Systematics and Biodiversity (2026), **24(2)**: 2684068

Research Article

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An old species with a new identity: resurrection and updated distribution of *Saron hemprichii* (Heller, 1861) (Hippolytidae: Decapoda) from the Mediterranean and Red Sea

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(Received 4 August 2025; accepted 6 May 2026)

The semi-enclosed Mediterranean marine fauna encompasses Atlantic taxa and endemic species. Global warming, the marine aquarium trade, and Suez Canal expansion have profoundly altered this ecosystem, facilitating the introduction and establishment of Indo-Pacific alien species, particularly in the Eastern Mediterranean Basin. These alterations necessitate the re-evaluation of native and alien marine fauna, especially caridean shrimps, to assess the effects on local biodiversity. Here, we apply an integrative taxonomic approach combining both morphological and genetic analyses, to reassess the identity and phylogenetic position of the marbled shrimp *Saron marmoratus* from the Mediterranean and Red Sea. We reinstate *Hippolyte hemprichii* (originally described from the Red Sea), currently a synonym of *S. marmoratus*, as a valid species for these populations, confirming their close affinities and supporting the Suez Canal as the likely introduction vector. This study underscores the need for ongoing monitoring and comparative taxonomic assessments of Mediterranean caridean fauna to clarify population assemblages, their identities, and biogeographic connections to Indo-Pacific lineages.

https://zoobank.org/urn:lsid:zoobank.org:pub:6BC83EA9-3C35-4112-B342-BEBDDEB1E896

Key words: Alien species, Caridea, cryptic species, Indo-Pacific Ocean, *Hippolyte hemprichii*, *Saron marmoratus*, Suez Canal

Introduction

The Mediterranean Sea is a semi-enclosed basin connected naturally to the Atlantic Ocean in the west and to the Black Sea in the northeast, and artificially to the Red Sea via the Suez Canal on its southeastern margin. Since the opening of the Suez Canal in 1869, the connection between the Mediterranean and the Gulf of Suez in the Red Sea has become a major pathway for species introductions, increasing over the years with the Canal's significant expansion, especially northwards (Boudouresque, 1999; Galil et al., 2021; Galil & Goren, 2014). While the Suez Canal is the major vector for introducing alien species to the Mediterranean, shipping constitutes an additional pathway and a primary vector for their dispersal across it, with species being transported incidentally through ballast water discharge or by attachment to hull biofouling and other submerged vessel surfaces (Ferreira et al., 2006; Gewing & Shenkar, 2017; Katsanevakis et al., 2016; Ojaveer et al., 2018; Ounifi-Ben Amor et al., 2016; Wanless et al., 2010). In addition, the rapidly growing popularity of ornamental fishkeeping and the global expansion of the aquarium industry constitute another potential introduction pathway for marine species, increasing both the frequency and success of alien species introductions and establishment along marine coastlines (Ojaveer et al., 2018; Tsiamis et al., 2020).

The introduction of Indo-Pacific species into the Mediterranean Sea, particularly within the Levant Basin, is considered one of the major threats to local marine biodiversity (Katsanevakis et al., 2016; Ojaveer et al., 2015). Such introductions may lead to homogenization, decline or loss of native and endemic species, alter ecosystem processes, and even impact on human health and economy (Galil & Goren, 2014; Özcan et al., 2008).

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ISSN 1477-2000 print / 1478-0933 online

https://dx.doi.org/10.1080/14772000.2026.2684068
Published online 09 Jul 2026

The significant enlargement of the Suez Canal over the years, along with the intensification of anthropogenic activities such as shipping and aquaculture, has further promoted the establishment and spread of alien species within new environments in the Mediterranean Sea (Galil et al., 2018; Galil & Goren, 2014).

Israel's geographic proximity to the northeastern entrance of the Suez Canal, combined with a relatively high sampling effort, has facilitated the early detection of numerous marine alien species, many of which were first recorded along the Israeli coast (Galil, 2011; Zenetos et al., 2010). To date, more than 40 species of the infraorder Caridea, representing 12 families, are known from the Mediterranean coast of Israel, with roughly one quarter being alien species (Galil et al., 2024; Galil & Shlagman, 2011; Katsanevakis et al., 2020; Levitt et al., 2014; Rothman et al., 2013).

