

## Description of *Metopograpsus cannicci*, new species, a pseudocryptic crab species from East Africa and the Western Indian Ocean (Decapoda: Brachyura: Grapsidae)

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**Abstract.** The Indo-Pacific genus *Metopograpsus* H. Milne Edwards, 1853, of the family Grapsidae (Decapoda: Brachyura: Thoracotremata) comprises six recognised species of intertidal crabs from sheltered rocky shores and mangrove forests. Recent molecular evidences suggest that *Metopograpsus thukuhar* (Owen, 1839) and *M. quadridentatus* Stimpson, 1858, could represent species complexes, each consisting of two species. Here we deal with *M. thukuhar* and its genetic separation into two clusters, one with all East African specimens, including samples from the Red Sea, Iran, and the Seychelles, and the other one comprising all the known specimens from Southeast Asia and Pacific islands. In this paper, we present new results of an in-depth morphological investigation of samples assigned to *M. thukuhar*, designate a neotype, and confirm the presence of an undescribed species by adding support from nuclear DNA comparisons. With respect to *M. thukuhar*, which was originally described from Hawaii, the new species corresponds to samples from the western Indian Ocean. The distinguishing morphological characters include differences in the shape of the first male gonopod. While the observed differences are relatively subtle, they nevertheless support the differentiation revealed by molecular findings. Therefore, we refer to the new species as a pseudocryptic taxon and name it *Metopograpsus cannicci*. The description of this new taxon elevates the species number within *Metopograpsus* to seven and adds another record to the list of newly described crabs from the Western Indian Ocean mangroves.

**Key words.** *Metopograpsus*, taxonomy, mitochondrial DNA, nuclear marker, pseudocryptic species

### INTRODUCTION

At present, the genus *Metopograpsus* H. Milne Edwards, 1853 (belonging to Grapsidae MacLeay, 1838), consists of six recognised species, here listed in chronological order: *M. messor* (Forskål, 1775); *M. thukuhar* (Owen, 1839) (type species, selected by Holthuis, 1977); *M. oceanicus* (Hombron & Jacquinot, 1846 [in Hombron & Jacquinot, 1842–1854]); *M. latifrons* (White, 1847); *M. quadridentatus* Stimpson, 1858; and *M. frontalis* Miers, 1880. The lateral carapace margins of *M. oceanicus* and *M. quadridentatus* show a tooth behind the external orbital angles, while the other four species have entire lateral carapace margins (Banerjee, 1960). The males of the latter four species are characterised

by species-specific first gonopods, which allow species identification of adult males (Tweedie, 1949).

In the past, the subdivision of the genus has been questioned by Tesch (1918), due to the apparent inconspicuous diagnostic morphological differences among species, particularly concerning *M. thukuhar* and *M. messor* (Ortmann, 1894: 702). However, their taxonomic separation was later supported by Tweedie (1949) and Banerjee (1960: 187, 188), based on newly recognised morphological characters. Recently, Fratini et al. (2018) published a molecular phylogenetic investigation which tested the taxonomic distinction of the six species of *Metopograpsus* across their respective distribution ranges and depicted the phylogeographic patterns within the widely distributed species. As a result, these authors indeed validated the monophyly of the six species of *Metopograpsus* in line with the partial analyses of Schubart (2011) and Ip et al. (2015). At the same time, this study recorded a high intraspecific mitochondrial genetic variation and possible phylogeographic patterns within the species *M. thukuhar* and *M. quadridentatus*. Consequently, the authors suggested the occurrence of distinct evolutionarily significant units within both species, possibly corresponding to undescribed species of *Metopograpsus* (see Fratini et al., 2018). This concerns the separation of *M. thukuhar* into two clusters, one including all the East African specimens together with samples from the Red Sea and Seychelles, and the other one comprising all the specimens from Southeast Asia and Pacific

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Table 1. Extraction number and origin of *Metopograpsus* specimens used for the reconstruction of a genotype network of *M. thukuhar* and *M. cannicci*, new species, based on the nuclear 28S locus (ZSMA, Zoologische Staatssammlung, Munich).

No.	Species and extraction number	Origin	Collection number
1	<i>M. cannicci</i> , new species T520-1	Egypt, Nabq	ZSMA2019408
2	<i>M. cannicci</i> , new species T546-4	Iran, Bandar Abbas	ZSMA2019410
3	<i>M. cannicci</i> , new species T546-6	Iran, Bandar Abbas	ZSMA2019410
4	<i>M. cannicci</i> , new species T546-1	Iran, Bandar Abbas	ZSMA2019410
5	<i>M. thukuhar</i> S107	Malaysia, Sabah	ZRC 2000.1644
6	<i>M. thukuhar</i> R43-9	Hawaii, Oahu Kewalo	ZRC 2000.0564
7	<i>M. thukuhar</i> R43-13	Guam, Pago Beach	ZRC 2001.0730

islands (Fratini et al., 2018). The geographic distribution of *M. quadridentatus* is less widespread, but samples from Singapore could still be separated from those of the South China Sea (see Fratini et al., 2018).

The occurrence of *M. thukuhar* is often associated with mangrove swamps, and this species is able to climb mangrove roots (Fratini et al., 2000; 2005). It is an opportunistic feeder with good predatory abilities (Fratini et al., 2000) and is presently known from the Red Sea and East African coast (north of Mozambique) to Japan, Taiwan, China, Indonesia, Australia, New Caledonia, Solomon Islands, Vanuatu, Tahiti, and to the Hawaiian Islands (e.g., Crosnier, 1965; Sakai, 1976; Takeda & Nunomura, 1976; Dai & Yang, 1991).

The present study builds on the results of Fratini et al. (2018) and performs an in-depth morphological investigation of the crabs identified as *M. thukuhar* from the Red Sea and East Africa to the Pacific Ocean, in particular from the type locality in Hawaii (Oahu; Owen, 1839), to verify the possible existence of two distinct species. In addition, sequences of the nuclear genome are compared for the first time within this genus in order to substantiate previous differences encountered among mitochondrial DNA sequences.

