

Ecology and systematics of mangrove crabs of the genus *Perisesarma* (Crustacea: Brachyura: Sesarmidae) from East Africa

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East Africa has a reduced mangrove crab species richness when compared to Asian mangroves. To date, only one species of *Perisesarma* de Man, 1895 has been reported in East Africa, despite more than 30 years of mangrove research in this region. Based on morphology, colour, mtDNA and behaviour, we describe a new species of *Perisesarma* from Kenya, *P. samawati* sp. nov. Surprisingly, when comparing molecular data from other species within this genus, *P. samawati* sp. nov. and the sympatric *P. guttatum* (A. Milne Edwards, 1869) are not sister species. Some aspects of the ecology of *P. guttatum* and *P. samawati* sp. nov. are compared and the differences discussed. Additionally, we compare *P. samawati* sp. nov. with the ecological literature of a possible sister species *P. eumolpe* de Man, 1895 from Malaysian mangroves. Our findings suggest that the new species is an ecologically important species in East African mangroves. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 141, 435–445.

ADDITIONAL KEYWORDS: 16S rRNA – Grapsoidea – Indian Ocean – Kenya – mangroves – morphology – mtDNA – new species – phylogeny – taxonomy.

INTRODUCTION

It is continuously being reported that grapsoid crabs, especially those from the species-rich family Sesarmidae, play an important ecological role in mangrove ecosystems (reviewed in Lee, 1998). For example, while many mangrove sesarmids do not assimilate much carbon from mangrove leaves and rely more on mangrove sediments (Bouillon *et al.*, 2002; Skov & Hartnoll, 2002), it appears that *Perisesarma* spp. do supplement their diet with mangrove leaves (Leh & Sasekumar, 1985; Slim *et al.*, 1997; Dahdouh-Guebas *et al.*, 1999; Ashton, 2002). The removal and processing of mangrove leaves by crabs helps to trap the energy stored in these leaves within the mangal before the tide can carry them away (see Lee, 1998; Skov & Hartnoll, 2002). Furthermore, their faecal material potentially contributes to secondary production via a coprophagous food chain (cf. Lee, 1997; Gillikin, De

Grave & Tack, 2001). *Perisesarma* spp. are reported to have the highest biomass of mangrove crabs in certain forests (Ashton, Macintosh & Hogarth, 2003).

East Africa, in general, has a limited number of brachyuran crabs associated with mangroves (about 35 species; cf. Hartnoll, 1975) compared with south-east Asia (>100 in Malaysia alone; Tan & Ng, 1994). In fact, there has not been a new grapsoid species described from East Africa since 1965, when Crosnier distinguished *Chiromantes ortmanni* from the well known *C. eulimene* de Man (1895), despite the large amount of ecological research concentrated in this area (e.g. Bright & Hogue, 1972; Hartnoll, 1975; Micheli, Gherardi & Vannini, 1991; Cannicci *et al.*, 1996; Ruwa, 1997; Slim *et al.*, 1997; Dahdouh-Guebas *et al.*, 1999; Fratini, Cannicci & Vannini, 2000; Flores, Paula & Dray, 2003). Currently, there is only one species of *Perisesarma*, *P. guttatum*, attributed to East Africa (Crosnier, 1965; Hartnoll, 1975; Vannini & Valmori, 1981), whereas there have been 19 species reported within the Indo-Pacific region as a whole (Davie,

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2003). Given the long planktonic phase of East African species of *Perisesarma* (22–25 days, see Pereyra Lago, 1993), and the presence of strong oceanic currents in the Indian Ocean (cf. Hartnoll, 1975), it is surprising that there are not more species of this genus present in East Africa. *Perisesarma guttatum*, endemic to East Africa, is an important element of the Kenyan mangrove fauna, removing almost anything that falls to the forest floor (Gillikin, 2000). These crabs are not at all shy, have wide distribution across the intertidal mangal [generally, from the *Cerriops tagal* (Perr.) C.B. Rob. zone down to the seaward front of the mangal] and are usually the first of the mangrove fauna to reach any potential food source (cf. Ruwa, 1997; Frattini *et al.*, 2000; Gillikin, 2000).

During field surveys in 1998, it was noticed that among the crabs that were referred to as *P. guttatum*, two forms with distinct colour patterns could be distinguished. Further investigations also revealed behavioural and ecological differences, the more colourful specimens not venturing out to forage as rapidly as the darker form, and seemingly returning to a specific shelter more regularly when retreating. This led us to believe that the crab was not in fact *P. guttatum*, but a different species of *Perisesarma*, previously unrecorded in East Africa. After detailed morphological examinations and careful comparisons with the literature describing other species of *Perisesarma*, it became apparent that this species was indeed different from *P. guttatum*, as well as from all other described members of the genus. In this study, we describe the new species of *Perisesarma* from Kenyan mangroves, where it occurs sympatrically with *P. guttatum*. Further evidence is provided by mtDNA sequences to show that, compared with other members of the genus, the new species is not the sister species of *P. guttatum*.

MATERIAL AND METHODS

All but one specimen of the studied material was collected from the eastern riverine mangroves of Mida Creek, Kenya (near the village of Dabaso, 80 km north of Mombasa) during September to November 1998 and 1999 by D. P. Gillikin and A. Verheyden. One female was found north of Kidogoweni Creek in the riverine forest type of the Gazi Bay mangrove system (40 km south of Mombasa) (forest types according to Lugo & Snedaker, 1974). *Perisesarma guttatum* was collected from both Mida Creek and Gazi Bay mangroves during the same time. All collections took place during field surveys for the European Union Project 'GRO-FLO' (contract IC18-CT96-0065).

