

REVISION OF THE *NEOSARMATIUM MEINERTI* SPECIES COMPLEX (DECAPODA: BRACHYURA: SESARMIDAE), WITH DESCRIPTIONS OF THREE PSEUDOCRYPTIC INDO–WEST PACIFIC SPECIES

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ABSTRACT. — Ragonieri et al. (2009) provided genetic and morphometric evidence that the widespread Indo-West Pacific sesarmid crab *Neosarmatium meinerti* (De Man, 1887) is a species complex composed of four species. The four have discrete ranges: one along the African mainland; one from islands in the western Indian Ocean; one from southern and eastern Asia; and one from northern Australia. The present paper clarifies the taxonomy of the four species and describes three new taxa. An updated identification key of all extant members of the genus is provided.

KEY WORDS. — *Neosarmatium meinerti*, species complex, three new species, western Pacific Ocean, Indian Ocean

INTRODUCTION

During the past 20 years, the number of species belonging to the genus *Neosarmatium* Serène & Soh, 1970, has increased considerably. Davie (1994) clarified some problems that arose after the classification by Serène & Soh (1970) and described two new species. Ng et al. (1997) reported new records of five species of *Neosarmatium* in Taiwan, describing new morphological diagnostic characters for them. Schubart & Ng (2002) described a new species from Sulawesi and transferred the Chinese *Chiromantes tangi* (Rathbun, 1931) to *Neosarmatium*. Finally, Rahayu & Davie (2006) described two more species from Papua, Indonesia, bringing the current number of species to 16 (Ng et al., 2008).

Within *Neosarmatium*, the majority of species are restricted to either the western Pacific Ocean or the eastern Indian Ocean: *N. daviei* Schubart & Ng, 2002; *N. fourmanoiri* Serène, 1973; *N. indicum* (A. Milne-Edwards, 1868); *N. inerme* (De Man, 1887); *N. integrum* (A. Milne-Edwards, 1873); *N. rotundifrons* (A. Milne-Edwards, 1869); *N. bidentatum* Rahayu & Davie, 2006; *N. papuense* Rahayu & Davie, 2006; *N. punctatum* (A. Milne-Edwards, 1873); *N. spinicarpus* Davie, 1994; *N. tangi* (Rathbun, 1931); *N. trispinosum* Davie, 1994. Only a few species have a broader

geographical range extending into the western Indian Ocean: *N. laeve* (A. Milne-Edwards, 1869); *N. meinerti* (De Man, 1887); *N. malabaricum* (Henderson, 1893); and *N. smithi* (H. Milne Edwards, 1853).

Neosarmatium meinerti is one of the better studied species of *Neosarmatium*, from both a behavioural and physiological point of view. A certain intraspecific morphological variability within *N. meinerti* was already reported by Davie (1994) who described two different colour morphs: the orange form with a “red-orange” chelar palm and the fingers fading to yellow distally, and the “yellow form” with evenly dirty pale yellow chelae. Both colour morphs occur sympatrically in north Australia, while in East Asia, the yellow morph seems to be much more common (Ng et al., 1997; Schubart & Ng, 2002). On the contrary, in the Indian Ocean, the orange morph seems to be more frequently encountered, and this observation led Schubart & Ng (2002) to speculate on the presence of two genetically differentiated groups. Recently, Ragonieri et al. (2009) investigated the phylogeography of *N. meinerti* throughout its geographical range, reporting the presence of a species complex with four evolutionary significant units (African mainland, western Indian Ocean islands, south-eastern Asia, and northern Australia) based on mitochondrial and nuclear genes as well as on morphological

and morphometric evidences. However, no genetic differences were found between the two colour morphs. The authors refrained from detailed morphological accounts and the description of new species, because it did not fit the initial scope of the paper and journal (Ragionieri et al., 2009: 833).

Neosarmatium meinerti suffers from a complex nomenclatural history (see Remarks). Based on photographs of *Cancer tetragonus* Fabricius, 1798, made available by Dr Meinert in Copenhagen, De Man (1887) noted that the description and figures of *Sesarma tetragona* by H. Milne Edwards (1853: 184) from Isle de France (= Mauritius) and those of A. Milne-Edwards (1873: 304, pl. 16, Fig. 4) did not correspond to *Cancer tetragonus* Fabricius, 1798 s. str. He therefore established a new name, *Sesarma meinerti*, for their material. De Man did not indicate if he studied any of these specimens. However, he commented that the species “bewohnt den ganzen Indischen Ocean und den Indischen Arcipel von Zanzibar, Madagascar und Mauritius” (De Man, 1887: 648). Until now, there was no need to determine which specimens may correspond to the type series (syntypes) or even to select a lectotype as there had been no confusion concerning the identity of this species (see discussion in Davie, 1994). In view of the study done by Ragionieri et al. (2009), however, there is now a need, so that a correct identification of all the members of the species complex can be carried out. According to the phylogeographic study of Ragionieri et al. (2009), the Mauritius specimens belong to the evolutionary significant unit (ESU, sensu Moritz, 1994) of the western Indian Ocean islands together with Rodrigues, Aldabra, and Seychelles. This ESU is reciprocally monophyletic to the ESU of the East African mainland, including specimens from western Madagascar (Nosy Bé) (according to mtDNA haplotypes), supporting the idea that these lineages share a common most recent ancestor prior to being historically isolated.

Cryptic and pseudocryptic (i.e., minor morphological differences only discovered after recognising genetic distinctness) species are the outcome of inconspicuous speciation, in agreement with the idea of subtle, but continuous genetic differentiation among natural populations. Previous biogeographical studies have shown that different genotypes, corresponding to different cryptic species, often exhibit different ecological and behavioural adaptations (Sáez et al., 2003). Therefore, a correct classification and delimitation of taxa, with the recognition of all species, is of fundamental importance for ethologists and ecologists, because even small genetic differences can be coupled with distinct ecological and behavioural adaptations. Will et al. (2005) argued that the real cutting-edge future for systematics and biodiversity research is integrative taxonomy, employing a large number of characters, including DNA, for delimiting, identifying, and describing natural species and taxa.

The aim of the present paper is thus to provide the morphological description of three undescribed species

belonging to the *N. meinerti* species complex (one from East Africa, one from south and eastern Asia, and one from north Australia; see Ragionieri et al., 2009). In addition, a lectotype for *N. meinerti* is selected from material from Mauritius, originally identified by H. Milne Edwards (1853) as “*Sesarma tetragona*” and which was subsequently used by De Man (1887) for the description of his *Sesarma meinerti*. This, together with an updated identification key, will clarify the taxonomy of *N. meinerti* and its sibling species.

MATERIAL AND METHODS

New material was collected from Phuket, Thailand; Mahé Island, Seychelles; and from Darwin, Northern Territories, Australia, between 1999 and 2006. Samples were preserved in 95% ethanol. In addition, many specimens were loaned or photographs requested from museums. Material examined originated or was deposited in the following institutions: MNHN – Muséum National d’Histoire Naturelle, Paris, France; MZUF – Museo Zoologico La Specola dell’Università di Firenze, Italy; NCHU – National Chung Hsing University, Taichung, Taiwan; NMNS – National Museum Natural Science, Taichung, Taiwan; QM-W – Queensland Museum, Brisbane, Australia; RMNH – Naturalis Museum Leiden, The Netherlands; ZMB – Zoologisches Museum, Berlin, Germany; ZRC – Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore. If historically reported material could not be re-examined, we attempted to attribute literature records based on the descriptions, figures, and distribution.

Morphological studies were carried out with stereomicroscopes and photographs were taken with a digital camera in order to present a more realistic view of the morphology of the species. Measurements of carapace width (taken at the widest point) and length (taken from frontal margin to the posterior border of the carapace) were taken with digital callipers in millimetres at the level of 0.01 mm. Only the first species in order of appearance, here *N. africanum* new species, is described in full. The other species are only diagnosed as they do not differ in other aspects.

TAXONOMIC ACCOUNT

Neosarmatium meinerti (De Man, 1887) has for long been considered a widespread species throughout the Indo-West Pacific. For this reason, many past accounts of *N. meinerti* included more than one of the recognised species accounted for in this paper, resulting in the fact that most of the new species described hereafter have been reported in the past as *N. meinerti* (Table 1). Papers which list the species but do not provide details of the specimens examined or where they were from (e.g., Serène (1968: 108, as *Sarmatium meinerti*); Serène & Soh (1970: 398, 406, as *Neosarmatium meinerti*); and Ng et al. (2008: 222, as *Neosarmatium meinerti*) are regarded as composite records and are not listed in the synonymy.

Table 1. Names, synonyms, and geographic distribution of *Neosarmatium meinerti* and the three new species.