## MATERIAL AND METHODS

**Morphological analysis – material examined.** In total, 75 specimens identified as *Metopograpsus thukuhar* were examined, including the synonymised taxa (*M. eydouxii* H. Milne Edwards, 1853; *M. intermedius* H. Milne Edwards, 1853; *Pachygrapsus parallelus* Randall, 1840). When possible, these samples corresponded to those genetically analysed in Fratini et al. (2018). A total overlapping between the material analysed for this paper and that analysed by Fratini et al. (2018), however, was not possible mainly because genetic analyses were also based on sequences downloaded from GenBank. The specimens belong to the following museum collections: Natural History Museum of the University of Florence (Italy) (MZUF); Muséum national d'Histoire naturelle, Paris (MNHN); Zoological Reference

Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC); Natural History Museum, London (NHM); Academy of Natural Sciences of Drexel University, Philadelphia (ANSP).

Photographs of the whole bodies and details were taken with a digital camera (Nikon D500 with micro-Nikkor 60 mm f. 2.8 lens). The specimens were examined and described using a stereomicroscope (Wild M7) and details of the male gonopods and female gonopores were examined with a photographic microscope (Leica M205 C). The type specimens of the new species are deposited in the Zoology Section of the Natural History Museum of the University of Florence (MZUF) (holotype and paratypes) and in the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (ZRC) (paratypes). The designated neotype of *M. thukuhar* also forms part of the collection of ZRC. The carapace width and length in millimetres are provided with the description of the examined material. The following abbreviations are used in the text: CW, carapace width; G1, male first gonopods.

## Molecular analysis – construction of genotype network.

The concept of genotype networks is often used to visualise genealogical relationships among and within species (Clement et al., 2000). For this purpose, a network of seven specimens covering the former range of *M. thukuhar* was created based on sequences of the 28S gene locus. As a first step, genomic DNA was isolated from muscle tissue of one walking leg of each animal with the Puregene method from Gentra Systems (Minneapolis, USA). Afterwards, polymerase chain reactions (PCR) took place targeting a relatively long (>1200 basepairs) DNA region of the nuclear 28S rRNA gene. This was achieved by combining the results of two primer combinations: 28L1 (5'-CGG AGG AAA AGA AAC CAA CAG-3') with 28D2H (5'-TGA CTC GCA CAC ATG TTA GA-3') (Mock & Schubart, in preparation) and 28D2L\* (5'-TAC CGT GAG GGA AAG TTG AAA AG-3') with 28H2 (5'-CGA TTT GCA CGT CAG AAT TGC T-3') (Thiercelin & Schubart, 2014).

Successfully amplified PCR products were outsourced to Macrogen Europe (The Netherlands) for sequencing. Aligned sequences of a length of 1286 basepairs (bp) were converted into a Nexus file that was subsequently used to infer the relationships among the individuals as a genotype TCS network with the software PopART v1.7 (Leigh & Bryant, 2015). This network reflects genetic distances as single mutation steps along the 1286 bp of the nuclear 28S gene among seven specimens, of which five belong to *M. cannicci*, new species (three from Iran and one from Egypt) and three to *M. thukuhar* (one each from Malaysia, Hawaii, and Guam) (Table 1).

## RESULTS

### Systematic Account

#### Order Decapoda Latreille, 1802

#### Family Grapsidae MacLeay, 1838

#### *Metopograpsus* H. Milne Edwards, 1853

#### *Metopograpsus cannicci*, new species

(Figs. 1A, 2A, 3A, 4A, 5A, 6)

**Material examined. Types.** Holotype. 1 male (34.5 × 28.1 mm) (MZUF 4865), Egypt: Ras Mohammad, mangrove channel, colls. S. Fratini, G. Innocenti, S. Barbaresi & A. Conti, 12 October 2004. Paratypes. 1 male (33.6 × 27.4 mm) (MZUF 5010), Egypt: Nabq, El Arwashie, colls. S. Fratini, G. Innocenti, S. Barbaresi & A. Conti, 15 October 2004; 1 male (27.6 × 21.5 mm) (ZRC 2019.1350), Nabq, El Monqata, colls. S. Fratini, G. Innocenti, S. Barbaresi & A. Conti, 13 October 2004; 1 male (24.4 × 19.2 mm) (MZUF 5007), same collection data as ZRC 2019.1350; 1 female (24.4 × 19.4 mm) (ZRC 2019.1351), same collection data as ZRC 2019.1350; 1 female (18.8 × 14.3 mm) (MZUF 5011), same collection data as ZRC 2019.1350.

**Others. Egypt:** 1 male (24.6 × 19.4 mm), 1 female (21.8 × 16.6 mm) (MZUF 5012), Egypt: Nabq, El Arwashie, colls. S. Fratini, G. Innocenti, S. Barbaresi & A. Conti, 15 October 2004; 1 male (18.9 × 14.0 mm) (MZUF 5013), Ras Mohammad, Mangrove channel, colls. S. Fratini, G. Innocenti, S. Barbaresi & A. Conti, 14 October 2004. **Somalia:** 1 male (23.3 × 17.8 mm), 4 females (27.4 × 20.8 mm, 27.9 × 22.0 mm, 27.8 × 21.0 mm, 23.0 × 17.9 mm) (MZUF 4935), Gesira, mangroves, coll. M. Vannini, 14 October 1981; 3 males (25.9 × 20.1 mm, 22.2 × 16.9 mm, 21.1 × 16.5 mm) (MZUF 647), Gesira, coll. M. Vannini, December 1976. **Kenya:** 2 males (24.9 × 19.0 mm, 25.0 × 19.1 mm), 1 female (25.4 × 19.1 mm) (MZUF 4940), Mida Creek, Dabaso, coll. S. Cannicci, December 1997; 1 male (22.1 × 17.8 mm), 1 female (25.5 × 19.6 mm) (MZUF 4943), Mida Creek, Sita, coll. M. Vannini, October 1988; 1 female (27.1 × 21.0 mm) (MZUF 4939), Mida Creek, coll. M. Vannini, October 1990; 1 female (25.2 × 19.2 mm) (MZUF 3654), Mida Creek, Sita, coll. M. Vannini, July 2000; 1 male