Ecological studies took place in both Mida Creek and Gazi Bay mangroves and are detailed in Gillikin (2000). In both forests, presence or absence of crab

species was determined by visual inspection in 10 m diameter plots along a transect perpendicular to the coastline, covering the full width of the forest. We investigated 15 plots along a 364 m long transect in Gazi Bay and 23 plots along a 1298 m long transect in Mida Creek. Each plot was first inspected using 10 × 42 binoculars from a distance of approximately 7 m for 15 min and the crab species recognized recorded. Afterwards, naked eye observations were made with two observers sitting on opposite sides of the plot for at least 30 min (cf. Hartnoll *et al.*, 2002; Skov *et al.*, 2002). On approaching the plot, a disturbance was created, causing all crab species to immediately take refuge. The time at which the first individual of a species would re-emerge was recorded. All observations took place at low tide during the day; no distinction of lunar cycle was made. To further assess the behavioural differences between the species of *Perisesarma*, one individual of each type was placed in a 50 cm diameter container and stimulated by moving a hand over the container. This experiment was replicated with males and females, each three times. At two plots, where numbers of both types appeared high, feeding experiments were conducted on three separate days. First, a fresh green leaf fragment ($\pm 2 \text{ cm}^2$) was placed on the forest floor and the first species to reach it was recorded (for discussions of crabs feeding on green leaves, see Ashton 2002; Gillikin, De Wachter & Tack, 2004). Secondly, ten or more leaves were fragmented and spread on the forest floor to create an abundance of leaf fragments. The behaviour following both of these experimental settings was recorded.

Type specimens have been deposited at the Senckenberg Museum (SMF), Frankfurt a. M., Germany; the Royal Belgian Institute of Natural Sciences (KBIN), Brussels, Belgium; the Nationaal Natuurhistorisch Museum (RMNH), Leiden, Netherlands; the Naturhistorisches Museum (NHMW), Vienna, Austria; the British Museum of Natural History (NHM), London, UK; the Zoological Reference Collection Raffles Museum (ZRC), Singapore; and the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., USA. Measurements of the studied material represent the carapace width and length in millimetres. Abbreviations and measurements used in this text are: cw, maximum carapace width; cl, carapace length; bh, body height; iw, interorbital width; el, extraorbital tooth length; 3mxl, third maxilliped length; 3mxw, third maxilliped width; pah, chelar palm height; prp4, propodus length of fourth pereiopod; 4merl, merus length of fourth pereiopod; 4merw, merus width of fourth pereiopod; 4dacl, dactylus length of fourth pereiopod; tell, telson length; telw, telson width; 6abl, length of sixth abdominal segment; 6abh, width of sixth abdominal segment.

The following material was examined: Holotype: (SMF 29333) male (24.63 × 20.00 mm), mangroves near village of Dabaso, Watamu, Kenya (S03°20.905' E039°59.498'), Sept.–Nov. 1998, coll. D. P. Gillikin and A. Verheyden, (DNA sequence). Paratypes: 1 male (28.61 × 23.45) and 1 female (23.98 × 19.56) (SMF 29334) same data as holotype; 1 female (23.47 × 19.28) (ZRC 2003.0202) same data as holotype; 1 female (22.63 × 18.34) (USNM 1020442) same data as holotype; 1 male (22.85 × 18.32) and 1 female (21.79 × 17.20) (KBIN: I.G. 29968); 1 male, 1 female, 1 chela (NHM 2004.72–73) same data as holotype; 2 males (19.75 × 16.13, 24.75 × 20.15) (ZRC 2003.0203) same locality as holotype, Sept.–Nov. 1999, coll. D. P. Gillikin and A. Verheyden; 1 male (24.03 × 19.08) (NHMW 19935) same data as ZRC 2003.0203; 1 male (24.18 × 19.80) (USNM 1020442) same data as ZRC 2003.0203; 1 male (26.37 × 21.33) (RMNH D 50430), same data as ZRC 2003.0203. Other material: 1 female (12.92 × 10.24) (SMF 29335) same data as holotype; 1 female (23.23 × 18.64) (SMF 29336), mangroves north of Kidogoweni Creek, Gazi Bay, Kenya (S04°25' E039°31'), Aug. 1999, coll. D. P. Gillikin. Comparative material of *P. guttatum*: 1 male (22.45 × 17.97) and 1 female (SMF 29337), mangroves near village of Dabaso, Watamu, Kenya (S03°20.905' E039°59.498'), Sept.–Nov. 1998, coll. D. P. Gillikin and A. Verheyden; 2 males (23.96 × 19.09, 15.78 × 12.63) (ZRC 2003.0204), same data as SMF 29338; 2 males (22.81 × 17.86, 18.06 × 14.50) (private collections Gillikin & Schubart) fringe mangroves of Gazi Bay, Kenya (S04°25' E039°31'), Aug. 1999, coll. D. P. Gillikin.

At the University of Regensburg, genomic DNA was isolated from the muscle tissue of one walking leg using Puregene tissue DNA extraction kits. Selective amplification of a 575 base pair product (excluding primer regions) from the mitochondrial 16S rRNA gene was carried out by PCR (polymerase chain reaction) (40 cycles: 45 s 94 °C, 45 s 48 °C, 1 min, 72 °C denaturing, annealing and extension temperatures, respectively) using primers 16Sar (5'-CGCCTGTT TATCAAAAACAT-3') and 1472 (5'-AGATAGAAAC CAACCTGG-3') (see Schubart, Neigel & Felder, 2000). PCR products were purified with Microcon-100 filters (Millipore Corp.) and sequenced with the ABI BigDye Terminator Mix (PE Biosystems) in an ABI Prism 310 Genetic Analyser (Applied Biosystems). Sequences were manually aligned and new sequences were accessioned to the European Molecular Biology Laboratory (EMBL) genomic library (accession numbers: AJ621183–AJ621186). Minimum evolution with neighbour joining and Kimura 2-parameter distances, as well as maximum parsimony with a heuristic search and random sequence addition (tree-bisection and reconnection as branch-swapping option, considering gaps a fifth character) analyses, were carried out

using the software MEGA 2.1 (Kumar *et al.*, 2001) and PAUP* (Swofford, 1998). Subsequently, significance levels were evaluated with the bootstrap method (Felsenstein, 1985) after 2000 replicates.

RESULTS

MORPHOLOGY

A morphological comparison of the collected specimens of *Perisesarma* from East Africa revealed that two distinct species were indeed present. One of the two forms agreed perfectly with previous descriptions of the mangrove crab *P. guttatum* (A. Milne Edwards, 1869) (see Crosnier, 1965; Vannini & Valmori, 1981). The other form seemed to be diagnostic in the following characters: a conspicuous blue colour on the lateral and frontal regions of the crab combined with a mottled blue on the otherwise dark carapace and dorsal surfaces of the legs. The legs of these crabs are comparatively short and broad with the meri of the third walking leg only slightly more than twice as long as broad. The most diagnostic feature on closer inspection is the tuberculation pattern of the cheliped dactyls, with a row of seven to nine rounded blunt tubercles of which the first is smaller, followed by six to eight more prominent and round tubercles, becoming progressively less distinct towards distal. This is not only different from the tuberculation of *P. guttatum*, it also distinguishes this crab from all other species of the genus *Perisesarma* currently described. Therefore, these crabs have to be considered representatives of an undescribed species, which is here described in its morphological details.