Species	Synonyms	Distribution	References
<i>Neosarmatium meinerti</i> (De Man, 1887)	<i>Sesarma tetragona</i>	Mauritius	H. Milne Edwards, 1837 A. Milne-Edwards, 1873
	<i>Sesarma tetragonum</i>	Rodrigues	Miers, 1879 Ortmann, 1894a Doflein, 1904
	<i>Sesarma rotundifrons</i>	Samoa Island	De Man, 1880
	<i>Sesarma meinerti</i>	Mauritius and Seychelles	De Man, 1887 Haig, 1984
<i>Neosarmatium africanum</i> , new species	<i>Sesarma tetragona</i>	East Africa, South Africa, and Mozambique	Krauss, 1843 Hilgendorf, 1869, 1879 A. Milne-Edwards, 1868 Hoffmann, 1874 Lenz & Richters, 1881
	<i>Sesarma africana</i>	Mozambique	Bianconi, 1869
	<i>Sesarma tetragonum</i>	South Africa	Stebbing, 1910, 1917a, 1917b
	<i>Sesarma meinerti</i>	Madagascar and Zambesi	De Man, 1887 Pfeffer, 1889 Ortmann 1894a Lenz, 1905 Gravier, 1920 Cott, 1930 Fourmanoir, 1953 Vannini & Valmori, 1981 Pereyra Lago, 1989 Emmerson & McGwynne, 1992 Emmerson, 1994 Tesch, 1917
	<i>Sesarma (Sesarma) meinerti</i>	East Africa and South Africa	Chace, 1942 Bernard, 1950 Crosnier, 1965
<i>Neosarmatium asiaticum</i> , new species	<i>Sesarma tetragona</i>	Madras	Henderson, 1893
	<i>Sesarma meinerti</i>	Andaman and Madras	De Man, 1887 Bürger, 1893 Alcock, 1900 Horikawa, 1940 Lin, 1949 Ortmann, 1894a, 1894b De Man, 1895
	<i>Sesarma (Episesarma) meinerti</i>	Borneo and Malacca Sea	
	<i>Sesarma (Sesarma) meinerti</i>	Micronesia, Madagascar, and Pacific	Tesch, 1917 Miyake, 1938
	<i>Sesarma (Sarmatium) meinerti</i>	Jolo Island	De Man, 1929
<i>Neosarmatium australiense</i> , new species	<i>Neosarmatium meinerti</i>	Australia	Davie, 1982, 1984, 1994, 2002, 2005

***Neosarmatium africanum*, new species**

(Figs. 1a, 2a, 3a,e, 4a,e, 5a, 6a,b)

Sesarma tetragona: Krauss, 1843: 44; Hilgendorf, 1869: 90, pl. 3, Fig. 3d; 1879: 809; A. Milne-Edwards, 1868: 71; Hoffmann, 1874: 23; Lenz & Richters, 1881: 425 [not *Cancer tetragona* Fabricius, 1798: 341].

Sesarma africana (?): Bianconi, 1869: 341 [fide Hilgendorf, 1879: 809; Tesch, 1917: 171] [not *Sesarma africana* H. Milne Edwards, 1837 = *Perisesarma huzardi* (Desmarest, 1825)].

Sesarma tetragonum: Stebbing, 1910: 321; 1917a: 438; 1917b: 10 [not *Cancer tetragona* Fabricius, 1798: 341].

Sesarma meinerti De Man, 1887: 648, 668–669 (in part); Pfeffer, 1889: 31; Ortmann, 1894a: 720 (in part); Lenz, 1905: 372; Gravier, 1920: 472; Cott, 1930: 679–692, pl. 1; Fourmanoir, 1953: 89; 1954: 5; Vannini & Valmori, 1981: 57; Pereyra Lago, 1989: 199; Emmerson & McGwynne, 1992: 41; Emmerson, 1994: 568.

Sesarma (Sesarma) meinerti: Tesch, 1917: 171–174 (in part); Chace, 1942: 201; 1953: 441; Bernard, 1950: 125–26, Fig. 25e, f; Crosnier, 1965: 61, Figs 81, 90, 91, 96, 103.

Neosarmatium meinerti: Davie, 1994: 35 (in part); Dahdouh-Guebas et al., 1997: 83; 1998: 345; Skov & Hartnoll, 2002: 1–7; Gillikin et al., 2004: 93; Skov et al., 2005: 1164; Fratini et al., 2005: 222, 225; Schubart et al., 2006: 195, 197; Berti

et al., 2008: 101; Cannicci et al., 2008: 186; Ragionieri et al., 2009: 825–834, 2010: 179–188.

Material examined. — Holotype: male (42.83 × 38.33 mm) (MZUF 678), Jumbo River, Somalia, coll. M. Vannini, Dec.1976. Paratypes: SOMALIA: 2 males (24.07 × 20.17 mm; 40.42 × 34.48 mm) (MZUF 677), Jumbo River, coll. M. Vannini, Dec.1976; KENYA: 1 male (37.65 × 32.36 mm) (MZUF 3666), Mida Creek, coll. M. Vannini, Jul.1997; 1 male (27.38 × 23.89 mm) (MZUF 2731), Mida Creek, coll. S. Fratini, 7 Feb.2005; 2 males (46.17 × 41.50 mm; 37.55 × 32.81 mm) (MZUF 1025), Gazi Bay, coll. M. Vannini, Jul.1997; 1 male (27.38 × 23.89mm) (MZUF 2731), Mida Creek, coll. S. Fratini, 7 Feb.2005; 3 males (36.72 × 34.03 mm; 38.31 × 33.09 mm; 34.09 × 29.57 mm) (MZUF 2967), Mida Creek, coll. S. Cannicci, Oct.1997; SOUTH AFRICA: 1 male (45.53 × 40.14mm) (MNHN-B31275), Natal, coll. B. Newman, 1997; AFRICAN COAST: 1 male, 1 female (ZRC 1968.1.22.6–7), coll. MacNae, Apr.1967; MADAGASCAR: 1 female (34.0 × 29.0 mm) (RMNH D171), Nosy Bé (former syntype of *Sesarma meinerti* De Man, 1887), coll. F. P. L. Pollen & D. C. van Dam, 1963–1966; 4 males (37.15 × 31.67 mm; 34.56 × 29.60 mm; 38.50 × 33.63 mm; 31.26 × 25.88 mm) (MNHN-B30342), Tuléar, coll. A. Crosnier 8 Oct.1961; 1 male (40.7 mm carapace width) (ZMB 12679) northwest Madagascar, coll. J. M. Hildebrandt, 1879.

Diagnosis. — Carapace narrowing towards posterior with slight concavity medially (Fig. 2a), without any indication of second anterolateral teeth. Male chela characterised by presence of single prominent line of tubercles along inner palm surface (Fig. 3e) with palm height 1.55 (± 0.12) times maximum chelar width. Descending slope of palm (with parallel prominent ridge) oblique at articulation with dactylus (Fig. 3a). Lower margin of chela straight. Dorsal surface of dactylus covered with tubercles until three-quarters of length (Fig. 4a, e). Male abdomen triangular; somite 6 with proximal width 1.35 (± 0.071) times length; telson length 1.24 (± 0.127) times width (Fig. 5a).

Description. — Carapace: smooth, bearing short setae in tufts on anterior half. Carapace ca. 1.14 (± 0.031; n = 19) times broader than long. Maximal carapace width ca. 1.23 (± 0.028; n = 19) times posterior carapace width. Carapace width ca. 1.61 (± 0.063; n = 19) times body height. Anterolateral tooth triangular. Lateral margin narrowing towards posterior slightly concave medially (Fig. 2a). Frontal border straight with front ca. 0.50 (± 0.021; n = 19) times carapace width. Postfrontal margin separated into 4 well-defined lobes,

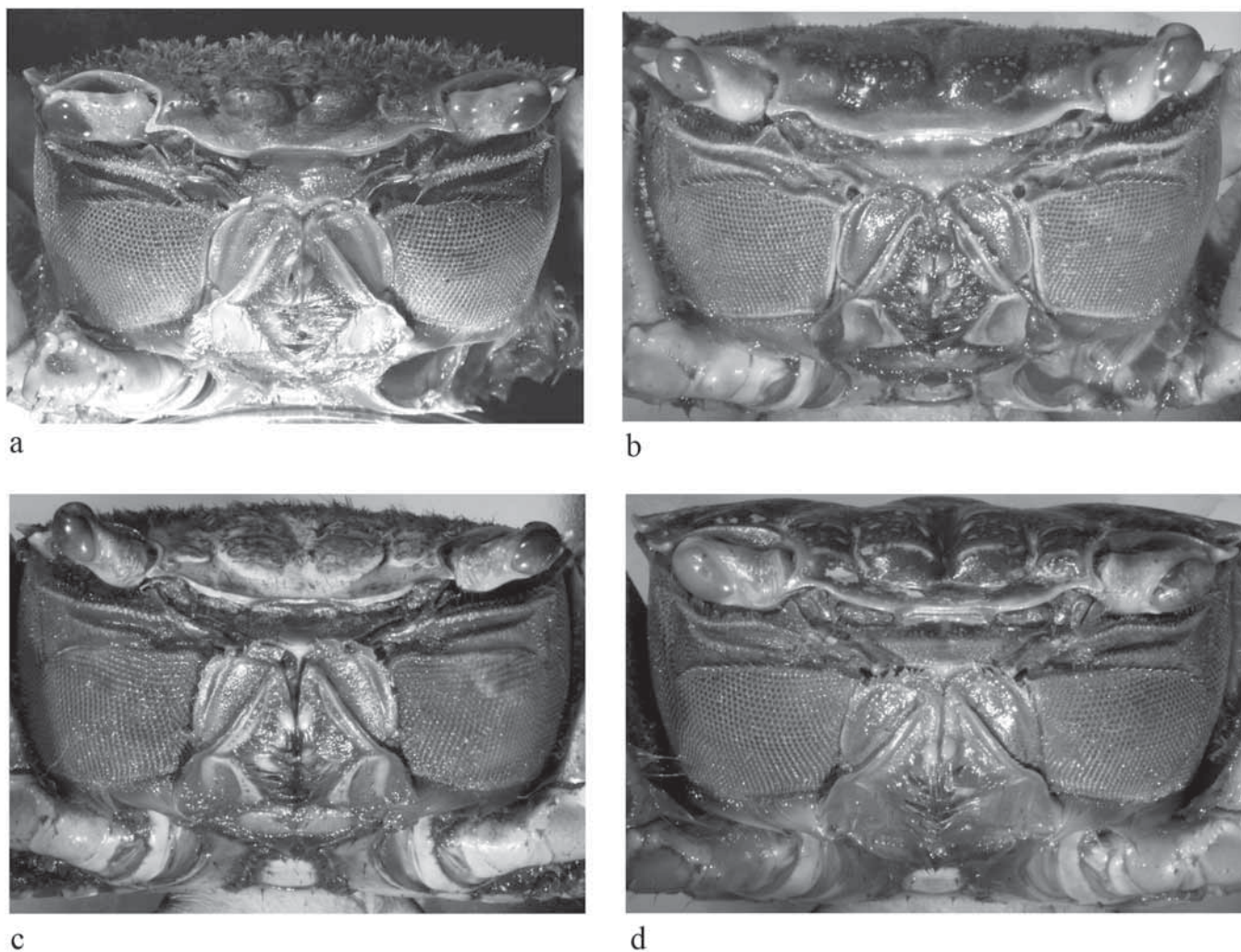


Fig. 1. Frontal view of four species of *Neosarmatium*: a, *N. africanum*, new species, holotype male (42.83 × 38.33 mm) (MZUF 678), Somalia; b, *N. meinerti* (De Man, 1887) paratype male (40.26 × 35.60 mm) (MZUF 2931), Seychelles; c, *N. asiaticum*, new species, holotype male (38.52 × 33.11 mm) (NMNS-6327-001), Taiwan; d, *N. australiense*, new species, holotype male (39.85 × 34.77 mm) (QM-W29085), Australia.

median lobes more prominent, than external ones, separated by deep concavity (Fig. 1a). Cardiac region with deep H-shaped gastro-cardiac groove. Branchial ridges prominent; other ridges arise laterally, near lateral margin of carapace (Fig. 2a).