The family Hippolytidae (infraorder Caridea) includes the colourful shrimps of the genus *Saron* Thallwitz, 1891, which currently comprises four recognized species (De Grave & Fransen, 2011). Two species have relatively narrow distributions, are well defined morphologically, and can be easily identified by their distinctive colour patterns, *S. inermis* Hayashi in Debelius, 1984 (occurs in Okinawa and Indonesia) and *S. rectirostris* Hayashi, 1984 (occurs in Indonesia) (Chace, 1997; Hayashi, 1984, 1989). The two remaining species, *S. neglectus* De Man, 1902, and *S. marmoratus* (Olivier, 1811), share similar morphological characters, diverse colour patterns, and are largely sympatric across the greater part of their wide distributional ranges throughout the Indo-West Pacific region, from the Red Sea and eastern Africa across the Indian Ocean to Japan and Australia, eastwards to Hawaii and French Polynesia. *Saron marmoratus* and *S. neglectus* are morphologically well differentiated, each showing low intraspecific morphological variation. Genetically however, their pronounced intraspecific divergence indicates that both likely represent species complexes that may include multiple cryptic species (Baeza et al., 2023; Chace, 1997; Minemizu, 2013).

Saron marmoratus was originally described as *Palaemon marmoratus* by Olivier (1811), based on material collected from Shark Bay, Western Australia. This nocturnal species is usually found hiding in crevices of rocks, corals, coral rubbles, or under rocks, in shallow waters down to approximately 50 m depth (Anker & De Grave, 2016; Chace, 1997; Davie, 2002; Holthuis, 1947; Sheibani-Tezerji & Sari, 2007). Its wide distribution, coupled with noticeable variability in morphology and colour patterns, has resulted in numerous synonyms over the years, including *Hippolyte gibberosus* H. Milne Edwards, 1837, *H. kraussii* Bianconi, 1869 (Indo-Pacific), and *H. hemprichii* Heller, 1861 (Red Sea), among others (see De Grave & Fransen, 2011, and references therein). The unclear morphological identification persists, with many colourful *Saron* specimens photographed by divers routinely identified only as *Saron* sp. (e.g., Debelius, 2001). Furthermore, *S. marmoratus* is a popular shrimp in the aquarium trade due to its distinctive colouration and minimal care requirements, commonly marketed under vernacular names such as "marble shrimp" or "common marble shrimp" (WoRMS Editorial Board, 2026).

The Indo-West Pacific marbled shrimp *S. marmoratus* was first recorded from the Levant Basin off northern Israel in 2013 (Rothman et al., 2013). In their report, Rothman et al. (2013) attributed the presence of the shrimp either to a release by aquarists or passive transport via hull fouling of slow-moving vessels but favoured Lessepsian migration via the Suez Canal from the Red Sea as the most likely pathway. Subsequent observations confirm this alien shrimp establishment along the Israeli Mediterranean coast on rocky bottoms from shallow lagoons down to approximately 30 m depth (Rothman et al., 2013; current study). The species has since been recorded along the eastern Mediterranean coasts of Lebanon, Syria, Cyprus, and Turkey (Ammar & Raya, 2019; Bianchi et al., 2022; Ergüden et al., 2018; Katsanevakis et al., 2020; Langeneck et al., 2022; Zenetos et al., 2015).

In this study, we evaluated the taxonomic and phylogenetic status of *S. marmoratus* specimens collected from the Mediterranean and Red Sea coasts of Israel using integrated morphological and genetic data. Our findings indicate that this alien shrimp represents a cryptic species previously known from the Red Sea, which subsequently invaded the Levant Basin. Accordingly, we reinstate *Hippolyte hemprichii* Heller, 1861, a Red Sea taxon currently regarded as a junior synonym of *Saron marmoratus*.

Materials and methods

Study material

Specimens of *Saron* sampled and examined in this study were collected along the Mediterranean and Red Sea coasts of Israel under permits from the Israel Nature and Parks Authority (2016/41165; 2017/41663), at depths of 0–26 m via snorkelling and scuba diving. An additional *S. marmoratus* specimen from the Gulf of Suez (Red Sea) was obtained from the Crustacea Collection of the Steinhardt Museum of Natural History, Tel Aviv University (SMNHTAU:Ar.27059). Nine *S. marmoratus* individuals, presumably of Indonesian

origin per the vendor, were acquired from a Tel Aviv pet shop (one sampled for molecular analysis, SMNHTAU:Ar.29994). All specimens were preserved in 70% ethanol. Comparative *Saron* material from the Indo-West Pacific and Red Sea was loaned from the following institutions: Naturhistorisches Museum Wien, Austria (NHMW); Muséum national d'Histoire naturelle, Paris, France (MNHN-IU); Senckenberg Museum, Frankfurt am Main, Germany (SMF); Museum für Naturkunde, Berlin, Germany (ZMB); and Oxford University Museum of Natural History, Zoological Collections, UK (OUMNH.ZC). Four tissue samples from Indo-West Pacific specimens, consisting of a single pleopod and, where available, embryos from ovigerous females, were excised and preserved in 100% ethanol for DNA extraction and analysis (see molecular methods detailed below).