PERISESARMA SAMAWATI SP. NOV.

Description

A medium-sized crab, largest male encountered measuring 28.61 mm cw. Body form relatively vaulted (bh/cw = 0.52 ± 0.01, *N* = 11). Carapace broader than long with greatest width between exorbital angles (cl/cw = 0.81 ± 0.01, *N* = 11). Carapace regions clearly delimited, especially mesogastrical region (Fig. 1A). Carapace covered with sparse transverse rows of granules and tufts of small setae, especially in frontal region and forming striae on branchial regions. Front more than half of carapace width (iw/cw = 0.60 ± 0.01, *N* = 11), sharply deflexed, with broad median indentation. Frontal borders smooth and parallel. Interorbital region subdivided into four prominent frontal lobes covered with short rows of transverse granules, median lobes broader than lateral ones. Exorbital angle triangular, anterolateral margin anterior to notch straight and relatively short (el/cl = 0.13 ± 0.01, *N* = 10). Single epibranchial tooth pointed and slightly

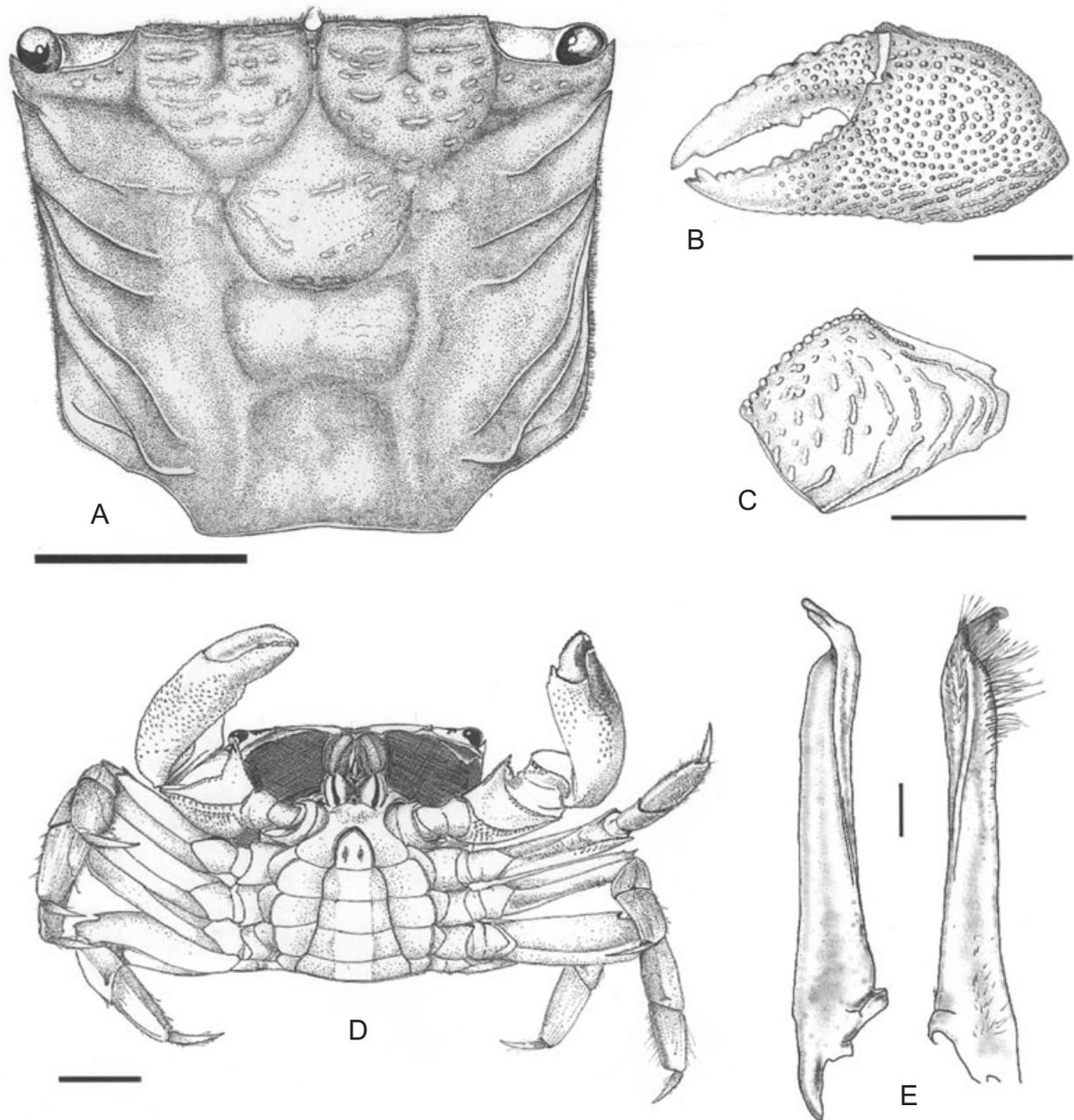


Figure 1. *Perisesarma samawati* sp. nov., male paratype (SMF 29334). A, dorsal view of carapace. B, outer face of chela. C, dorsal view of carpus of cheliped. D, male abdomen and sternum. E, first gonopods, one of them denuded. Scale bars: A, D = 10 mm; B, C = 5 mm; E = 1 mm.

elevated, no indication of a second epibranchial tooth. Posterior lateral margins slightly concave and sloping ventrally, fringed by six rows of setae on pterygostomial region. Pterygostome and branchiostegite with dense cover of geniculate setae. Posterior border of orbit slightly perpendicular to front running posterio-laterally. Eyes pigmented, cornea large and wider than eyestalk. Suborbital ridge granular and setose.