Third maxilliped: Suture between merus and ischium of third maxilliped oblique. Ischium with shallow submedian sulcus; slender exopod with tip reaching half length of outer margin of merus. Inner margin of both ischium and merus with dense setae (Fig. 1a).

Chelipeds: Merus of chela with tubercles on inner face and along dorsal margins. Carpus with row of short setae on dorsal margin and weak tubercles along anterior and posterior

margins. Outer surface of palm glabrous with microscopic granules (Fig. 3a). Chela length ca. $1.39 (\pm 0.09; n = 19)$ times dactylus length. Inner surface of palm with single prominent row of tubercles that forms angular structure (Fig. 3e). Descending slope of palm (with parallel prominent ridge) at articulation with dactylus oblique, especially visible from outer side (Fig. 3a). Proportion of chelar length to maximum chelar width ca. $2.61 (\pm 0.27; n = 19)$. Dactylus strongly curved, forming wide gap with pollex (Fig. 3a, e). Dorsal surface of dactylus with minute granules extending towards two-thirds of length (Fig. 4a, e). Immobile finger moderately curved inwards, ventral border straight (Fig. 4a).

Ambulatory legs: Third and second legs (pereiopods 3 and 4) longest. Length of merus of third walking leg ca. $2.1 (\pm 0.17;$

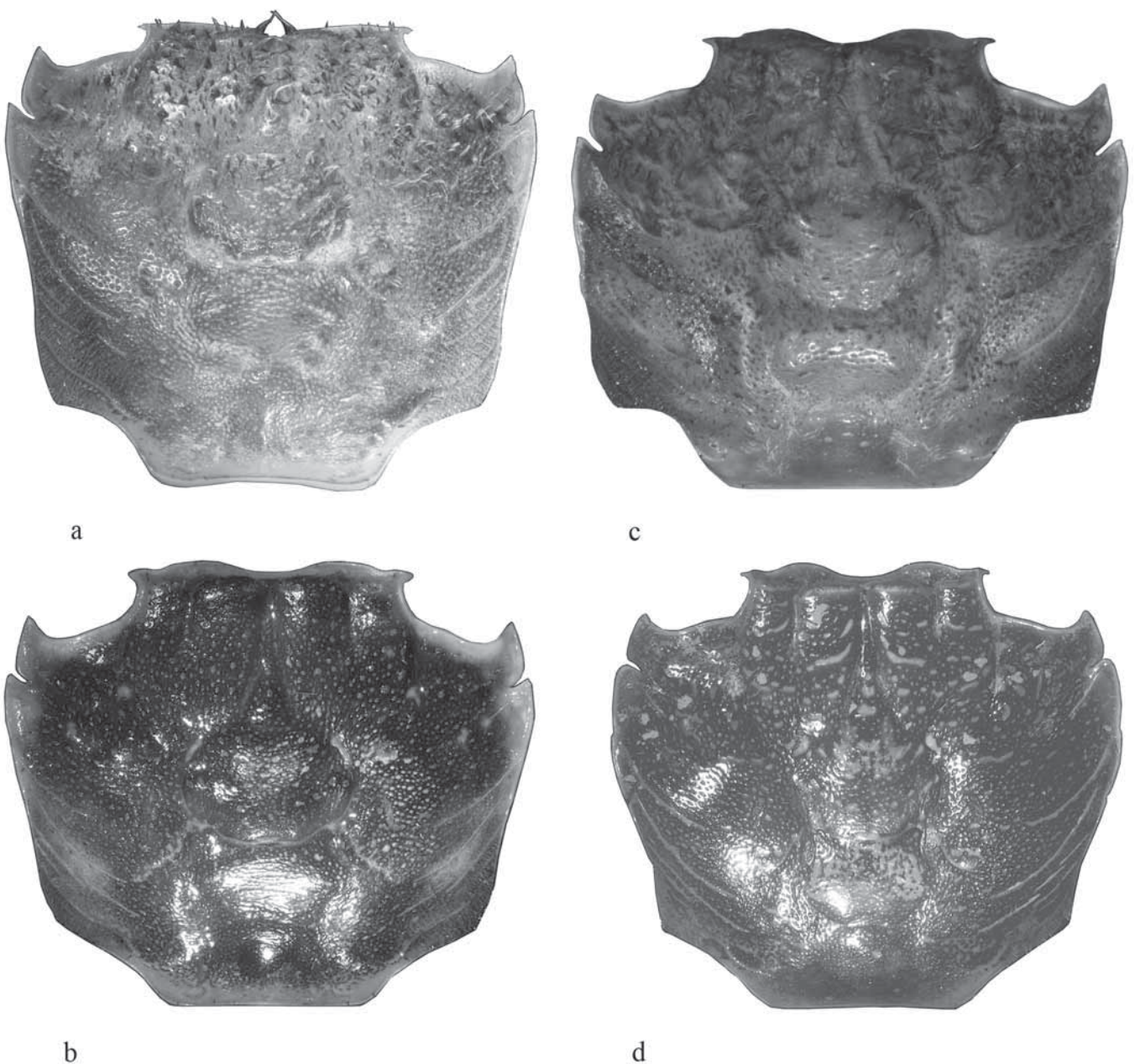


Fig. 2. Dorsal view of carapaces of four species of *Neosarmatium*: a, *N. africanum*, new species, holotype male (42.83×38.33 mm) (MZUF 678), Somalia; b, *N. meinerti* (De Man, 1887), paratype male (40.26×35.60 mm) (MZUF 2931), Seychelles; c, *N. asiaticum*, new species, holotype male (38.52×33.11 mm) (NMNS-6327-001), Taiwan; d, *N. australiense*, new species, holotype male (39.85×34.77 mm) (QM-W29085), Australia.

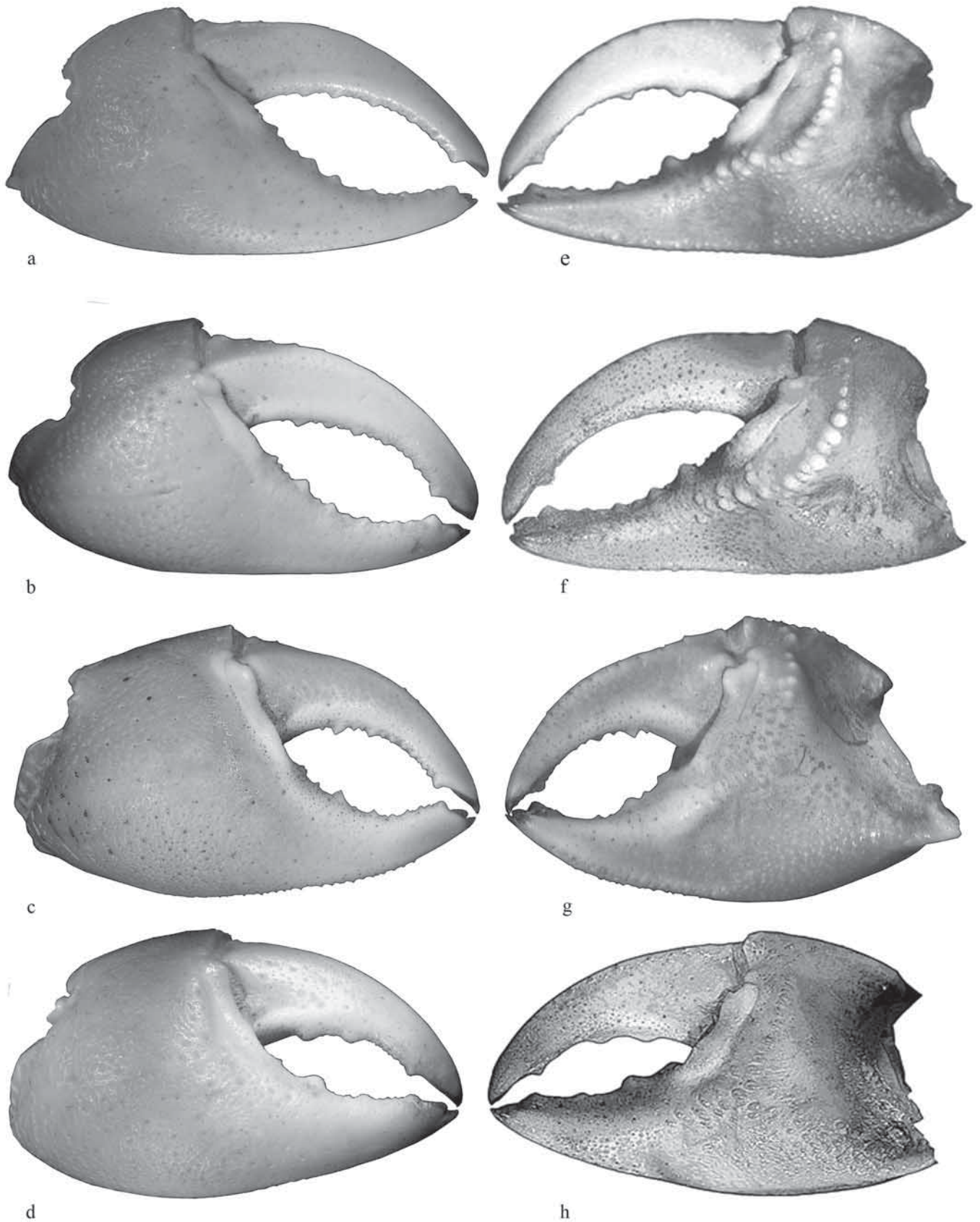


Fig. 3. Outer and inner surfaces of the right chelae of four species of *Neosarmatium*: a, e, *N. africanum*, new species, holotype male (42.83 × 38.33) (MZUF 678), Somalia; b, f, *N. meinerti* (De Man, 1887), paratype male (40.26 × 35.60) (MZUF 2931), Seychelles; c, g, *N. asiaticum*, new species, holotype male (38.52 × 33.11 mm) (NMNS-6327-001), Taiwan; d, h, *N. australiense*, new species, holotype male (39.85 × 34.77 mm) (QM-W29085), University of Darwin, Darwin, Australia.