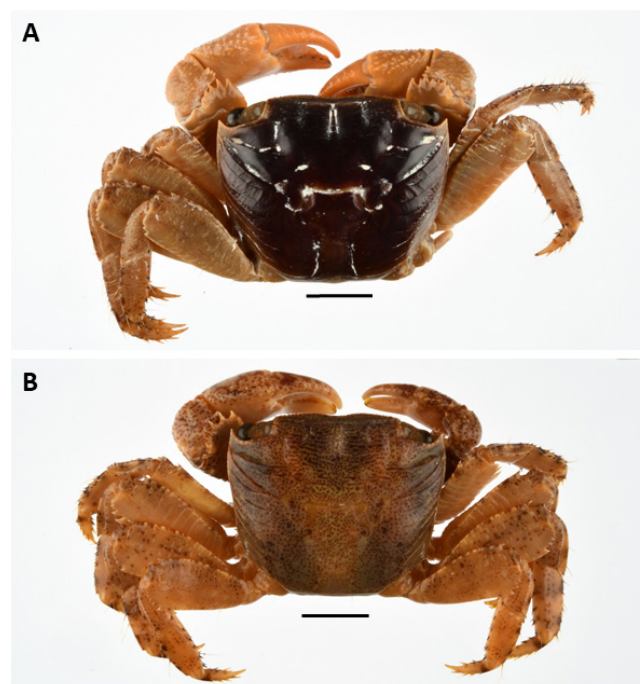


Fig. 1. A, *Metopograpsus cannicci*, new species, holotype, male, Egypt: Ras Mohammad (MZUF 4865); B, *Metopograpsus thukuhar* (Owen, 1839), neotype, male, Hawaii: Oahu, Kewalo, Ala Moana area, Waikiki (ZRC 2020.0219). Scale bar = 10 mm. Photographs by S. Bambi.

(25.8 × 20.3 mm) (MZUF 4945), Mida Creek, Dabaso, coll. M. Vannini, 15 October 1990; 1 male (22.0 × 16.9 mm) (MZUF 2544), Mida Creek, coll. V. Vigiani, September 2000. **Tanzania:** 2 males (20.8 × 15.5 mm, 18.7 × 13.9 mm) (MZUF 5003), Pangane, Muchojo, Macomia, mangrove swamp, coll. F. Tarducci, 26 August 1995. **Mozambique:** 2 males (17.3 × 13.3 mm, 15.4 × 12.2 mm), 1 female (19.5 × 14.8 mm) (MZUF 2508, one chela for genetic analysis as MZUF 4866), Mozambique: Inhaca I., Saco da Inhaca, colls. S. Cannicci & F. Porri, July 1997. **Seychelles:** 1 male (16.9 × 13.3 mm) (MZUF 2980), Seychelles: Mahé, coll. S. Fratini, December 2005; 2 males (25.6 × 19.5 mm, 20.0 × 15.9 mm) (MZUF 2934), Mahé, Port Launay, coll. S. Fratini, December 2005; 1 female (17.0 × 13.1 mm) (MZUF 2937), Mahé, Port Launay, coll. S. Fratini, December 2005. **Rodrigues I.:** 1 male (22.0 × 17.3 mm), 1 female (19.0 × 14.4 mm) (MZUF 4934), Baie Topaze, coll. M. Vannini, 9 July 1989; 1 male (19.1 × 15.2 mm), 2 females (28.0 × 21.5 mm, 23.6 × 18.0 mm) (MZUF 5004), Baie au Huitres, coll. M. Vannini, 8 July 1989. **Mauritius I.:** 2 females (24.5 × 18.8 mm, 18.7 × 13.8 mm) (MZUF 5005), Melville, coll. M. Vannini, 1 July 1989. **Aldabra:** 2 males (23.3 × 18.9 mm, 25.6 × 19.8 mm), 1 female (24.2 × 17.8 mm) (MZUF 5006), lagoon behind the headquarter, coll. M. Vannini, March 1979. **Iran:** 1 male (30.8 × 25.5 mm), 1 female (30.2 × 24.4 mm) (MZUF 5014), Bandar Abbas, behind the airport, coll. A. Shahdadi, 10 April 2013.

**Comparative material examined. Metopograpsus thukuhar (Owen, 1839):** Neotype (here designated), male (32.5 × 27.1 mm) (ZRC 2020.0219; Figs. 1B, 2B, 3B, 4B, 5B), Hawaii: Oahu, Kewalo, on sea wall, surf zone, Ala Moana area,

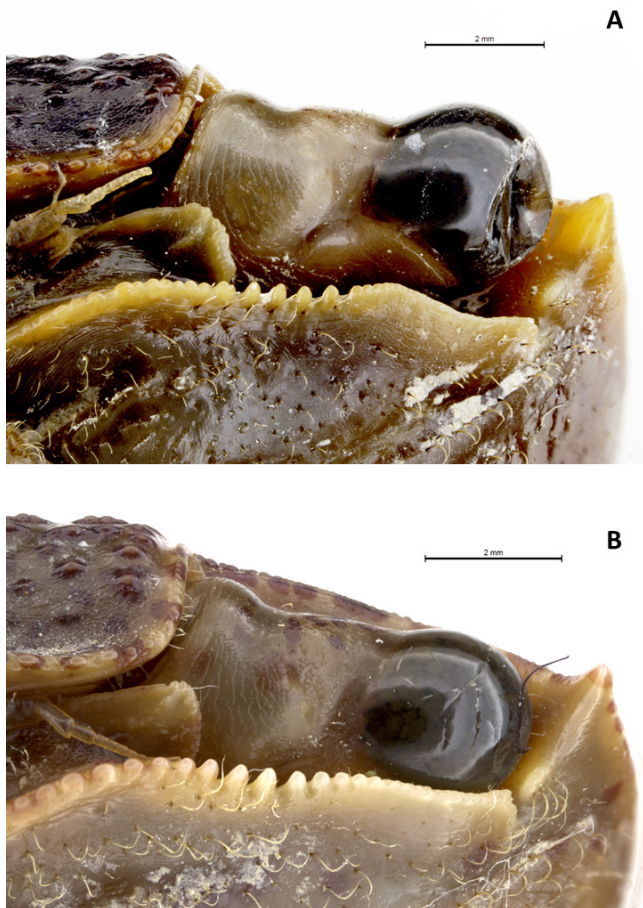


Fig. 2. A, *Metopograpsus cannicci*, new species, holotype, male (MZUF 4865); B, *Metopograpsus thukuhar* (Owen, 1839), neotype, male (ZRC 2020.0219), detail of the suborbital tooth. Photographs by S. Bambi.