Epistome granular and glabrous except for Verwey's groove, which is delimited by two rows of setae. Ventral border of epistome lined by row of tubercles (endostomial crista). Third maxillipeds granular, merus concave and broad ($3\text{mxl}/3\text{mxw} = 0.73 \pm 0.02$, $N = 10$). Exopod with well developed setose flagellum.

Chelipeds equal and sexually dimorphic. Male chelae larger and stronger ($\text{pah}/\text{cw} = 0.36 \pm 0.04$,

$N = 8$) than female chelae ($\text{pah/cw} = 0.26 \pm 0.01$, $N = 4$). Inner row of merus smooth with two longitudinal rows of setae, ventral row more prominent and continuous with longer setae, dorsal one interrupted with setal cover extending to dorsal border. Ventral face smooth, triangular with transverse row of tubercles distally; outer face covered with granules directed distally. All three borders serrate, prominent subdistal tooth on ventral border less serrate, smaller tooth on dorsal border. Carpus dorsally trapezoidal with smooth inner angle, inner border lined with pointed tubercles. Outer face of carpus granular, granules forming transverse groups; inner face with longitudinal row of minute granules and distal tuft of long setae (Fig. 1C). Upper surface of palm in males with 2 transverse pectinated crests. Proximal crest composed of 8–14 teeth (most larger males 11–14), distal crest with 12–18 teeth, teeth of both crests similar in size. Both pectinated crests preceded and followed by several blunt tubercles and on inner side pronounced hump. In some cases, an additional proximal accessory crest comprising four teeth visible. In females, pectinated crests are less conspicuous and with shorter teeth; proximal crest in most cases replaced by row of tubercles. Upper margin of palm with strong blunt tubercles. Outer surface of palm bulbous and granular, granules forming indistinct median longitudinal line and ventral longitudinal groups (Fig. 1B); inner surface with smaller granules. Palm glabrous except for tuft of short setae in front of first pectinated crest. Distal third of surface of both fingers almost smooth. Cutting edge less than half the propodus length measured ventrally (0.37 ± 0.02 , $N = 10$) with irregular number of triangular teeth. Ventral border of chela slightly concave at base of fixed finger, granular. Dorsal surface of dactylus bearing 7–9 blunt tubercles; first tubercle smaller, elongate and positioned more towards outer side, followed by 6–8 more prominent and round tubercles, becoming progressively less distinct and almost indiscernible towards tip (Fig. 1B). Dactylar tubercles are less distinct in females. Row of sharp, distinct tubercles (5–12) on proximal two thirds of inner edge of dorsal surface and scattered granules on outer edge of dorsal surface. Fingers with tips chitinous; adult males with variable gape width.

Third and fourth pairs of pereopods longest (fourth tends to be slightly longer) ($\text{prp4/cw} = 1.49 \pm 0.09$, $N = 9$). Meri of walking legs relatively broad, roughly twice as long as wide ($4\text{merl}/4\text{merw} = 2.06 \pm 0.13$, $N = 9$); dactylus medium-sized ($4\text{dacl}/\text{prp4} = 0.17 \pm 0.01$, $N = 9$). Walking legs mostly glabrous, scattered long setae on dorsal and ventral borders, forming dense tufts at the dorsal propodus of all walking legs. Males with mat of setae on ventral propodus of pereopod-2 and fringe of setae on ventral border of pereopod-3. Dorsal face of meri granulate. Dorsal border of

meri with row of small tubercles and sharp subdistal tooth.

Male abdomen with telson slightly shorter than width at base ($\text{tell}/\text{telw} = 0.88 \pm 0.05$, $N = 8$), moderately pointed and longer than sixth abdominal segment ($\text{tell}/6\text{abl} = 1.16 \pm 0.08$, $N = 8$); penultimate segment roughly half as long as wide ($6\text{abl}/6\text{abh} = 0.52 \pm 0.02$, $N = 8$) (Fig. 1D). Second segment with median length slightly longer than lateral length. Abdomen of females fringed with long setae, evenly rounded, broadest at segment-5. In adult female specimens, abdomen touches coxae of walking legs. Taking this as a reference of adulthood, the smallest adult female encountered measured 21.79 cw (KBIN: I.G. 29968) and the largest juvenile female measured 12.92 cw (SMF 29335). Thoracic sternites in both sexes smooth and almost glabrous; episternites fringed with small setae on outer border. First male gonopods relatively slender, almost straight; apical process bent by approximately 45° , with corneous tip (Fig. 1E). Few and scattered short setae along most of the gonopod, apical end covered by longer setae, almost completely covering corneous tip (Fig. 1E). Female gonopores prominent, located near the bottom of sternal cavity.

The coloration in life is characterized by a dark carapace with many aqua blue spots, black ocular peduncles mottled with sky blue blotches, corneas grey-black (Fig. 2). Front and epistome dark with many sky blue spots. Pterygostomial region violet-blue, becoming mottled with sky blue spots on branchiostegal region (Fig. 2); suborbital region sky blue with blotches of violet-blue. Ischium and merus of maxilliped sky blue with black blotches. Merus of cheliped brown to dark red with few sky blue spots on outer face and larger spots on inner face; carpus dark red, occasionally with sky blue spots; palm and dactylus bright red. Ambulatory legs with meri mottled sky blue and dark; carpus, propodus and dactylus with fewer or no sky blue spots. Colours fade quickly after preservation.

Etymology: The name of this new species, *Perisesarma samawati*, is derived from the Swahili word 'Samawati', which means 'the sky, sky colour, azure' (Oxford Swahili-English dictionary). It refers to the sky blue coloration of the front and of the dots on the carapace and walking legs (Fig. 2), expressed in the language of the people from where this crab was discovered. Samawati is used as a noun in apposition.