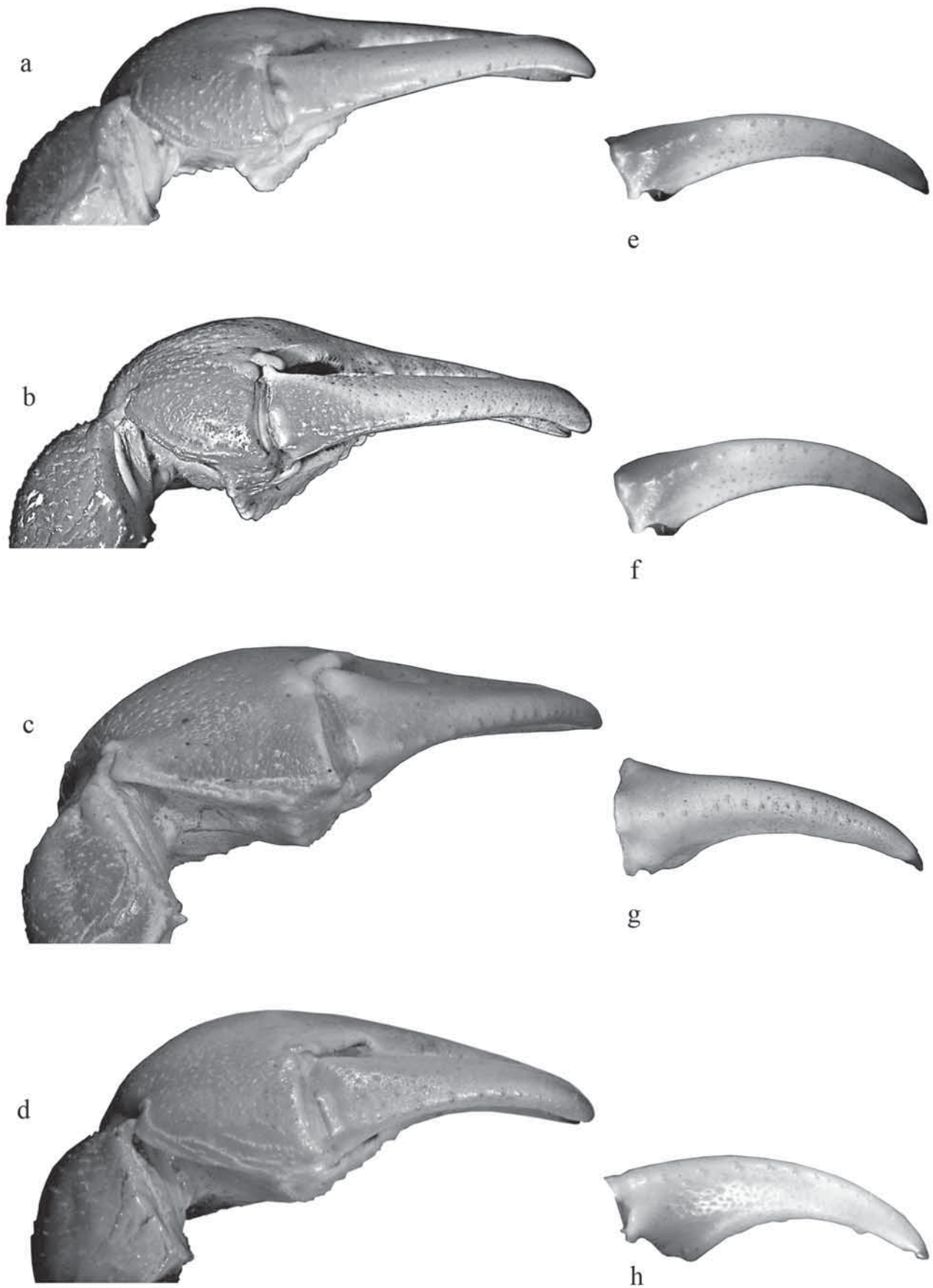


Fig. 4. Dorsal view of distal chelipeds and dactyli: a,e, *Neosarmatium africanum*, new species, holotype male (42.83 × 38.33 mm) (MZUF 678), Somalia; b,f, *N. meinerti* (De Man, 1887), paratype male (40.26 × 35.60 mm) (MZUF 2931), Seychelles; c, g, *N. asiaticum*, new species, holotype male (38.52 × 33.11 mm) (NMNS-6327-001), Taiwan; d, h, *N. australiense*, new species, holotype male (39.85 × 34.77 mm) (QM-W29085), Australia.

n = 19) times its width. All legs with bristles along ventral margins of coxae, basis-ischia and meri. Outer surfaces of meri strongly rugose. Carpi and propodi with short mat of soft setae on dorsal and ventral margins of pereopods 2 and 3, only present on dorsal margin of fourth pereopods. Bristles present on both margins along carpi and propodi. Dactyli shorter than propodi with 6 longitudinal lines of setae proximally.

Male abdomen: Width of somite 3 ca. 2.24 (\pm 0.098; n = 19) times carapace width. Somite 6 elongated with proximal width 1.35 (\pm 0.071; n = 19) times length. Telson shorter than somite 6; ca. 1.24 (\pm 0.127; n = 19) times longer than wide (Fig. 5a).

Gonopods: First male gonopods almost straight, distally curved inward with outer margins convex. Distal part of stem straight, broad, with setae around apex (Fig. 6a); apex moderately fold towards medial plane of body (Fig. 6b).

Etymology. — The species name *Neosarmatium africanum* makes reference to the geographical distribution of this species along the East African coast, from Somalia to South Africa, including parts of Madagascar.

Colour. — This species occurs in East Africa with exclusively red-orange chelae, the colouration extending onto two-thirds of the proximal part of the palm and the fingers fading to yellow distally.

Habitat. — *Neosarmatium africanum*, new species, lives in burrows in the dry and muddy area of the upper intertidal belt associated with mangroves and estuaries. Burrow entrances usually are surrounded by a mound of mud. The burrows have secondary channels, with a mean length of around 80 cm usually extending to the water table (Berti et al., 2008).

Ecology. — *Neosarmatium africanum*, new species, as many other species of Sesarmidae, plays an important role in the biochemical cycle of mangrove leaves degradation. Analysis of stomach content showed that its diet mainly consists of mangrove leaves, especially of *Avicennia marina*, completed with little animal matter (Dahdouh-Guebas et al., 1997). Nevertheless, Skov & Hartnoll (2002) showed that the mangrove leaves are unlikely to fulfil the nitrogen requirements of crabs. Leaf fragmentation may enrich the nutritional quality of the substrate detritus, with the sediment detritus being a richer source of nitrogen, regularly ingested by crabs (Skov & Hartnoll, 2002). Moreover, this species seems to be a strong mangrove propagule consumer and may even affect the regeneration potential of mangroves (Dahdouh-Guebas et al., 1998). As the density reached by *N. africanum* in most of East African mangroves can be high (see Fratini et al., 2011), bioturbation due to its excavation activity contributes to a rapid nutrient enrichment of soil and as a consequence, enhances mangrove primary production. These observations lead Cannicci et al. (2008) to review the ecological function of many crab species inhabiting the mangal ecosystem and highlighted the importance of crab

bioturbation in producing a rapid enrichment of the primary production of mangroves. From a physiological point of view, *N. africanum* is able to resist large salinity fluctuations as congeneric species, like *N. smithi*, and this appears to be typical of species living along the landward fringe of the East African mangal (Gillikin et al., 2004).

Breeding and larvae. — The breeding season of *Neosarmatium africanum*, new species, varies according to its latitudinal distribution along the East African coast. In Kenya and Tanzania, the highest occurrence of ovigerous females is during the dry season (between February and April), while in sub-temperate areas such as South Africa, most ovigerous females occur during the summer season (between January and February) (Emmerson, 1994; Skov et al., 2005). Pereyra Lago (1989) described five zoeal stages and one megalopa stage of *N. africanum* (as *N. meinerti*), highlighting important morphological characters useful for distinguishing their larvae from those of other sesarmid species sympatric in the same mangal and estuary areas.

Distribution. — East African coast from middle of Somalia to Natal in South Africa. It is also present in Madagascar, at least along the north-western coast of Madagascar close to Nosy Bè. We have not been able to study material from other parts of the island.

Neosarmatium meinerti (De Man, 1887)

(Figs. 1b, 2b, 3b,f, 4b,f, 5b, 6c,d)

Sesarma tetragona: H. Milne Edwards, 1837: 73; 1853: 184–185; A. Milne-Edwards, 1873: pl.16: Fig.4 [not *Cancer tetragona* Fabricius, 1798: 341].

Sesarma tetragonum: Miers, 1879: 490; Ortmann, 1894a: 720; Doflein, 1904: 130 [not *Cancer tetragona* Fabricius, 1798: 341].

Sesarma rotundifrons: De Man, 1880: 24 [not *Sesarma rotundifrons* A. Milne-Edwards, 1869; see Davie, 1994].

Sesarma meinerti: De Man, 1887: 648, 668–669 (in part); Haig, 1977: 127.

Neosarmatium meinerti: Serène & Soh, 1970 (localities not listed); Serène, 1977: 51; Davie, 1994: 35 (in part).