Wakiki, coll. P.K.L. Ng & S.H. Tan, 22 January 2000; 3 males (21.3 × 17.0 mm, 20.5 × 16.4 mm, 17.5 × 13.7 mm), 1 female (28.6 × 23.6 mm) (ZRC 2000.0405), Hawaii: Oahu, Kewalo, on sea wall, surf zone, Ala Moana area, Waikiki, coll. P.K.L. Ng & S.H. Tan, 22 January 2000; 1 male (20.3 × 16.4 mm) (NHM 1948.5.3.1), Sandwich Islands (= Hawaii): further collection data unknown; 1 male (22.1 × 18.5 mm), 2 females (21.8 × 17.6 mm; 20.5 × 16.9 mm) (NHM 1883.22), presented by the Hawaiian Government from the International Fisheries Exposition, 1883; 2 males (27.6 × 22.5 mm; 18.0 × 14.2 mm), 3 females (ovigerous: 22.6 × 17.9 mm; 17.2 × 13.1 mm; 13.4 × 10.8 mm) (NHM 1884.31), Hilo, coll. HMS Challenger; 1 female (ovigerous: 22.6 × 16.7 mm) (NHM not registered), Samoa: Upolu I., coll. Buxton & Hopkins, further collection data unknown; 1 male (22.0 × 17.9 mm) (NHM not registered), collection data unknown; 2 males (17.6 × 13.1 mm; 13.8 × 10.2 mm), 2 females (ovigerous: 19.4 × 15.00 mm; 15.2 × 11.9 mm) (NHM 1884.31), French Polynesia: Tahiti, near the reefs, coll. HMS Challenger, collection data unknown; 2 males (22.2 × 17.5 mm; 21.6 × 17.8 mm), 2 females (ovigerous: 23.0 × 18.2 mm; ovigerous: 15.1 × 10.9 mm; 12.5 × 9.5 mm) (NHM 1884.31), Tahiti, Papeete, coll. HMS Challenger, further collection data unknown; 1 male (13.5 × 10.0 mm) (NHM 1884.31), Fiji: Kandavu, coll. HMS Challenger; 1 male (18.5 × 15.2 mm) (MNHN-IU-2011-9039), Marquesas Islands:

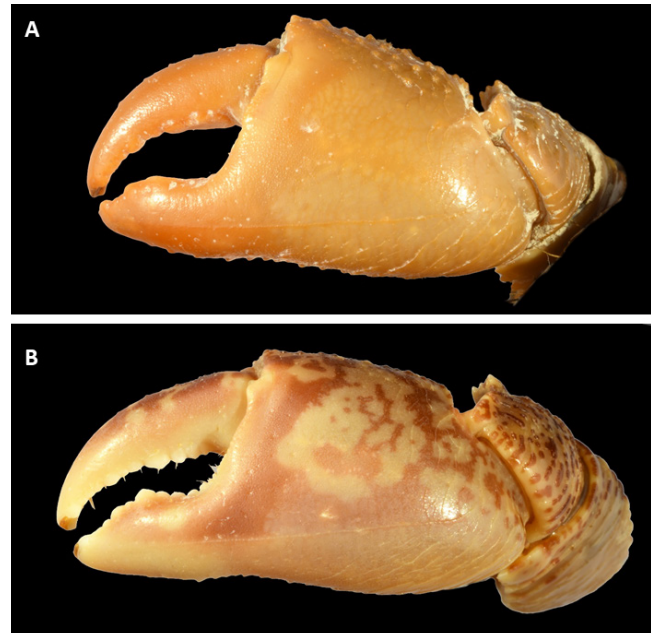


Fig. 3. A, left cheliped of *Metopograpsus cannicci*, new species, holotype, male (MZUF 4865); B, left cheliped of *Metopograpsus thukuhar* (Owen, 1839), neotype, male (ZRC 2020.0219). Photographs by S. Bambi.

Nuku Hiva, Hakatea Cove, 8°56'6"S, 140°10'6.006"E, coll. Agence des Aires Marines Protégées, 28 January 2012. ***Metopograpsus eydouxi* H. Milne Edwards, 1853:** 1 male (20.2 × 15.2 mm) (MNHN-IU-2000-3547; Fig. 6), Sandwich Islands (= Hawaii), designated as lectotype by Ng et al. (2019: 114); 1 male (25.1 × 19.6 mm), 1 female (21.0 × 16.2 mm) (MNHN-IU-2000-3551, not types (Ng et al., 2019: 114)), Sandwich Islands (= Hawaii). ***Metopograpsus intermedius* H. Milne Edwards, 1853:** 1 male (23.1 × 16.8 mm) (MNHN-IU-2014-11210), unknown locality, designated as lectotype by Tweedie (1954: 128). ***Pachygrapsus parallelus* Randall, 1840:** Syntypes: 2 males (32.7 × 28.0 mm, 11.1 × 8.0 mm), 3 females (26.2 × 22.0 mm, 23.1 × 18.1 mm, 22.0 × 15.0 mm) (ANSP CA3545), Sandwich Islands (= Hawaii), colls. T. Nuttall & J.K. Townsend, before 1839.