Molecular phylogenetic dataset and analyses

To assess the phylogenetic relationships and position of *Saron* from the Mediterranean and Red Sea, two datasets were constructed for the genus using amplified genetic markers (detailed below). We included five specimens collected from Israel's shores and one from a pet shop (from SMNHTAU), four specimens from the Indo-West Pacific (MNHN-IU, OUMNH.ZC, SMF), and additional sequences retrieved from GenBank and the Barcode of Life Data Systems (BOLD) from previous studies. Representatives of the genera *Hippolyte*, *Tozeuma*, *Thor*, and *Lysmata* were used as outgroup (De Grave et al., 2014). Specimen codes, localities, and GenBank/BOLD accession numbers are detailed in Supplemental Table S1.

Molecular procedures were performed at the molecular laboratory of SMNHTAU. DNA was extracted from ethanol-preserved tissue samples using DNA isolation kits (SIGMA GenElute Mammalian Genomic DNA Miniprep, Germany; Qiagen DNeasy, CA, USA) following the manufacturer's protocol. Two datasets were constructed, each comprising a distinct mitochondrial marker: the 16S ribosomal rRNA gene (*16S*; 571 bp; $n = 65$ sequences) and the barcoding protein-coding gene cytochrome *c* oxidase subunit I (*COX1*; 657 bp; $n = 34$ sequences). Primers and PCR conditions used for amplification and sequencing of the two markers are detailed in Supplemental Table S2. PCR products were cleaned of residual primers using exonuclease and alkaline phosphatase (Thermo Scientific). Sequencing of both strands of the PCR products was carried out using the BigDye Terminator Cycle Sequencing Kit on an ABI 3500xl Genetic Analyzer, and sequence analysis was performed with ABI GeneScan software (Tel Aviv University, Israel). Chromatograms were checked, assembled, and edited using Geneious v.7.1.9 (Biomatters Ltd). The sequences for each marker were aligned using the MAFFT online server v.7 (Katoh et al., 2019; Katoh & Standley, 2013). The Q–INS–i strategy, which considers the secondary structure of RNA, was applied for the *16S* gene fragment, while the *COX1* sequences were aligned using default settings. The *COX1* sequences were translated into amino acids, and no stop codons were detected, suggesting they were not pseudogenes.

For the phylogenetic analyses, substitution models were selected for each marker independently using jModelTest v.2.1.7 (Darriba et al., 2012; Guindon & Gascuel, 2003). The best models according to the BIC model selection criterion were as follows: HKY + G for *16S* and TrN + G for *COX1*. The dataset for each marker was analysed separately under Maximum likelihood (ML) and Bayesian inference (BI). Alignment gaps were treated as missing data. ML analyses were performed using IQ-TREE v.1.6.12 (Nguyen et al., 2015) through the web interface W-IQ-TREE (Trifinopoulos et al., 2016). Branch support was assessed with the Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon et al., 2010) and the ultrafast bootstrap approximation algorithm (UFBoot; Hoang et al., 2018; Minh et al., 2013), each with 1000 replicates. BI analyses were conducted using MrBayes v.3.2.7 (Ronquist et al., 2012). Two simultaneous parallel runs were performed with four chains per run for 2 and 1.5 million generations, with sampling every 200 and 150 generations for the *16S* and *COX1* datasets, respectively. The standard deviation of split frequencies between the two runs and the potential scale reduction factor (PSRF) diagnostic were examined. The first 25% of trees were conservatively discarded as burn-in. *Saron* inter- and intraspecific uncorrected *p*-distances for *16S* and *COX1* were calculated with pairwise deletion in MEGA11 (Tamura et al., 2021).

