are not very clear and fail to include the number of setae of coxal and basial endites. However, this may not be relevant to the present comparison given that the setation of these endites often exhibits intra- and interspecific variability (e.g. Guerao et al., 1999). Another important difference is found in the setation of pleopods and uropods: *P. d. squamosa* exhibits one or two plumose setae on the protopod of the pleopods, whereas the same segment is unarmed in *P. d. depressa*. The protopod of the uropod carries nine plumose setae in *P. d. squamosa*, but only five in *P. d. depressa* (see Table 3).

16S mtDNA sequence. – The 16S mtDNA is a widely applicable genetic marker for molecular systematics. Due to the presence of variable and more conserved regions, it can be used for population studies as well as higher order phylogenies (Schubart et al., 2000a). In the present case, two subspecies of *Plagusia depressa* are characterized by a sequence divergence of a minimum of 5.1% along the studied 546 basepairs of 16S mtDNA (Table 4). This is a level that is clearly within the documented range of genetic distance between congeneric species among grapsoid crabs (approx. 1-15% sequence divergence, Schubart, unpubl.). It is comparable to the genetic divergence (4.6%) found between 16S mtDNA sequences of the two Mediterranean species of *Pachygrapsus*, *P. marmoratus* and *P. maurus* (see Schubart & Cuesta, 1996), which show marked differences in adult morphology.

Based on three independent analyses presented in this study, we conclude that *Plagusia squamosa* (Herbst, 1790) should be considered a distinct species. The type locality of this species is «Ostindien» (East Indies), and the range covers the entire tropical Indo-Pacific, the Indo-Australian warm temperate region (Dawson, 1987) and the eastern Mediterranean (Shiber, 1981). *Plagusia squamosa* is a senior synonym of *Plagusia tuberculata* Lamarck, 1818, and *Plagusia orientalis* Stimpson, 1858 (see Schubart & Ng, 2000). A description and picture of this species are presented in Rathbun (1918: 334, pl. 102, as *P. d. tuberculata*). A colour picture is available in Wang & Liu (1998: Fig. 173, as *P. tuberculata*).

Clear differences in zoeal and megalopal morphology as well as in the 16S mtDNA sequences between *P. depressa* and *P. squamosa* contrast with a striking similarity of the adult morphs. Since these two species (plus *P. immaculata*) are probably sister taxa, as suggested by preliminary results from molecular phylogenetics (Schubart, unpubl.), the morphological similarity is most likely due to morphological stasis under stabilizing selection. Adult habitats of these two allopatric species seem to be identical, thus favoring the same phenotypes. In our comparison of the two species of *Plagusia*, the only material available for zoeal comparisons of *P. squamosa* was from Taiwan, and for DNA comparisons from Taiwan and Hawaii. The megalopal description by Muraoka (1965) is from Japan. As mentioned above, the range of *Plagusia squamosa* in addition to East Africa and Asia also comprises western America. Due to the lack of data, the status of *P. squamosa* populations from the Indian Ocean and the eastern Pacific remains currently unresolved. For most species of coastal crabs, one would expect clear genetic differences on both sides of the Pacific. *Plagusia*, however, shows a great facility to raft by clinging to floating objects (Dawson, 1897, and citations therein). This behaviour, the long planktonic development of *Plagusia* (a minimum of 60 days for zoeal development according to Wilson & Gore, 1980), and the vast number of Pacific Islands that can be used as stepping stones between the American and Asian continents (e.g. Hawaii) makes it plausible that differentiation across the Pacific is low in *P. squamosa* (see also Rosenblatt & Waples, 1986, for trans-Pacific gene flow in shore fishes). Results from the present study demonstrating the absence of diagnostic differences in portions of the 16S mtDNA between *P. depressa* from both sides of the Atlantic and the close genetic similarity of *P. squamosa* from Taiwan and Hawaii (Table 4) corroborate the assumption of low divergence between transoceanic populations of *Plagusia*. We hope to be able to test this hypothesis in the future by including zoeae, megalopae and mtDNA sequences from the eastern Pacific and western Indian Oceans in this analysis.

Based on the current distributions of *P. depressa* and *P. squamosa*, it becomes evident that the north-south oriented landmasses surrounding the Atlantic Ocean serve as geographical barriers between these two tropical crab species. Speciation must therefore date back around 3 mya when the emerging Panama Isthmus blocked a free movement between Caribbean and Pacific marine biota (see Knowlton & Weigt, 1998). Our present results suggest that these rafting tropical crabs are not able to circumnavigate the cold temperate to arctic continental tips (e.g. South Africa and South America) and thus became isolated from each other within the tropical basins of the major oceans.

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