**Diagnosis.** Carapace flat, quadrangular, slightly broader than long; branchial groove distinct, branchial region with distinct oblique ridges, urogastric grooves distinct, cardiac and intestinal regions smooth, without any ridge or tubercle. Lateral margins of the carapace entire. Front broad, more than half of greatest width of carapace, deflexed with rugose surface and crenulated free margin, 4 depressed post-frontal lobes along line of frontal deflexion. Suborbital tooth triangular, keeled from tip to base. Exposed surface of base of antenna densely pubescent. Chelipeds subequal, without obvious handedness, fingers stout with spooned tip. Ambulatory legs compressed and with broad merus, dorsal and ventral ridges of 3 distal joints bearing bristles, dactylus with spines. Third and fourth pereopods with pubescence on lower border of base and ischium. Male pleon with 6 distinct segments, basal one as broad as thoracic sternum, somite 6 rectangular, telson triangular. G1 slender, straight, with twisted ridge along longitudinal axis, apical corneous process elongate.

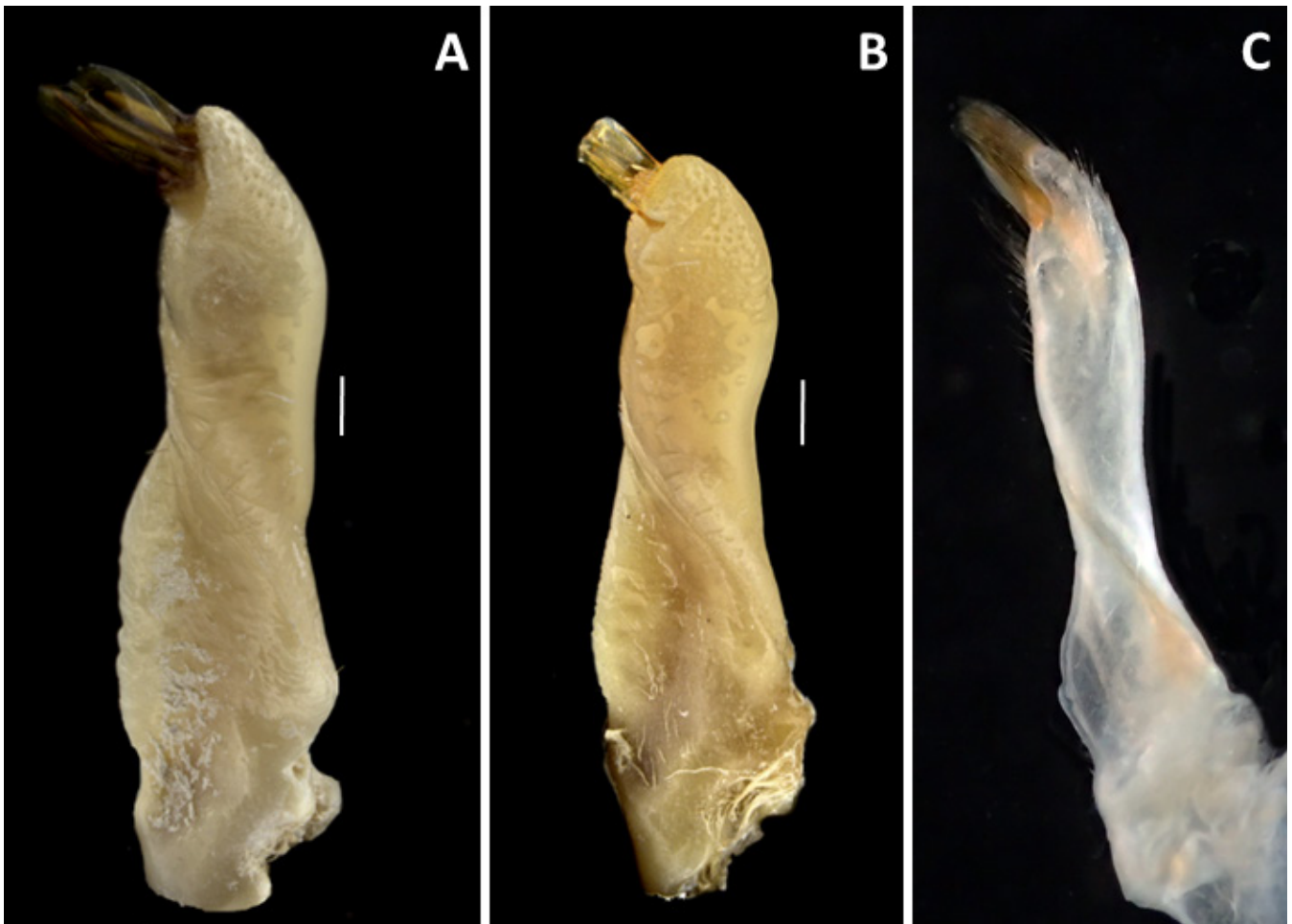


Fig. 4. First left pleopod (G1), dorsal view. A, *Metopograpsus cannicci*, new species, holotype, male (MZUF 4865); B, *Metopograpsus thukuhar* (Owen, 1839), neotype, male (ZRC 2020.0219); C, *Metopograpsus intermedius* H. Milne Edwards, 1853, lectotype, male (MNHN-IU-2014-11210). Scale bar = 0.5 mm. Photographs by S. Bambi (A, B) and L. Corbari (C).

**Description.** Small- to medium-sized crab (maximum observed CW 34.5 mm). Carapace almost quadrangular, slightly broader than long, greatest width just behind exorbital angles; surface smooth, with transverse ridges lined in rows on branchial region, urogastric grooves evident (Fig. 1A). Front  $0.6 (\pm 0.02)$  times carapace width (N=6), quite deflexed, slightly concave medially. Post-frontal lobes evident, median ones slightly smaller than lateral ones in width and separated by furrow. Dorsal carapace regions moderately indicated, hepatic region demarcated, cardiac region separated from urogastric region, lateral branchial ridges evident, mid upper orbital border eyelet-shaped, lower orbital border granulate, anterolateral margin with sharp exorbital tooth, lateral margin weakly concave. Suborbital tooth triangular, distally crenulated, with central keel (Fig. 2A).