Material examined. — Lectotype: 1 male (34.00 × 39.30 mm) (MNHN-IU-2011-278), Ile de France (Mauritius), coll. M. Mathieu (1837 or earlier) (identified as *Sesarma tetragona*, ex-MNHN-B3688); Paralectotypes: MAURITIUS: 2 females (28.20 × 33.90 mm; 30.60 × 36.00 mm) (MNHN-IU-2011-279 ex-MNHN-B3688) same data as lectotype. Other material: SEYCHELLES: 2 males, 1 female (ZRC 1972.8.25.2), Mahé Island, coll. R. Serène, May 1972; 1 male (40.26 × 35.60 mm) (MZUF 2931), Mahé Island: Port Launary, coll. S. Fratini, 11 Dec.2005; 1 male (15.34 × 12.35 mm) (MZUF 2940), Mahé Island, Port Launary, coll. M. Fusi, 4 Dec.2005; REPUBLIC OF MAURITIUS: 1 male (27.00 × 22.00 mm) (RMNH D 17503), Barkley Island, Port Louis, coll. C. Miquel, Feb.1960; 1 male (34.5 × 28.83 mm) (MZUF 3661), Rodrigues, coll. M. Vannini, 8 Jul.1987; 1 male (15.74 × 12.85 mm) (MZUF 3662), Rodrigues, coll. M. Vannini, 8 Jul.1987; 1 male (12.70 × 10.35 mm) (MZUF 3660), Mauritius, coll. M. Vannini, 1 Sep.1989; male (20.47 × 17.00 mm) (MZUF 3665), Mauritius, coll. M. Vannini, 1 Sep.1989.

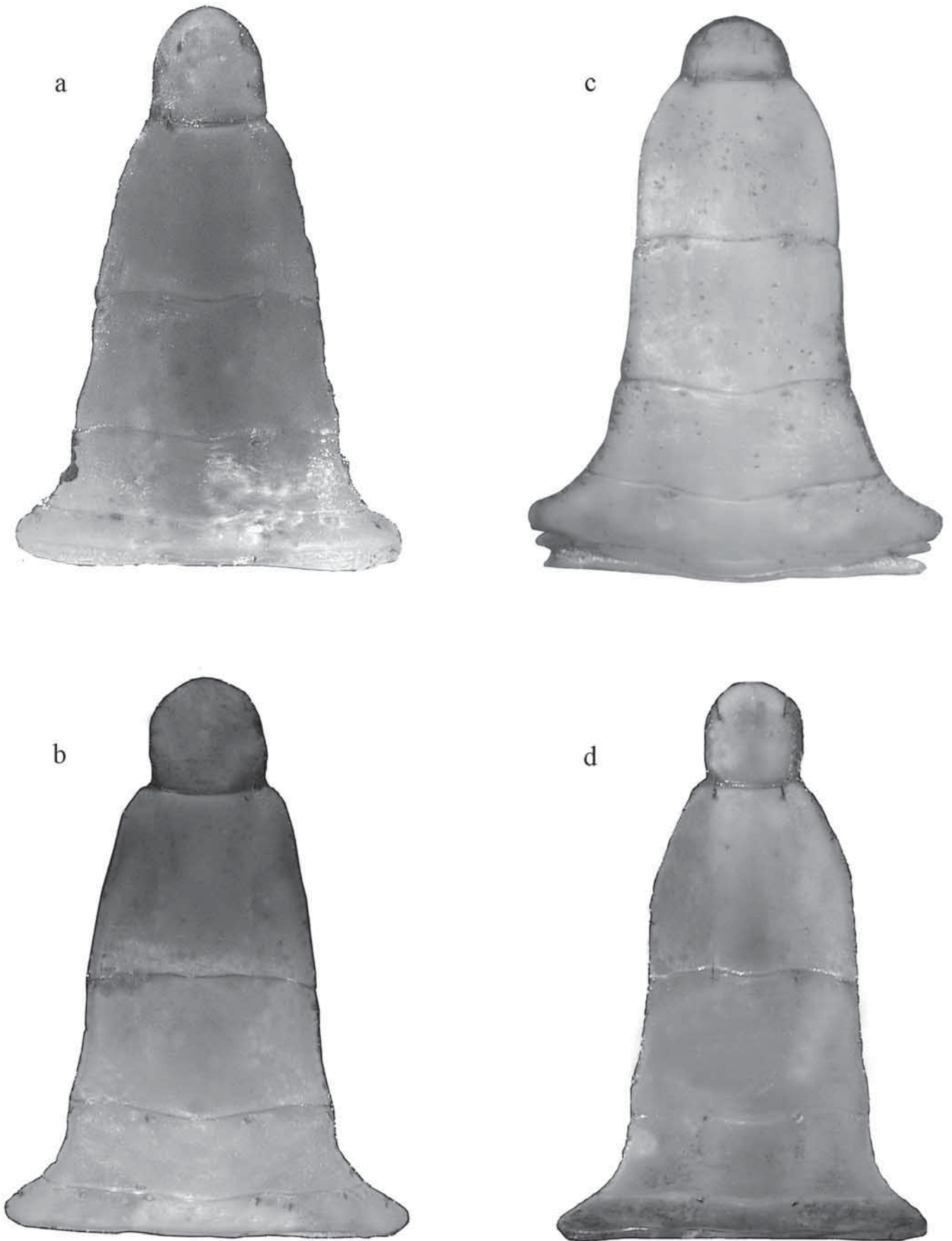


Fig. 5. Male abdomens: a, *Neosarmatium africanum*, new species, holotype male (42.83 × 38.33 mm) (MZUF 678), Somalia; b, *N. meinerti* (De Man, 1887), paratype male (40.26 × 35.60 mm) (MZUF 2931), Seychelles; c, *N. asiaticum*, new species, holotype male (38.52 × 33.11 mm) (NMNS-6327-001), Taiwan; d, *N. australiense*, new species, holotype male (39.85 × 34.77 mm) (QM-W29085), Australia.

Diagnosis. — Carapace gently concave posteriorly, without any indication of second anterolateral tooth (Fig. 2b). Male chela characterised by presence of single prominent line of tubercles along inner palm surface (Fig. 3f), with palm height 1.58 (± 0.18 ; $n = 8$) times maximum chelar width. Descending slope of palm (with parallel prominent ridge) at articulation with dactylus oblique (Fig. 3b). Lower margin of chela straight. Dorsal surface of dactylus covered with tubercles until three-quarters of length (Fig. 4b, f). Male abdomen triangularly shaped; somite 6 with proximal width 1.29 (± 0.124 ; $n = 8$) times length; telson length 1.15 (± 0.141 ; $n = 8$) times width (Fig. 5b).

Colour. — All specimens examined correspond to the morph with red-orange chelae, with the colouration extending to two-thirds of the proximal part of the outer margin of the palm and the fingers fading to yellow.

Remarks. — Regarding the missing holotype of this species, Peter Ng, Danièle Guinot, and Charles Fransen offered useful and extensive information based on the nomenclatural rules and material to be found in the collections of Paris and Leiden. Davie (1994: 57) noted that the holotype of this species was “unidentifiable”, with the type locality being Mauritius. The same paper (p. 56) does not list any specimens from H. Milne Edwards, A. Milne-Edwards, or De Man under the material examined; although the author notes later (p. 57) that in the Paris Museum there is a bottle with three female specimens (MNHN-B 10887) from Mauritius that had been labeled as *S. meinerti*, but dated 10 Jun. 1890, three years after De Man’s (1887) paper. As such, he argued that these could not be the types. Davie thus considered the types to be lost, but deferred from designating a neotype because at that time, there was no confusion over the identity of *N. meinerti* and the stability of the nomenclature was not threatened.