Ecological observations

Perisesarma samawati sp. nov. is a semi-terrestrial (adults terrestrial; cf. Schubart, Cuesta *et al.*, 2000) crab inhabiting the intertidal mangrove forests domi-

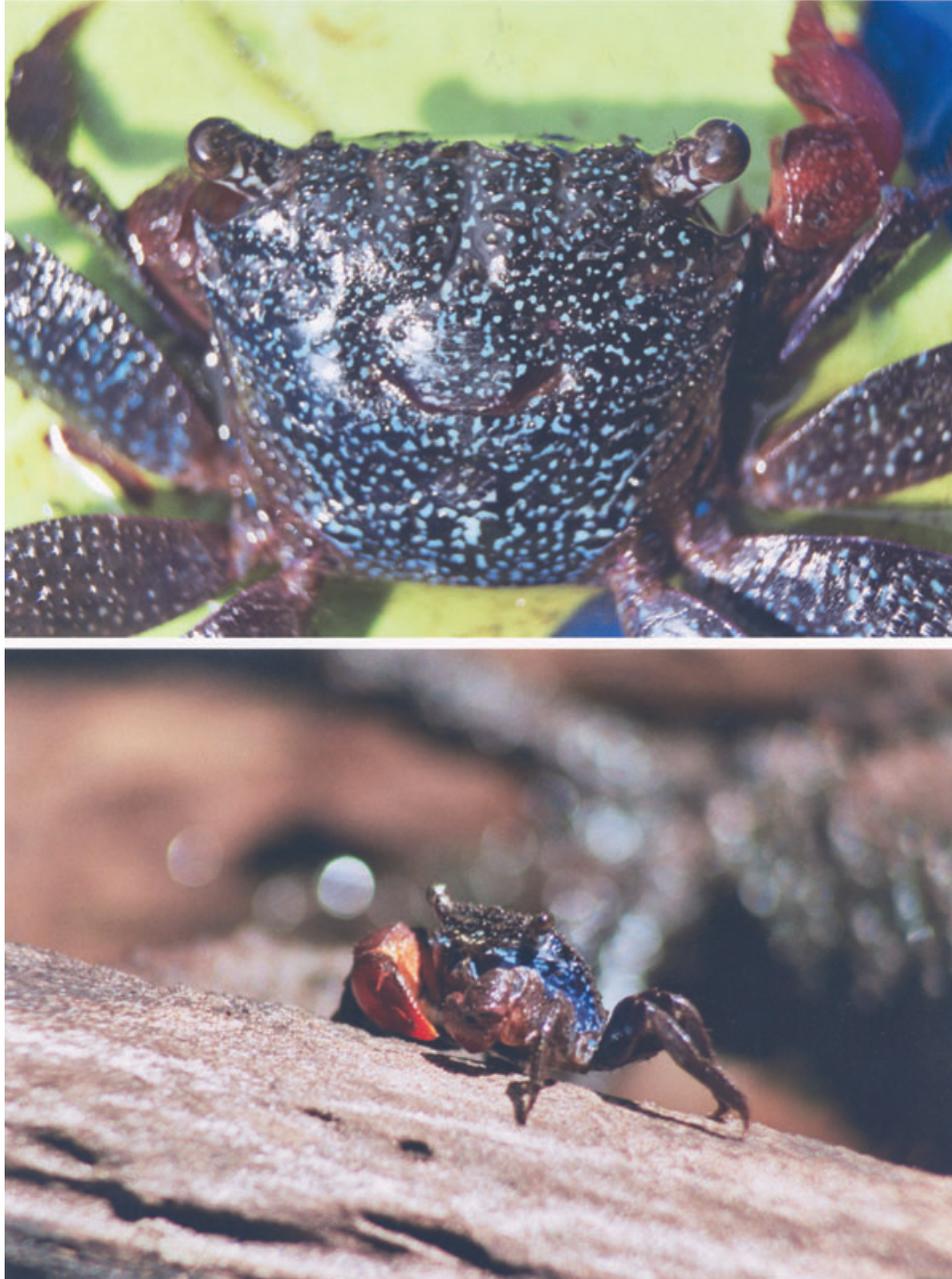


Figure 2. *Perisesarma samawati* sp. nov., life colours.

nated by *Rhizophora mucronata* Lam. The crab occurs sympatrically with *P. guttatum*, but was not found to be distributed as extensively as *P. guttatum*. In the eastern riverine Mida Creek mangroves they occur across the full width of the muddy *R. mucronata*-dominated zones. No specimens were found in the more sandy sediments of the *Ceriops tagal*-dominated forests where *P. guttatum* was found to be common. In Gazi Bay (120 km south of Mida Creek), only a single female was found in a riverine forest type. In the

fringe mangroves of Gazi Bay, no individual of *P. samawati* sp. nov. was ever found after hundreds of hours of field work, indicating that they are rare in this forest or do not inhabit fringe mangrove forests. Of the 23 plots investigated in Mida Creek, *P. guttatum* was found to occur in 95.7% of the plots (66.7% of 15 plots in Gazi), whereas *P. samawati* sp. nov. was found in 56.5% of the plots (0% in Gazi). *Perisesarma samawati* sp. nov. were always found sheltering in crevices under roots from which they did

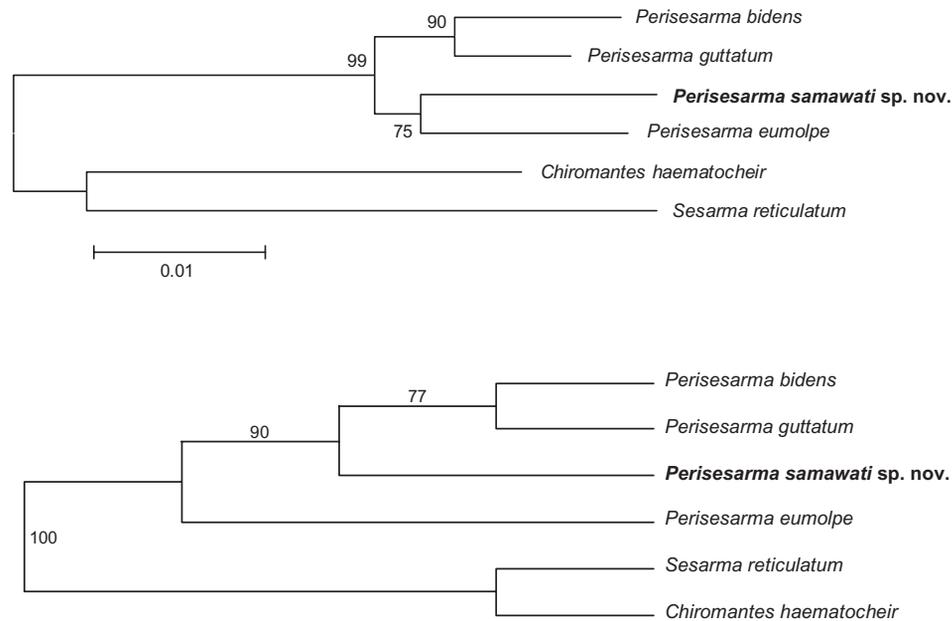


Figure 3. Phylogenetic relationships among four Indo-Pacific species of the genus *Perisesarma* based on 575 base pairs of mtDNA coding for the 16S rRNA. Minimum evolution (neighbour joining, Kimura 2-parameter distances) (upper) and maximum parsimony (lower) trees with confidence values established after 2000 bootstrap replicates.

not readily venture far and quickly retreated to when approached. *Perisesarma samawati* sp. nov. was never recorded climbing on roots or trees and was active during daylight hours.