Male chelipeds subequal (51% with right enlarged; 49% with left enlarged, N=10) (Fig. 3A). Chela large (palm length  $0.68 \pm 0.05$  times CW, N=3 males), robust (length/width ratio =  $0.53 \pm 0.02$ , N=3 males). Merus with grooves on dorsal border and with spines on inner (3 or 4) and upper (4 or 5) borders; ventral border crenulate; inner upper border of carpus with 3 small spines. Upper surface of palm in males with 3 or 4 transverse granulated lines; outer surface of palm smooth, along ventral border a hardly evident ridge crossing

several (6 or 7) transverse ridges, ventral border coarsely granular until outer surface of fixed finger, centrally gently hollowed; inner surface of palm coarsely smooth except area facing carpus; length of cutting edge of fixed finger  $0.39 \pm 0.04$  (N=3 males) times maximum propodus length. Dactylus relatively stout, slightly curving in dorsal view, length  $0.57 \pm 0.05$  (N=3) times maximum propodus length. Fingers with chitinous spoon-shaped tips, with gape when closed. Cutting edge of both fingers with series of inconspicuous teeth. Female chelipeds smaller than in males, subequal as in males, ratio of palm length to carapace width ca. 0.60 in female paratype (MZUF 5008). Merus and carpus as in males, upper surface of palm with 3 or 4 transverse and sparse granules, inferior border of palm with line along its length and 4 lines of not relevant transverse ridges, both fingers with chitinous spoon-shaped tips.

Ambulatory legs relatively long, with broad merus (length/width ratio =  $0.46 \pm 0.01$ , N=11 males), flattened; fourth and fifth pereopods longest (Fig. 1A). Edges of last three joints bearing bristles, dactylus with spines. Lower border of third and fourth base and ischium pubescent.

Male pleon triangular; telson triangular and slightly longer than somite 6. Somite 6,  $1.60 \pm 0.04$  (N=3) times wider than



Fig. 5. Female gonopores. A, *Metopograpsus cannicci*, new species, paratype (MZUF 5008); B, *Metopograpsus thukuhar* (ZRC 2000.0405).

long. Somites 4 and 5 trapezoidal. Somite 3 widest, laterally convex. Somite 2 following lateral edges. G1 slender, straight, with twisted ridge along its axis, distal part slender, apical corneous process elongate (Fig. 4A). Female pleon fringed with long setae, broad, evenly rounded, in adults laterally touching coxae of walking legs; telson half-moon shaped, ca. 0.4 times wider than long. Vulva in depression at the border of sternite 6 with sternite 5, operculum on inner part with an evident trapezoidal sternal vulvar cover in adult females (Fig. 5A).

**Colour.** In life, crabs are mottled brown-green and cream, and distinctly glossy (Fig. 7). Crabs with CW > 24 mm are purple on the outer face of the chelar palm. Preserved specimens have brown spots, still visible on a creamy patterned carapace, cheliped cream-coloured with brownish-orange tips.

**Etymology.** The new species is dedicated to our colleague and friend, Dr Stefano Cannicci, who devoted his research career to study mangrove fauna, especially of East Africa; the name here is used as a noun in apposition.

**Remarks.** The description of *M. cannicci*, new species, is quite challenging as, at first sight, all the examined specimens from the Red Sea to the central Pacific Ocean are morphologically very similar. However, the G1 of *M. cannicci*, new species, is slightly different in shape from that of *M. thukuhar*, being more slender and less inflated at its distal end, with a more acute hump (Fig. 4A). Moreover,

the general shape of the G1 in *M. thukuhar* is distally more swollen, with a rounded hump and a shorter corneous tip (Fig. 4B). However, only fully adult specimens can be distinguished by their G1, as in males with CW < 23 mm such differences are not always marked (see Fig. 4C). Adult females of *M. cannicci*, new species, have a trapezoidal sternal vulvar cover (Fig. 5A), while in female *M. thukuhar* the cover is wider and higher (Fig. 5B). The live colouration is also very variable between and within both species, thus not helping in possible identification. It is hypothesised that it probably depends upon the background on which the crabs thrive.

Owen's (1839) original description of *Grapsus thukuhar*, based on a single specimen (without sex specification) collected from Oahu (Hawaii), provided diagnostic characters that are very common for all species of *Metopograpsus*: “*Grapsus clypei lateribus striatis; humeris, ulnis, carpisque interne spinosis; femoribus supra et subtus spinosis [...]* Color, fulvus brunneo-punctatissimus. Carapace quadrilateral, broadest in front; the sides slightly converging to the posterior angles, which are truncated. Rostrum very broad, inclined, supporting four prominences, of which the laterals are the largest. No teeth at the sides of the shell, but the anterior angles produced and acute; oblique lines over the branchial regions. Chelae equal, short, obtuse; humeri with two spines; carpi with one or two spines internally; manus slightly tuberculated at the upper part, the remainder smooth and mottled with purple. Claws compressed, the femora with two or three spines at their apices, the other joints hairy, the terminal ones armed with short brown spines, sprinkled over with minute brown spots, like the skin of *Sepia officinalis*” (Owen, 1839: 80). Unfortunately, the holotype was destroyed during the 1941 bombing of the Royal College of Surgeons (London, UK), where it was deposited (Sarah Pearson, personal communication).

Banerjee (1960: 174) reported the following diagnostic characters for *M. thukuhar*: “lateral margins of the carapace scarcely convergent backwards, upper surface of the base of the antenna densely pubescent, 6th segment of the male abdomen equal to or slightly longer than fifth, compressed finger-shaped chitinous projection present at the top of the male pleopod”. He also mentioned a blunt sub-orbital tooth, not keeled from tip to base, but this character was found to be extremely variable in the examined specimens, finding in many of them a central keel, as already pointed out by Vannini & Valmori (1981) in their remarks on specimens of *M. thukuhar* from Somalia. The specimens from Hawaii have an evident keel in the suborbital tooth too (Fig. 2B).