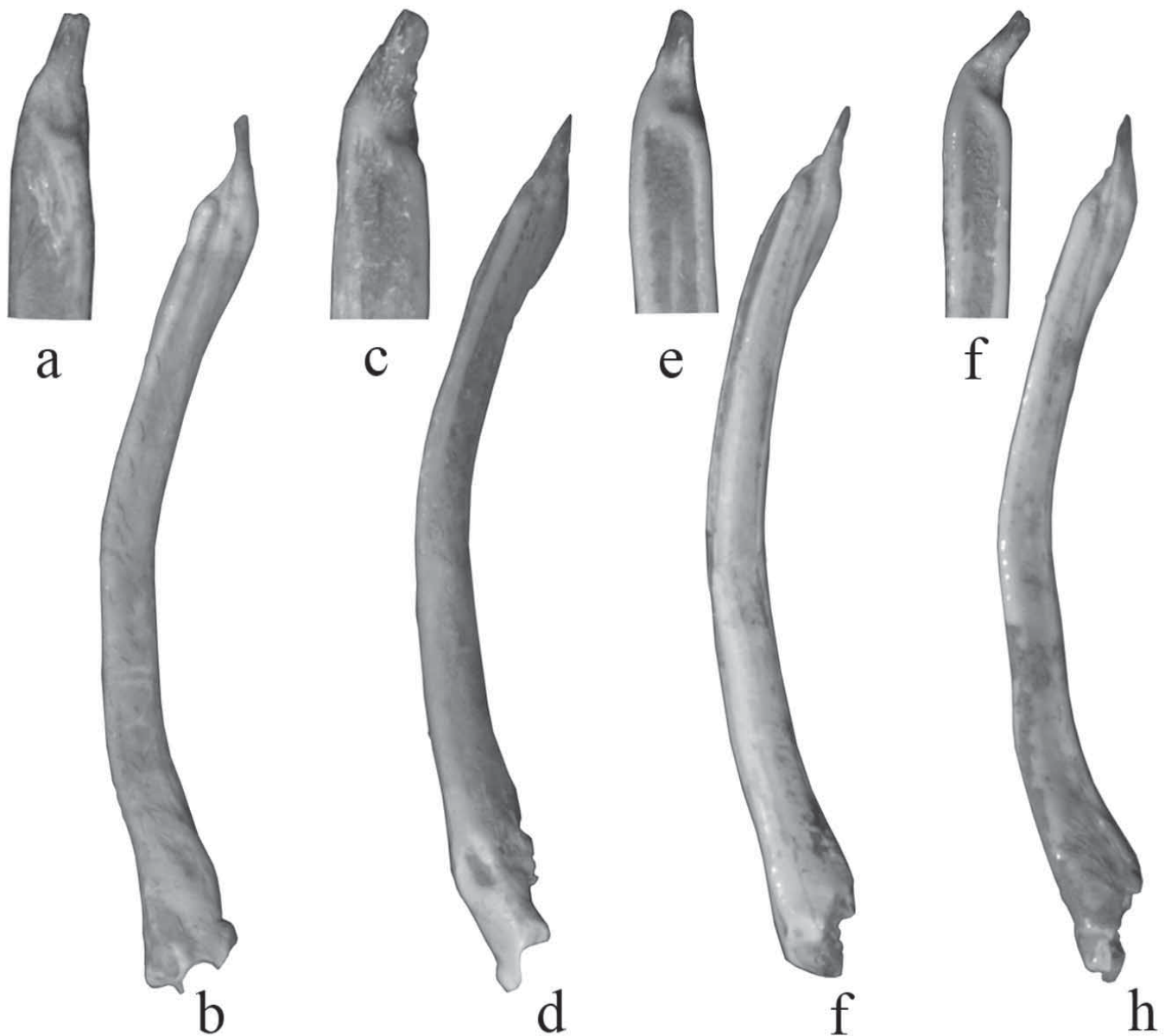


Fig. 6. Male left first gonopods and corresponding distal parts: a, b, *Neosarmatium africanum*, new species, holotype male (42.83 \times 38.33 mm) (MZUF 678), Somalia; c, d, *N. meinerti* (De Man, 1887), paratype male (40.26 \times 35.60 mm) (MZUF 2931), Seychelles; e, f, *N. asiaticum*, new species, holotype male (38.52 \times 33.11 mm) (NMNS-6327-001), Taiwan; g, h, *N. australiense*, new species, holotype male (39.85 \times 34.77 mm) (QM-W29085), Australia.

According to article 72.4.1 of the International code of Zoological Nomenclature (ICZN) “the type series of a nominal species-group taxon consists of all the specimens included by the author in the new nominal taxon (whether directly or by bibliographic reference)”. This means that all the material De Man (1887: 648) had in his hands at the time of the description or the specimens listed by the given bibliographic reference (i.e., H. Milne Edwards, 1853 and A. Milne-Edwards, 1873) are syntypes. Now H. Milne Edwards (1853: 184, 185) did not have any figure or material listed for “*Sesarma tetragona*”, and only noted that the species in his report was found in “Ile de France” (= Mauritius). Alphonse Milne-Edwards (1873: 304–305) gave a longer account and indicated the species occurred in New Caledonia, Mauritius and Madagascar. However, A. Milne-Edwards (1873) also did not indicate how many specimens he had from each location or provide any other data. Presumably, most, if not all the material used by both H. Milne Edwards (1853) and A. Milne-Edwards (1873) were in Paris.

Unfortunately, even De Man (1887) did not list which specimens were studied by him, and he also did not indicate a holotype for *Sesarma meinerti*. Peter Ng brought to our attention (personal communication) an important and very revealing comment made by De Man in the introduction which he wrote in Jan.1887. De Man (1887: 640) thanked Milne Edwards (presumably Alphonse-Milne Edwards) for his kindness in letting him examine material from the Paris Museum. He also noted that he examined material from Leiden Museum (De Man, 1887: 641). According to article 72.4.1.1 of the ICZN, for all the taxa established before 2000, “any evidence, published or unpublished, may be taken into account to determine what specimens constitute the type series”. Taking these facts into account, all the material of “*Sesarma tetragona*” of H. Milne Edwards that were examined or seen by De Man up to Jan.1887 from Mauritius can be regarded as types. The same applies for all the material of “*Sesarma tetragona*” from Mauritius, Madagascar, and New Caledonia that A. Milne-Edwards (1873) had up to Jan.1887. As noted above, there is also a good chance that De Man had, in fact, examined this material from the Paris Museum. Whether this material was renamed as *S. meinerti* or it kept the original identification, we do not know. Moreover, the fact that De Man listed Zanzibar, even though it was not mentioned by H. Milne Edwards (1853) or A. Milne-Edwards (1873), is interesting and suggests that De Man had examined material from this location as well.

It is also possible that any specimens in the Leiden Museum which may have been labeled as *S. meinerti* up to Jan.1887, would have been examined by De Man and can be regarded as syntypes. Charles Fransen, the curator of Crustacea at RMNH, noted that: “apart from the material of Mauritius (RMNH D 17503) we also have two specimens from Madagascar (RMNH D 171) that were collected in 1863–1866 by F. P. L. Pollen & D. C. van Dam and are indicated as syntypes.” These two specimens were collected from Nosy Bé, northwestern Madagascar. However, according to Ragionieri et al. (2009), all the samples genetically and morphometrically

examined from Nosy Bé belong to the African clade, which is named *N. africanum*, new species, in the present paper. The material from Mauritius now present in the Leiden Museum was collected in 1960, so it could not have been seen by De Man and cannot be considered a syntype.

Fortunately, Danièle Guinot from MNHN was able to relocate the material presumably examined by De Man. She, together with Tohru Naruse and Peter Ng, clarified the origin of the type of *N. meinerti* as follows: there is a strong presumption that the material initially used by H. Milne Edwards (1837) for *Sesarma tetragona* (indicated from Indian Ocean) was collected by Mathieu M. in Ile de France (= Mauritius), because the dates of Mathieu’s life correspond to this period. Also, the fact that H. Milne Edwards in 1853 used the same material is indicative of Ile de France as the locality. Thus, the *Sesarma tetragona* of H. Milne Edwards, 1837, is the same as that of 1853. Alphonse Milne-Edwards (1873: pl. 16, Fig. 4) depicted the *Sesarma tetragona* specimens of H. Milne Edwards (1837) and (1853). They correspond to the specimens, which De Man (1887) described as new under the name “*Sesarma meinerti*” and hence they are also types of *Sesarma meinerti*.

Consequently, here we have designated a male (34.00 × 39.30 mm) from the series collected by M. Mathieu in Mauritius (MNHN-IU-2011-278) as the lectotype of *Sesarma meinerti* De Man, 1887. The two remaining specimens of this series are to become paralectotypes. The lectotype of *N. meinerti* (MNHN-IU-2011-278) has similar morphological characteristics as other studied specimens of *N. meinerti* from the western Indian Ocean islands: carapace shape without any indication of second anterolateral tooth (Fig. 7a); frontal border straight with the postfrontal margin separated into four well-defined lobes, with median lobes much more prominent than external ones, and separated by a deep concavity (Fig. 7d); inner palm of the chela characterised by the presence of a single prominent line of tubercles (Fig. 7b), dorsal surface of dactylus covered with tubercles until three-quarters of its length (Fig. 7b), and descending slope of palm at articulation with dactylus oblique (Fig. 7c). This lectotype selection conclusively fixes the name *Sesarma meinerti* De Man, 1887, for the Mauritius taxon.

With regard to the specimens from New Caledonia mentioned by A. Milne Edwards in 1873, all previously identified specimens of *N. meinerti* from the western Pacific Ocean (such as Guam and Fiji; see Ragionieri et al., 2009) and Papua New Guinea (unpublished data) have been morphologically and genetically identified as *N. fourmanoiri*. Therefore, we assume that the specimens collected in New Caledonia previously identified as *N. meinerti* by De Man (1887) and others belong to *N. fourmanoiri* Serène, 1973.

Habitat. — Similar to *N. africanum*, new species (M. Vannini pers. obs.).

Ecology. — Similar to *N. africanum*, new species (M. Vannini pers. obs.).

Distribution. — The range of distribution of this species extends into the western Indian Ocean from Mauritius (type locality) to Rodrigues, including the islands Aldabra and Mahé Island belonging to the Seychelles.

***Neosarmatium asiaticum*, new species**

(Figs. 1c, 2c, 3c,g, 4c,g, 5c, 6e,f)

Sesarma tetragona: Henderson, 1893: 392 [not *Cancer tetragona* Fabricius, 1798: 341].

Sesarma meinerti: De Man, 1887: 648 (in part); Bürger, 1893: 617; Alcock, 1900: 417; Horikawa, 1940: 30; Lin, 1949: 30; Ortmann, 1894a: 720; 1894b: 56.

Sesarma (Episesarma) meinerti: De Man 1895: 166.

Sesarma (Sesarma) meinerti: Miyake, 1938: 108; Tesch, 1917: 171–174 (in part).

Sesarma (Sarmatium) meinerti: De Man, 1929: Fig 4.

Neosarmatium meinerti; Dai et al., 1986: 496, Fig. 280, pl. 70(3); Dai & Yang, 1991: 543–44, Fig. 280, pl. 70(3); Ng et al., 1997: 145–159, Figs. 1b, 2b,f,k, 3b, 4b, 5b,d, 6b,g, 7e,f, pl. 49 (2); Dahdouh-Guebas et al., 2011: 188.

Material examined. — Holotype: male (38.52 × 33.11 mm) (NMNS-6327-001), Tainan City, Sihcao, Dajhong Temple, Taiwan, coll. J.-H. Lee & W.-J. Wang, 23 Jan.2005. Paratypes: TAIWAN: 1 male (37.10 × 32.15 mm) (MZUF 2516), Pingtung, Kenting, Pao Li stream, coll. H. C. Liu, 14–16 Jun.1995; 1 male (39.40 × 30.40 mm), 1 female (31.40 × 24.70 mm) (ZRC 1997.660) Pingtung County, mouth of Paoli River, coll. H. C. Liu & C. H. Wang, 15 Aug.1996; 1 male

(38.47 × 32.83 mm) (NCHU 13076), Tainan City, Sihcao, Dajhong Temple, coll. J.-H. Lee & W.-J. Wang, 18 Dec.2004; THAILAND: 1 female (ZRC 2000.1899), Phuket, Ao Teng Khen, coll. C. D. Schubart et al., 22 Aug.1999; 1 male (32.90 × 28.83 mm) (ZRC 2001.1083), Phuket, Thailand, coll. Yeo D. C. J. & Y. Cai, 22 Feb.2001; INDONESIA: 1 male (23.47 × 21.91 mm) (MNHN-B31277), aquarium trade; 1 male (34.68 × 28.15 mm) (MNHN-B31276), aquarium trade (possibly Sulawesi).