At the nine plots where both species of *Perisesarma* were found together, *P. guttatum* would re-emerge first after a disturbance (after 2.06 ± 1.86 min, $N = 9$), then *P. samawati* sp. nov. would re-emerge (4.56 ± 1.42 min, $N = 9$, Wilcoxon matched pairs, $P < 0.012$). However, *P. samawati* sp. nov. was not as shy as *Neosarmatium smithi* (H. Milne Edwards, 1853) (9.89 ± 5.40 min, $N = 9$, Wilcoxon matched pairs vs. *P. samawati* sp. nov., $P < 0.03$) which also inhabits the same areas. Distinct behavioural differences were noticed, in both males and females, when both species of *Perisesarma* were placed in an artificial situation and stimulated. All *P. guttatum* except for one female vigorously ran (83.3% ran, $N = 6$), whereas all *P. samawati* sp. nov. except for one male retracted all appendages and remained still (16.7% ran, $N = 6$).

When one leaf fragment was placed on the forest floor, *P. guttatum* was the first to reach it 100% of the time ($N = 6$). Although they would usually consume the leaves where they found them, they would also carry them off to other areas. In the case of abundant green leaves, *P. samawati* sp. nov. were observed to carry off fresh green leaf fragments. They were always observed to manipulate the leaf fragments at the edge of the refuge from which they came.

Molecular phylogeny

A phylogenetic analysis of 576 base pairs (70 variable and 21 parsimony-informative) revealed that the four included species of Indo-Pacific *Perisesarma* cluster together with high bootstrap support. The topologies vary according to the method used (Fig. 3). The minimum evolution distance tree suggests a sister species relationship of the similarly coloured *P. eumolpe* and *P. samawati* sp. nov., while in maximum parsimony *P. eumolpe* forms an outgroup to the other species of *Perisesarma*. In both cases, however, *P. guttatum* is the sister species of the East Asian species *P. bidens*, thereby indicating that the two East African species are not sister species and thus probably colonized East African mangroves independently.

DISCUSSION

With the description of *P. samawati* sp. nov., the genus *Perisesarma* in the Indo-Pacific region is now represented by 20 species. This is the fourth new species of *Perisesarma* to be recently described (Rahayu & Davie, 2002; Davie, 2003). *Perisesarma samawati* sp. nov. is closely related to *P. eumolpe* (de Man, 1895) based on mtDNA (Fig. 3). Interestingly, they are also similarly pigmented and are the only two species of this genus that have a strikingly blue coloration. However, they can be distinguished by the number of tubercles on the dorsal surface of the che-lipeds (*P. samawati* sp. nov. 7–9; *P. eumolpe*: 20–26,

C. D. Schubart, unpubl. data, 23 according to de Man, 1895). From our current knowledge of distribution, these two species do not inhabit the same geographical regions. The only congeneric sympatric species, *P. guttatum*, can be distinguished from *P. samawati* sp. nov. by the striking colour difference (in life) (Fig. 2), the number and shape of tubercles on the dorsal surface of the cheliped dactyls (*P. guttatum*: 11–13, Fig. 4A and Fig. 1B) and the characters detailed in Table 1. Additionally, in *P. samawati* sp. nov., the gonopod apical process is bent by approximately 45° (Fig. 1E), whereas it is more strongly bent in *P. guttatum* (Fig. 4B). Based on the material examined above, sexual maturity in

females of *P. samawati* sp. nov. is probably achieved between 12.92 and 21.79 mm cw. This agrees with the observations of Flores, Saraiva & Paula, (2002) for *P. guttatum*, who calculated sexual maturity to be 15.3 mm cw in females and between 9.3 and 9.4 mm cw in males.

As the difference between these two species had so far not been recognized, all previous studies on the ecology and behaviour of *P. guttatum* could have included both species. However, the study by Slim *et al.* (1997) took place in the mangroves of Gazi Bay and most likely only included *P. guttatum*. They found that *P. guttatum* is an ecologically important species due to its leaf litter processing behaviour. Similar find-

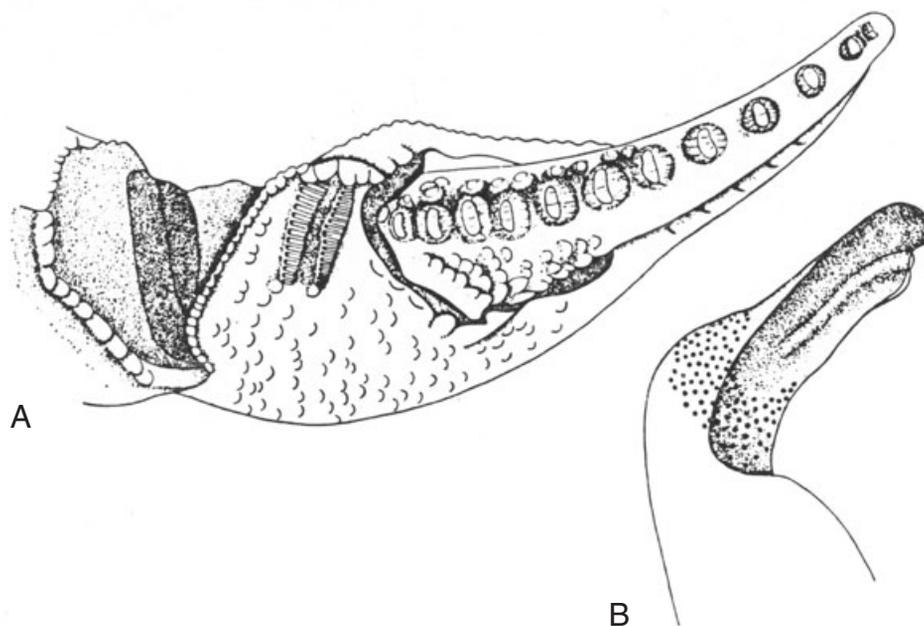


Figure 4. *Perisesarma guttatum*. A, dorsal view of chela. B, first gonopod (denuded) (after Crosnier, 1965).