The male specimen from ZRC (Figs. 1B, 2B, 3B, 4B, 5B) is very similar to the specimen figured by Owen (1839: pl. 24, figs. 3, 3a), and it was collected from the same locality. Therefore, we decided to designate it as the neotype of *M. thukuhar* to stabilise its taxonomy, and to serve as the primary point for comparison with *M. cannicci*, new species.

Three other names have been treated as synonyms of *Metopograpsus thukuhar* (Owen) by previous workers (e.g.,

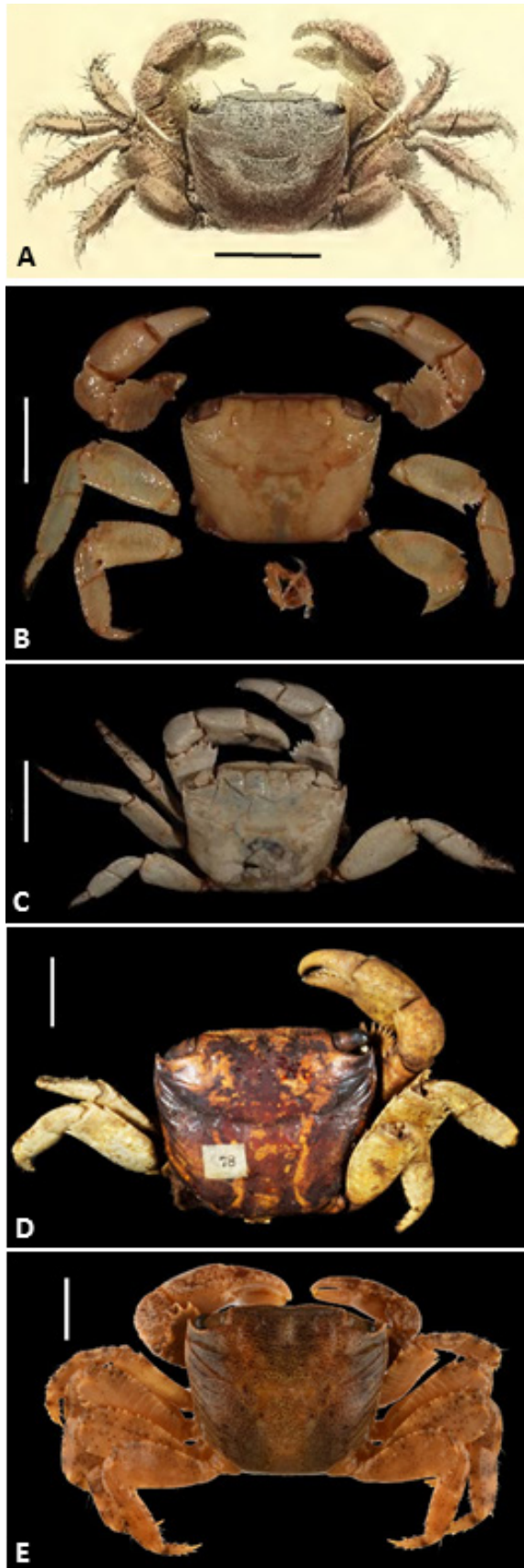


Fig. 6. A, *Grapsus thukuhar* Owen, 1839, original plate; B, *Metopograpsus intermedius* H. Milne Edwards, 1853, lectotype, male (MNHN-IU-2014-11210); C, *Metopograpsus eydouxi* H. Milne Edwards, 1853, lectotype, male (MNHN-IU-2000-3547); D, *Pachygrapsus parallelus* Randall, 1840, syntype, male (ANSP CA3545); E, *Metopograpsus thukuhar* (Owen, 1839), neotype, male (ZRC 2020.0219). Black or white bar = 10 mm.



Fig. 7. *Metopograpsus cannicci*, new species, live male from Mida Creek mangrove forest (Kenya), July 2004, specimen not collected. Photograph by S. Cannicci.

Tweedie, 1949, 1954; Banerjee, 1960; Davie, 2002; Ng et al., 2008), viz. *Metopograpsus eydouxi* H. Milne Edwards, 1853 (type locality: Hawaii), *Metopograpsus intermedius* H. Milne Edwards, 1853 (type locality: unknown), and *Pachygrapsus parallelus* Randall, 1840 (type locality: Hawaii), and their type material have also been examined in this work. The description of *Pachygrapsus parallelus* by Randall (1840) is based on the external shape of the carapace, claws and legs with no mention of gonopods. The lectotype of *M. eydouxi* was selected and figured recently by Ng et al. (2019: 114, fig. 6F). The G1s of *M. eydouxi* and *P. parallelus* could not be observed, however, as the specimens have been dried and are very fragile. As for *Metopograpsus intermedius* H. Milne Edwards, 1853, Ng et al. (2019: 115, fig. 7B) reconstructed the intricate history of the type specimen as follows: Tweedie (1949) indicated that *Metopograpsus intermedius* H. Milne Edwards, 1853, was represented in the collection of the MNHN by two syntypes belonging to two distinct species; the smaller of them being a *M. thukuhar*, whereas the larger agreed with the description of *M. gracilipes* De Man, 1891, according to the examination of the G1 sketches by Isabella Gordon. Tweedie (1954) designated the smaller syntype as the lectotype of *M. intermedius*, in order to define *M. intermedius* as a junior synonym of *M. thukuhar* and to establish *M. gracilipes* (presently a synonym of *M. frontalis* Miers, 1880) as the valid name for the species represented by the larger co-type of *M. intermedius*. Figure 6 shows the neotype of *M. thukuhar* and compares it with Owen's figure of *M. thukuhar*, and photographs of the types of *M. intermedius*, *M. eydouxi*, and *P. parallelus*.