Diagnosis. — Carapace narrowing to posterior, straight borders with gentle cleft, corresponding to second anterolateral tooth (Fig. 2c). Male chela characterised by presence of a double line of weak tubercles along inner palm surface (Fig. 3g), with palm height 1.70 (± 0.12; n = 6) times maximum chelar width. Descending slope of palm (with parallel prominent ridge) at articulation with dactylus almost transverse (Fig. 3c). Lower margin of chela convex. Dorsal surface of dactylus covered with tubercles until tip (Fig. 4c, g). Male abdomen relatively more quadrate; somite 6 with proximal width 1.13 (± 0.093; n = 6) times length; telson length 1.09 (± 0.11; n = 6) times width (Fig. 5c).

Colour. — The most common colour morph of *N. asiaticum*, new species is the yellow one (mostly in East Asia), whereas specimens from Sri Lanka (S. Cannicci, pers. obs.), Thailand, and Indonesia are characterised by red-orange chelae. Ragionieri et al. (2009) did not record any genetic differences among specimens with different colour morphs.

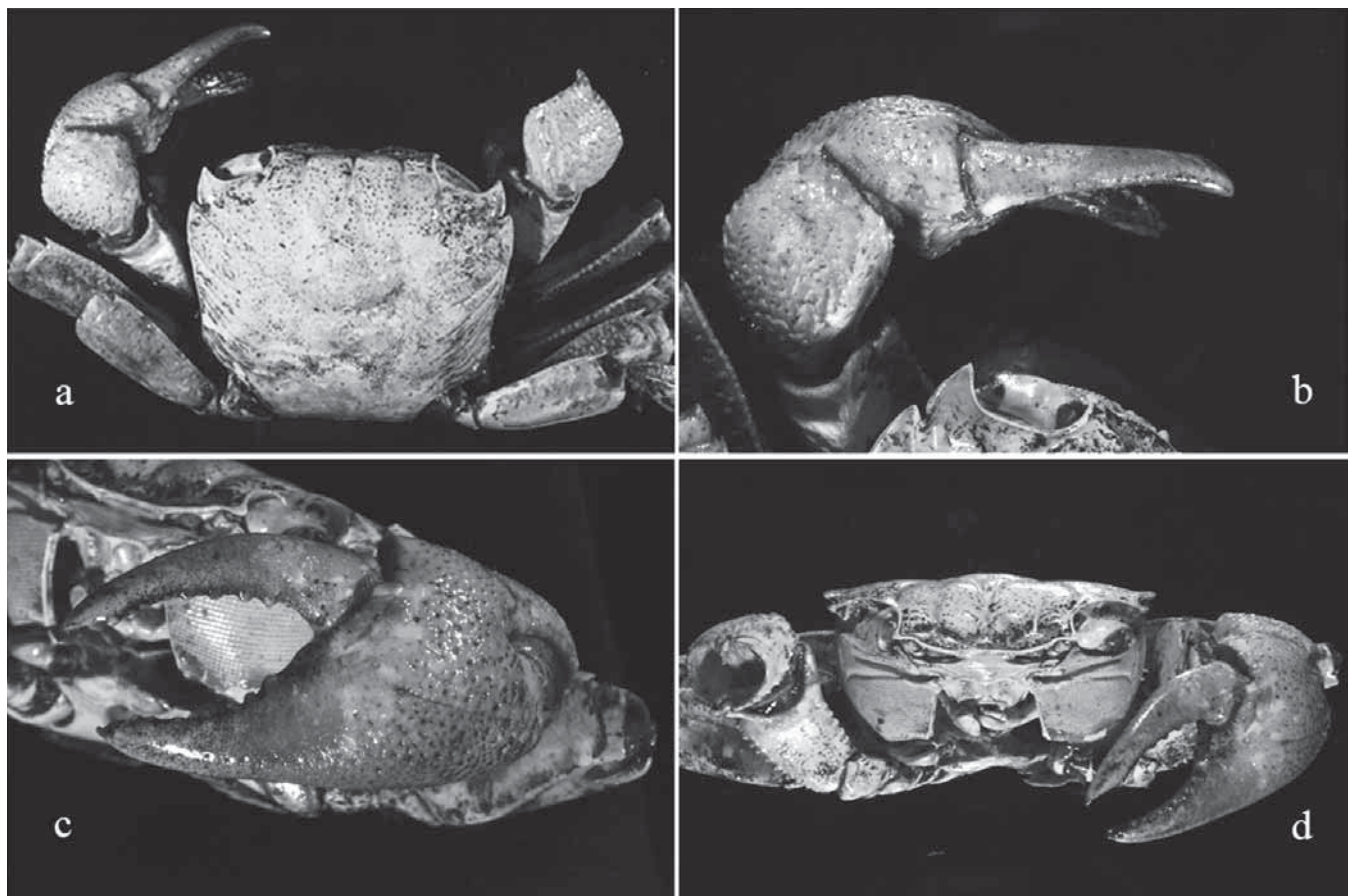


Fig. 7. Lectotype of *Neosarmatium meinerti* (De Man, 1887) (34.00 × 39.30 mm) (MNHN-IU-2011-278), Isle de France, Mauritius: a, dorsal view of carapace; b, dorsal view of left cheliped and dactylus; c, outer and inner surface of right chela; d, frontal view.

Etymology. — *Neosarmatium asiaticum*, new species, is named after its distribution from South Asia (Sri Lanka) to East Asia (Taiwan) including Indonesia.

Habitat. — *Neosarmatium asiaticum*, new species inhabits mangroves and estuaries with grassy banks which are under the influence of tides. In Taiwan, this species occurs sympatrically with its putative sister species *N. fourmanoiri*, and the land crab *Cardisoma carnifex* (Gecarcinidae) (Ng et al., 1997). All specimens examined from Guam were identified as *N. fourmanoiri*.

Ecology. — Until now, there is limited information on the ecology of this species deduced from a paper on the herbivorous feeding habitus of Asiatic sesarmid crabs (Ashton, 2002), but a recent study performed in Sri Lanka (Dahdouh-Guebas et al., 2011) confirmed that the species consumes leaf litter and mangrove propagules.

Distribution. — Its distribution range extends from Sri Lanka through the Andamans, ending in Indonesia and Taiwan (Alcock, 1900; Davie, 1994; Ng et al., 1997).

***Neosarmatium australiense*, new species**

(Figs. 1d, 2d, 3d,h, 4d,h, 5d, 6g,h)

Neosarmatium meinerti: Robertson, 1986: 237; 1988: 235; Camilleri, 1989: 453; Robertson & Daniels, 1989: 191; Davie, 1982: 207 (in part); 1984: 262 (in part); 1994: 35 (in part); 2002 (in part); 2005: 152.

Material examined. — Holotype: male (39.85 × 34.77 mm) (QM-W29085; former MZUF 3659), Darwin, Australia, coll. L. Ragionieri, 13 Aug.2006. Paratypes: AUSTRALIA: 1 male (41.71 × 36.98 mm) (MZUF 2968), Darwin, East Point, coll. L. Ragionieri, 13 Aug.2006; 1 male (39.27 × 29.07 mm) (MZUF 2970), Darwin Mindil Beach, coll. L. Ragionieri, 13 Aug.2006; 4 males (36.50 × 31.39 mm; 35.68 × 30.15 mm; 24.93 × 20.95 mm; 22.18 × 18.65 mm) (MZUF 2971), Darwin, Charles Darwin National Park, coll. L. Ragionieri, 13 Aug.2006; 1 male (35.05 × 30.08 mm) (MZUF 3658), Darwin, University of Darwin, coll. L. Ragionieri, 13 Aug.2006; 2 males (26.50 × 23.03 mm; 27.23 × 23.71 mm) (MZUF 2969), Darwin, University of Darwin, coll. L. Ragionieri, 13 Aug.2006; 1 female yellow morph (QM-W25080), NT: Kakadu N.P.: East Alligator Estuary, coll. P. Davie, Jun.1981.

Diagnosis. — Carapace borders convexly rounded, with gentle cleft corresponding to second anterolateral tooth (Fig. 2d). Male chela characterised by presence of a single line of weak tubercles along inner palm surface (Fig. 3h), with palm height 1.78 (± 0.08; n = 10) times maximum chela width. Descending slope of palm (with parallel prominent ridge) at articulation with dactylus almost transverse (Fig. 3d). Lower margin of chela convex. Dorsal surface of dactylus covered with tubercles until tip (Fig. 4d, h). Male abdomen straight, relatively more quadrate; somite 6 with proximal width 1.14 (± 0.081; n = 10) times length; telson length 1.18 (± 0.07; n = 10) times width (Fig. 5d).

Remarks. — Northern Australia is the only area where the two colour morphs occur sympatrically. Notwithstanding

the coexisting presence of the two colour morphs, the main diagnostic morphological characters of this species are consistent. Ragionieri et al. (2009) did not record any genetic differences between the two colour morphs.

Etymology. — *Neosarmatium australiense*, new species has been named according to its geographic distribution which is the western Australian coast, Kimberly coast, to northern Australia, till the Gulf of Carpentaria.

Habitat. — *Neosarmatium australiense*, new species lives in the rearward mangrove zone which receives water just during the spring tide (Davie, 1994). Usually it is associated with well-developed forests of *Avicennia marina*, but it is not uncommon in *Avicennia marina* parkland.

Ecology. — Currently there is no information about the feeding behaviour or bioturbation activity of this species in Australia. However, there are some studies on *Neosarmatium* which suggest similar feeding behaviour and ecological function of Australian species compared to African ones (Robertson, 1986; 1988; Camilleri, 1989; Robertson & Daniels, 1989).

Distribution. — North-western Australia from Gulf of Carpentaria to the Kimberly Coast.