Table 1. Comparison of morphometric relationships between adult males of *Perisesarma guttatum* and *P. samawati* sp. nov. from Kenyan mangroves. Due to the small sample sizes, a Mann–Whitney *U*-test was used to test for statistical significance. Values represent means, standard deviations and sample size

	<i>P. guttatum</i>	<i>P. samawati</i> sp. nov.	<i>P</i> ≤
Carapace length/width	0.80 ± 0.01 (5)	0.81 ± 0.01 (8)	0.01
Body height/carapace width	0.51 ± 0.01 (5)	0.53 ± 0.01 (8)	0.01
Interorbital width/carapace width	0.57 ± 0.01 (5)	0.60 ± 0.01 (8)	0.01
Posterior margin/carapace width	0.41 ± 0.01 (5)	0.42 ± 0.01 (8)	0.05
Extraorbital tooth/carapace length	0.16 ± 0.01 (5)	0.13 ± 0.01 (8)	0.01
Periopod-3 merus length/width	2.18 ± 0.07 (5)	1.92 ± 0.08 (6)	0.01
Telson width/length	0.96 ± 0.02 (5)	0.88 ± 0.05 (8)	0.01
Palm height/propodus length	0.52 ± 0.02 (5)	0.56 ± 0.01 (8)	0.01
Dactylus cutting edge/propodus length	0.43 ± 0.00 (5)	0.37 ± 0.02 (8)	0.01

ings have also been reported for other species of *Perisesarma* (e.g. Ashton, 2002). As *P. samawati* sp. nov. also readily consumes mangrove leaves and was common in the Mida Creek mangroves, it too is probably an ecologically important species, although it undoubtedly fills a different niche on the forest floor. In Malaysian mangroves, Ashton (2002) found differences in preference of leaf species consumed between the sympatric *P. eumolpe* and *P. onychophorum* (de Man, 1895) that may help reduce competition. Furthermore, she found evidence for differences in feeding strategies, with *P. onychophorum* being 'fast shredders' that consume leaves where they find them and *P. eumolpe* being 'slow shredders' that drag leaves into their burrows to feed. In addition to these differences, Leh & Sasekumar (1985) found that *P. eumolpe* had a more diverse diet than *P. onychophorum*, eating more invertebrates and green algae. We suggest that similar ecological differences may be present between *P. guttatum* and *P. samawati* sp. nov. in East African mangroves. Based on our feeding experiments, we suggest that *P. samawati* sp. nov. are 'slow shredders', similar to their proposed sister species *P. eumolpe*, whereas *P. guttatum* would behave more like the 'fast shredders' *P. onychophorum*.

Although more in-depth surveys are needed, our ecological observations on behaviour point towards higher shelter fidelity in *P. samawati* sp. nov. than in *P. guttatum*, which would also fit with the hypothesis above. It is difficult to draw conclusions about this from the literature as previous studies have not separated these species. Skov *et al.* (2002) found that >70% of the Zanzibar *Perisesarma* spp. are faithful to restricted areas of $\pm 16 \text{ m}^2$, whereas Flores *et al.* (2002) found that *Perisesarma* juveniles do not shelter in specific microhabitats and indistinctly use any available shelter in the mangroves of Inhaca Island. If, in fact, *P. samawati* sp. nov. is more dependent on a fixed shelter, shelter fidelity may also prevent competition between *P. samawati* sp. nov. and the larger *N. smithi*, which we have observed stealing leaves from *P. guttatum* and is known to steal leaves from the gastropod *Terebralia palustris* (Linnaeus, 1758) (see Fratini *et al.*, 2000). Although it is not certain whether *P. samawati* sp. nov. actively burrows or maintains these crevices, the seemingly faithful use of shelters and shy behaviour probably aid in both reduced competition and predator avoidance.

The geographical distribution of *P. samawati* sp. nov. remains unknown, although it can be assumed that it has a more restricted distribution than *P. guttatum* as it does not seem to occur (or is rare) in fringe mangrove forest types. *Perisesarma* spp. are among mangrove crab species with the highest densities in East Africa (Cannicci *et al.*, 1996; Flores *et al.*, 2002). Cannicci *et al.* (1996) recorded a higher activity

of *Perisesarma* spp. at night during neap tides, suggesting that *P. samawati* sp. nov. may also possibly be seen in higher numbers at night. This alone would further substantiate *P. samawati* sp. nov. as an ecologically important species.

The discovery of *P. samawati* sp. nov. raises many new ecological questions, including competition with *P. guttatum*, burrowing and feeding behaviour, geographical distribution, ecophysiology etc., all of which will give us a better understanding of the ecological contributions made by this new species. It may also have an influence on some of the earlier ecological work carried out in East Africa, as *P. samawati* sp. nov. must have been pooled with *P. guttatum* in at least some of the studies. The hypotheses discussed in this study need to be tested to fully understand the ecology of this beautiful, newly discovered species.

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REFERENCES

- Ashton EC. 2002. Mangrove sesarmid crab feeding experiments in Peninsular Malaysia. *Journal of Experimental Marine Biology and Ecology* **273**: 97–119.
- Ashton EC, Macintosh DJ, Hogarth PJ. 2003. A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia. *Journal of Tropical Ecology* **19**: 127–142.
- Bouillon S, Koedam N, Raman AV, Dehairs F. 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. *Oecologia* **130**: 441–448.