**Ecology.** Within its geographical range, *M. cannicci*, new species, is often associated with mangrove forests. Among the specimens analysed in this study, the Red Sea crabs were collected among the pneumatophores of *Avicennia marina* shrubs, while all the other specimens were collected in marine creeks and fringing mangroves (Vannini & Valmori, 1981; Fratini et al., 2000). However, populations of *M. cannicci* are also known to colonise man-made structures in sheltered areas, such as harbours and vertical jetties, where they can be abundant on wooden and concrete vertical surfaces. In East Africa, *M. cannicci* colonises both the seaward fringe, where it can be found in sympatry with *M. messor* and *M.*

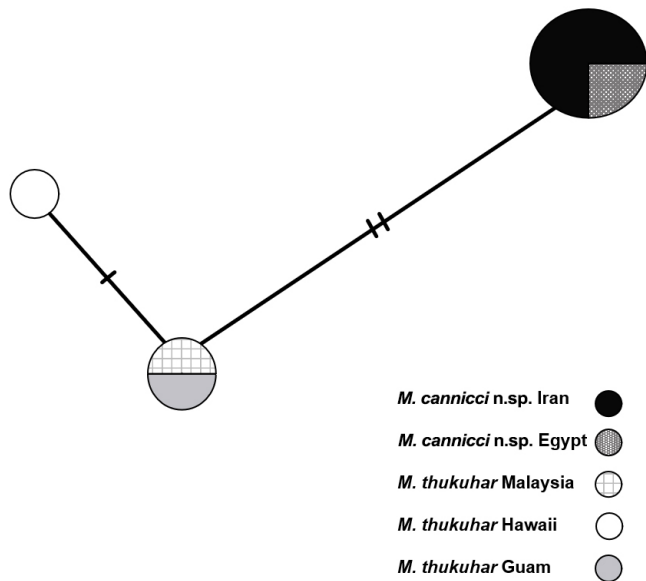


Fig. 8. Genotype network of *Metopograpsus thukuhar* and *Metopograpsus cannicci*, new species, based on an alignment of seven 28S sequences (1286 bp) and constructed with PopART v1.7. The size of the circles is proportional to the number of individuals carrying that genotype. Transverse lines indicate the number of mutational steps between genotypes.

*oceanicus*, and the denser part of the *Rhizophora mucronata* forests, where it is usually the only species of *Metopograpsus* present (see Cannicci et al., 1996). This species is known to be a generalist feeder and a very fast and agile predator of fiddler and sand bubbler crabs (Fratini et al., 2000).

**Distribution.** Red Sea, East African coast (from Somalia (Vannini & Valmori, 1981, quoted as *M. thukuhar*) to Mozambique), Seychelles; Dar es Salaam (Hartnoll, 1975, quoted as *M. thukuhar*); Madagascar, Toliara and Toamasina (Crosnier, 1965, quoted as *M. thukuhar*); Mauritius (Michel, 1964, quoted as *M. thukuhar*; present paper); Iran (Naderloo & Türkay, 2012; Naderloo, 2017, in both papers quoted as *M. thukuhar*; present paper).

**Nuclear genetic evidence.** The TCS genotype network (Fig. 8) shows the clustering of seven individuals of *Metopograpsus*, formerly treated as *M. thukuhar*, across three individual 28S genotypes. A genotype is here defined as a specific sequence of nucleotides within the 28S nuclear gene region and is visualised as a circle in Figure 8. Short transverse lines indicate the number of mutations separating the different genotypes. The most common genotype is shared by the four individuals from Iran and Egypt and is separated by two mutations from a second genotype comprising specimens from Guam and Malaysia. A third genotype is separated by one additional mutation from the latter ones and was found in a sample from Hawaii.

## DISCUSSION

In this study, we were able to confirm what had been suggested based on mitochondrial DNA by Fratini et al.

(2018), now providing morphological and nuclear DNA evidences that the former species *Metopograpsus thukuhar* consists of a complex of two pseudocryptic species, one of which is here described as *Metopograpsus cannicci*, new species.

The term pseudocryptic is hereby used in the sense of Ragionieri et al. (2012) and Fratini et al. (2019), i.e., minor morphological differences discovered, after recognising the genetic distinctness. With *M. cannicci*, new species, the number of species belonging to *Metopograpsus* increases to seven. Since the type specimen used by Owen (1839) for the description of *M. thukuhar* was from Hawaii, the original name remains associated to populations occurring in the eastern Indian and Pacific oceans, while *M. cannicci*, new species, refers to populations from the Red Sea, East Africa, western Indian Ocean islands, and the Persian Gulf.

We must assume that these two species do not occur in sympatry and their geographic distribution ranges are well separated. Geographic barriers are typically implicated as a likely driver of allopatric speciation of widely distributed intertidal marine species with planktonic larvae (see Keenan et al., 1998; Shih & Suzuki, 2008; Ragionieri et al., 2009; Lai et al., 2010, 2017; Shih et al., 2012). In this case, the two species are possibly isolated by the geographic break between the western Indian Ocean and the eastern Indian/Western Pacific Ocean, caused by the mid-Indian Ocean Oceanic Barrier, west of the Lakshadweep Maldives-Chagos archipelagos (see Borsa et al., 2016; Fratini et al., 2018).

While the two species are strongly differentiated at the mtDNA 12S and 16S gene level (with a genetic pairwise p-distance of  $3.2 \pm 0.5$ ; Fratini et al., 2018), we found only minor morphological differences, mainly related to the shape of the first gonopod of adult males. Since these morphological differences were only discovered after Fratini et al. (2018) reported the genetic distinctness, we define these taxa as pseudocryptic species in line with the definitions provided by Ragionieri et al. (2012), Chu et al. (2015), and Fratini et al. (2019) for other brachyuran species.

Also the genetic differences recovered from the 28S gene are more subtle than the ones from the mitochondrial markers, despite the fact that all of these molecular markers correspond to ribosomal structural genes, which are characterised by an alternation of conserved (stems) and variable regions (loops) (e.g., Schubart et al., 2000). In the present case, the compared sequences encompass the loop regions defined as D2 and D3 of the 28S rRNA gene. Nevertheless, only two consistent differences can be found between the two studied species, which on the other hand appear to be reliable enough for their use in diagnostic species identification. The reduced genetic divergence of the 28S DNA compared to mitochondrial markers in thoracotreme crabs was recently also demonstrated in a genetic comparison of sesarmid species from East Africa (Cannicci et al., 2017: table 3).



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