Key to species of *Neosarmatium* Serène & Soh, 1970

(modified from Davie, 1994; Schubart & Ng, 2002; Rahayu & Davie, 2006)

1. Lateral carapace margins more or less straight, without clear antero- and posterolateral separation 2
- Lateral carapace margins more or less sinuous, antero- and posterolateral margins relatively clearly demarcated 3
2. Carapace rectangular, lateral margins weakly convergent posteriorly; anterolateral margin with distinct tooth behind exorbital angle; dorsal margin of cheliped dactylus with 4 evenly spaced tubercles; chelipeds subequal *N. leave*
- Carapace trapezoidal, lateral margins strongly convergent posteriorly; anterolateral margin without tooth; dorsal margin of cheliped dactylus with 4 large submedian tubercles and row of numerous small granules along proximal margin; chelipeds distinctly unequal *N. tangi*
3. Anterolateral margin entire, or if a low angular tooth behind exorbital angle then not separated by deep notch from rest of margin (exorbital breadth subequal to length of carapace; male unknown) *N. integrum*
- Side of carapace with 1 or 2 anterolateral teeth (second often reduced to angular projection) 4
4. Dactylus of male cheliped with strong chitinous teeth on dorsal margin 5
- Dactylus of male cheliped either without strong chitinous teeth on dorsal margin, or bearing small, sharp, chitinous spinules only 13
5. Dactylus of male cheliped with 2 teeth on dorsal margin ... 6
- Dactylus of male cheliped with 3–5 teeth on dorsal margin 9
6. Male chela with protruding basal shelf on outer face of fixed finger below gape; 1 dactylar tooth placed medially, other subproximally *N. indicum*

- Male chela without protruding basal shelf on outer face of fixed finger below gape 7
- 7. Inner surface of palm without strongly raised, granular, vertical crest (4 or 5 granules may be prominent on large males but are not raised onto a protruding crest); dorsal dactylar tubercles restricted to proximal quarter; distal-most tooth placed dorsal to large subproximal tooth on cutting margin; first tooth placed halfway towards base of dactylus *N. bidentatum*
- Inner surface of palm with a strongly raised, granular, vertical crest; dactylar tubercles otherwise positioned 8
- 8. Distal tooth on upper surface of dactylus placed close to middle; upper surface of palm of cheliped with strong longitudinal rim marking outer edge; carapace 1.15–1.25 times longer than wide *N. malabaricum*
- Distal tooth on upper surface of dactylus placed clearly less than half-way to tip; longitudinal rim present on upper surface of palm of cheliped but not strongly differentiated; carapace 1.25–1.35 times longer than wide *N. punctatum*
- 9. Dactylus of male cheliped with 3 tubercles (one may be smaller, non-chitinous) on dorsal margin 10
- Dactylus of male cheliped with 4 or 5 teeth on dorsal margin *N. rotundifrons*
- 10. Carapace distinctly vaulted, more or less rectangular (1.2–1.28 times wider than long); carapace dorsal surface almost smooth, setae present as very short, small tufts, hardly discernible; somite 6 of male abdomen not markedly elongated (much wider at base than long) 11
- Carapace squarish (less than 1.2 times wider than long); carapace dorsal surface with prominent tufts and rows of setae; somite 6 of male abdomen markedly elongated (length equal to width) 12
- 11. First anterolateral carapace tooth sharply angular, prominent, anteriorly directed, separated from exorbital angle by deep V-shaped notch; dorsal surface of dactylus typically with 3 chitinous teeth on proximal half *N. daviei*
- First anterolateral carapace tooth low, blunt, separated from exorbital angle by broad U-shaped sulcus; dorsal surface of dactylus bearing 3 teeth on proximal third, a pair of closely-set chitinous teeth, and 1 very small, proximal, non-chitinous tooth *N. papuense*
- 12. Dactylar teeth truncate, spaced evenly over proximal half *N. smithi*
- Dactylar teeth acute, set close together over proximal two-fifths *N. trispinosum*
- 13. Dactylus of cheliped smooth, unarmed (walking legs relatively slender, length of merus of third walking leg 2.6–2.7 times width; male first gonopod short, with distal portion not strongly narrowing, and strongly twisted) 14
- Dactylus of cheliped armed with small, sharp, chitinous spinules (length of merus of third walking leg 1.9–2.1 times width; male first gonopod straight and distally curved inward with outer margins convex; apex of gonopod moderately fold towards medial plane of body) 15
- 14. Inner angle of carpus of cheliped unarmed; inner face of palm with vertical row of granules behind gape *N. inermis*
- Inner angle of carpus of cheliped armed with acute granular projection; inner face of palm with a patch of granules ventrally but not extending as a vertical row behind gape *N. spinicarpus*
- 15. Male chela ca. 1.6 to 1.7 times longer than high; chelar dactylus spinules in a single row, vertical granular row on inside of chela relatively strong 16
- Male chela ca. 1.8 times longer than high; lower margin straight behind fixed finger; chelar dactylus spinules numerous, not confined to a single row; vertical granular row on inside of chela relatively low *N. fourmanoiri*

- 16. Carapace borders gently concave in middle section without indication of second anterolateral tooth; chelar dactylus spinules evenly spaced in a single row, extending only to about two-thirds length of dactylus; a single vertical granular row on inside of chela strongly developed 17
- Carapace borders straight or convexly rounded with second anterolateral tooth weakly marked; chelar dactylus spinules in a single row, extending to the tip of dactylus 18
- 17. Male abdomen with male abdominal somite 6 width 1.29 its length, telson length 1.15 times width *N. meinerti*
- Male abdomen with male abdominal somite 6 width 1.35 times length, telson length 1.24 times width *N. africanum*
- 18. Carapace border straight; male chela ca. 1.7 times longer than high; double row of weak granules on inside of chela; male abdomen with abdominal somite 6 width 1.13 times length, telson length 1.1 times width *N. asiaticum*
- Carapace border convexly rounded; male chela ca. 1.6 times longer than high; single row of weak granules on inside of chela; male abdomen with abdominal somite 6 width 1.14 times length, telson length 1.2 times width *N. australiense*

DISCUSSION

Neosarmatium meinerti has long been considered one of the most widespread representatives of its genus. Recently, Ragionieri et al. (2009) reported the presence of four evolutionary significant units within *N. meinerti* sensu lato, differing genetically and morphometrically. According to two mitochondrial genes (16S and Cox1), all the clades within the *N. meinerti* species complex form a monophyletic group, within which three main clades are recognised: one from southern and eastern Asia (Indonesia, Sri Lanka, Taiwan, and Thailand = *N. asiaticum*, new species), one from Australia (north-western Australia; = *N. australiense*, new species), and one from the western Indian Ocean (Pan-African populations). This latter clade can be subdivided into two distinct and reciprocally monophyletic subclades: the East African mainland group (from Somalia to South Africa, including populations of western Madagascar = *N. africanum*, new species), and the western Indian Ocean island group (Seychelles, Aldabra, Rodrigues, and Mauritius = *N. meinerti*). The samples of *N. fourmanoiri*, a well-supported morphological species, occupy a basal position in the mtDNA trees with respect to the clades of the *N. meinerti* species complex. Genetic distances (as percent values of the 16S rRNA and Cox1) of *N. fourmanoiri* to all former populations of *N. meinerti* (here described as species) range between 1.8 and 3.6, whereas distances among the former populations of *N. meinerti* range between 1.6 and 3.2 (Ragionieri et al., 2009: Table 5). In the highly conserved nuclear 28S rRNA gene, *N. fourmanoiri* is even identical to *N. asiaticum* and *N. australiense*, whereas there is a consistent genetic separation to the Pan-African species (*N. meinerti* and *N. africanum*). We therefore consider *N. fourmanoiri* to also belong to the *N. meinerti* species complex, at least from the genetic data.

Time estimates for the divergence set the separation between the Pan-African species (*N. meinerti* and *N. africanum*) and *N. asiaticum* around 3.58 ± 0.42 ma, while the separation between *N. asiaticum* and *N. australiense* is around 3.16 ± 0.42 ma. Similar time estimates were also calculated for the

separation between *N. asiaticum* and *N. fourmanoiri* with 3.58 ± 0.42 ma. Finally, the separation between *N. africanum* and *N. meinerti* is $1.6-1.96 \pm 0.34$ ma (Ragionieri et al., 2009; Ragionieri et al., 2010). In addition, the morphometrics of the four genetically identified clusters supports significant separation between all clades, with the strongest differentiation by *N. asiaticum*, which appears to be well separated from the other groups (Ragionieri et al., 2009). On the other hand, there is no clear difference in pairwise comparisons between *N. fourmanoiri* and the different groups of *N. meinerti*.

The main morphological character able to discriminate among the species of the *N. meinerti* complex is the presence of a single prominent row of tubercles (*N. meinerti* and *N. africanum*), a double row of weak tubercles (*N. asiaticum*) or a single row of weak tubercles (*N. australiense*) on the inner palm of the male chela. The discrimination between *N. africanum* and *N. meinerti* is mostly based on the ratio of the proximal width of the adult sixth abdominal somite to the width of the telson as well as the ratio between the telson length and width.

The morphological and genetic (mtDNA) evidences reported here and in Ragionieri et al. (2009) support an early split of a common ancestor to the *N. fourmanoiri* and *N. meinerti* species complex s. str. Almost simultaneously, the common ancestor of the *N. meinerti* complex s. str. radiated into three geographic groups, which later became four with the subsequent separation of *N. meinerti* and *N. africanum*. An alternative hypothesis based on nuclear DNA phylogeny, suggests the differentiation of a common ancestor of the *N. meinerti* species complex s. l. (including *N. fourmanoiri*) within the Indian Ocean into a western and eastern form, the former subsequently splitting into three Asian taxa, of which *N. fourmanoiri* is one, with a second later splitting into the two African species (Ragionieri et al., 2009). Independent of the scenario, we provide enough evidence for several evolutionary significant units previously included within the species *N. meinerti* and herewith confer full species status to all of them.

ACKNOWLEDGEMENTS

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