- Bright DB, Hogue CL. 1972.** A synopsis of the burrowing land crabs of the world and list of their symbionts and burrow associates. *Contributions in Science – Los Angeles County Natural History Museum* **220**: 1–58.
- Cannicci S, Ritossa S, Ruwa RK, Vannini M. 1996.** Tree fidelity and hole fidelity in the tree crab *Sesarma leptosoma* (Decapoda: Grapsidae). *Journal of Experimental Marine Biology and Ecology* **196**: 299–311.
- Crosnier A. 1965.** Crustacés décapodes. Grapsidae et Ocypodidae. *Faune de Madagascar* **18**: 1–143.
- Dahdouh-Guebas F, Giuggioli M, Oluoch A, Vannini M, Cannicci S. 1999.** Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. *Bulletin of Marine Science* **64**: 291–297.
- Davie PJF. 2003.** A new species of *Perisesarma* (Crustacea: Brachyura: Grapsidae) from the Bay of Bengal. *The Raffles Bulletin of Zoology* **51**: 387–391.
- Felsenstein J. 1985.** Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783–791.
- Flores AAV, Paula J, Dray T. 2003.** First zoal stages of grapsoid crabs (Crustacea: Brachyura) from the East African coast. *Zoological Journal of the Linnean Society* **137**: 355–383.
- Flores AAV, Saraiva J, Paula J. 2002.** Sexual maturity, reproductive cycles, and juvenile recruitment of *Perisesarma guttatum* (Brachyura, Sesarminidae) at Ponta Rasa mangrove swamp, Inhaca Island, Mozambique. *Journal of Crustacean Biology* **22**: 143–156.
- Fratini S, Cannicci S, Vannini M. 2000.** Competition and interaction between *Neosarmatium smithi* (Crustacea: Grapsidae) and *Terebralia palustris* (Mollusca: Gastropoda) in a Kenyan mangrove. *Marine Biology* **137**: 309–316.
- Gillikin DP. 2000.** Factors controlling the distribution of Kenyan brachyuran mangrove crabs: salinity tolerance and eco-physiology of two Kenyan *Neosarmatium* species. Unpublished MSc. Thesis, Vrije Universiteit Brussel, Belgium.
- Gillikin DP, De Grave S, Tack JF. 2001.** The occurrence of the semi-terrestrial shrimp *Merguia oligodon* (De Man, 1888) in *Neosarmatium smithi* H. Milne Edwards, 1853 burrows in Kenyan mangroves. *Crustaceana* **74**: 505–508.
- Gillikin DP, De Wachter B, Tack JF. 2004.** Physiological responses of two ecologically important Kenyan mangrove crabs exposed to altered salinity regimes. *Journal of Marine Biology and Ecology* **301**: 93–109.
- Hartnoll RG. 1975.** The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. *Journal of Zoology* **177**: 305–328.
- Hartnoll RG, Cannicci S, Emmerson WD, Fratini S, Macia A, Mgaya Y, Porri F, Ruwa RK, Shunula JP, Skov MW, Vannini M. 2002.** Graphical trends in mangrove crab abundance in East Africa. *Wetlands Ecology and Management* **10**: 203–213.
- Kumar S, Tamura K, Jakobsen IB, Nei M. 2001.** MEGA2: Molecular Evolutionary Genetics Analysis software. Arizona: Arizona State University.
- Lee SY. 1997.** Potential trophic importance of the faecal material of the mangrove crab *Sesarma messa*. *Marine Ecology Progress Series* **159**: 275–284.
- Lee SY. 1998.** Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research* **49**: 335–343.
- Leh CMU, Sasekumar A. 1985.** The food of sesarmid crabs in Malaysian mangrove forests. *Malayan Nature Journal* **39**: 135–145.
- Lugo AE, Snedaker SC. 1974.** The ecology of mangroves. *Annual Review of Ecology and Systematics* **5**: 39–64.
- de Man JG., 1895.** Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Zweiter Theil. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Thiere* **9**: 75–218.
- Micheli F, Gherardi F, Vannini M. 1991.** Feeding and burrowing ecology of two East African mangrove crabs. *Marine Biology* **111**: 247–254.
- Pereyra Lago RP. 1993.** Larval development of *Sesarma guttatum* A. Milne Edwards (Decapoda: Brachyura: Grapsidae) reared in the laboratory, with comments on larval generic and familial characters. *Journal of Crustacean Biology* **13**: 745–762.
- Rahayu Dwi L, Davie PJF. 2002.** Two new species and a new record of *Perisesarma* (Decapoda: Brachyura: Grapsidae: Sesarminae) from Indonesia. *Crustaceana* **75**: 597–607.
- Ruwa RK. 1997.** Zonation of burrowing crabs in the mangroves of the east coast of Kenya. In: Kjerfve B, Drude de Lacerdaand L, Diop HS, eds. *Mangrove ecosystem studies in Latin America and Africa*. UNESCO Technical Papers in Marine Science, Paris: UNESCO, 316–324.
- Schubart CD, Cuesta JA, Diesel R, Felder DL. 2000.** Molecular phylogeny, taxonomy, and evolution of nonmarine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Molecular Phylogenetics and Evolution* **15**: 179–190.
- Schubart CD, Neigel JE, Felder DL. 2000.** The use of the mitochondrial 16S rRNA gene for phylogenetic and population studies of Crustacea. *Crustacean Issues* **12**: 817–830.
- Skov MW, Hartnoll RG. 2002.** Paradoxical selective feeding on a low nutrient diet: why do mangrove crabs eat leaves? *Oecologia* **131**: 1–7.
- Skov MW, Vannini M, Shunula JP, Hartnoll RG, Cannicci S. 2002.** Quantifying the density of mangrove crabs: Ocypodidae and Grapsidae. *Marine Biology* **141**: 725–732.
- Slim FJ, Hemminga MA, Ochieng C, Jannink NT, Cocheret de la Morinière E, van der Velde G. 1997.** Leaf litter removal by the snail *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). *Journal of Experimental Marine Biology and Ecology* **215**: 35–48.
- Swofford DL. 1998.** *PAUP*: phylogenetic analysis using parsimony (*and other methods)*, Version 4. Sunderland, Mas-

sachusetts: Sinauer Associates.

Tan CGS, Ng PKL. 1994. An annotated checklist of mangrove brachyuran crabs from Malaysia and Singapore. *Hydrobiologia* **285**: 75–84.

Vannini M, Valmori P. 1981. Researchers on the coast of Somalia. The shore and the dune of Sar Uanle. 30. Grapsidae (Decapoda Brachyura). *Monitore Zoologico Italiano (N.S.)* **14** (Supplement): 57–101.