Distinct lineages within each *Saron* dataset were delimited by applying a single-locus, tree-based species delimitation analysis, the multi-rate Poisson Tree Process (mPTP; Kapli et al., 2017). For these analyses, ingroup haplotypes of the *16S* and *COX1* datasets were used, and individual ultrametric trees were reconstructed using BEAST v.1.10.4 (Drummond et al., 2012; Suchard et al., 2018), executed on the CIPRES Science Gateway (Miller et al., 2010). Each analysis was configured with the following priors (otherwise by default): TN93 + G model, Yule process tree model, random starting tree, alpha prior (uniform; 0–10), and an uncorrelated relaxed clock (uniform distribution; mean 1, 0–1). Three independent runs of 10 million generations were performed for each

dataset, with sampling every 1000 generations. Convergence diagnostics, posterior trace plots, effective sample sizes (>200), and burn-in were assessed using Tracer v.1.7.2 (Rambaut et al., 2018). For each analysis, the three runs were combined in LogCombiner, with the first 10% of trees discarded as burn-in, and the ultrametric tree was generated using TreeAnnotator (both provided within the BEAST package).

Morphological dataset and analyses

Saron specimens from the Mediterranean and Red Sea coasts of Israel were morphologically compared to pet shop material, Indo-West Pacific *S. marmoratus* specimens, and type material, including the syntypes of *Hippolyte hemprichii* from the Red Sea (NHMW-CR1029), paratypes of *S. inermis* (SMF 11123), *S. rectirostris* (SMF 12257), and *S. neglectus* (SMF 7991), as detailed in Supplemental Table S3. Additionally, all examined specimens were compared to literature data, encompassing classical taxonomic keys and their original descriptions, as well as more recent taxonomic revisions (Anker & De Grave, 2016; Balss, 1914, 1915; Barnard, 1950; Bianconi, 1869; Boone, 1935; Borradaile, 1899; Bruce, 1976, 1989; Chace, 1997; Dana, 1852; De Grave et al., 2012; De Grave & Goulding, 2011; de Lamarck, 1838; Guérin-Méneville, 1838; Hayashi, 1989; Heller, 1861a, 1861b; Hilgendorf, 1879; Holthuis, 1947; Kemp, 1914, 1916; Kubo, 1940; Ledoyer, 1969; Man, 1888, 1902; Milne Edwards, 1837; Miyake & Hayashi, 1966; Nobili, 1901, 1906a, 1906b; Olivier, 1811; Ortmann, 1890, 1894; Pearson, 1905; Randall, 1840; Rathbun, 1906; Sheibani-Tezerji & Sari, 2007; Stebbing, 1914; Streets, 1877; Thallwitz, 1891; Tirmizi & Kazmi, 1971; Whitelegge, 1897).

Morphometric and meristic characters were recorded using a Zeiss SteREO Discovery.V12 stereomicroscope as follows: number of articles in the carpus of the second pereiopods (p2 carpus articles); number of spines on the dactyls of pereiopods 3–5 (p3–5 dactyls spines); number of spines on the propodus of pereiopods 3–5 (p3–5 propodus spines); number of spines on the merus of pereiopods 3–5 (p3–5 merus spines); and number of teeth on the rostrum's dorsal (Dorsal male/female) and ventral (Ventral male/female) margins of males and females (see Table 1). Size is expressed as carapace length (cl.), measured as the distance from the posterior orbital edge, to the posterior border of the carapace, using a digital calliper for relatively small specimens and with a digital hand calliper for larger specimens. All measurements were made to the nearest 0.1 mm. Drawings were prepared using a Zeiss Stemi 508 stereomicroscope with a drawing tube and digitized using a Wacom Bamboo CTL471 pen tablet with Adobe Illustrator.

To determine morphological differences between populations, linear and generalized linear models (GLM) were used. For meristic data, a GLM with a Poisson family was employed (Zuur et al., 2009). The 'lm' and 'glm' functions from the 'lme4' package in R (v.1.1-25; Bates et al., 2015) were used. To examine the effects of habitat and sex, a likelihood ratio test (LRT) was performed using the 'lrtest' function from the 'lmtest'

Table 1. Comparison of meristic characters of *Saron hemprichii* comb. nov. from the Mediterranean and Red Sea (Med & RS) and *Saron marmoratus* from the Indo-Pacific Ocean (Indian, Pacific).

	***Saron hemprichii* comb. nov.**			***Saron marmoratus***					
	Med & RS			**Indian**			**Pacific**		
Characters	**N**	**Average**	**SD**	**N**	**Average**	**SD**	**N**	**Average**	**SD**
p2 carpus articles	15	12.7	1.2	44	11.4	0.9	12	10.8	0.8
p3 dactyls spines	14	5.6	0.5	20	4.6	0.8	9	4.3	0.5
p4 dactyls spines	15	5.5	0.5	20	4.5	0.8	9	4.3	0.5
p5 dactyls spines	15	5.3	0.7	24	4.4	1.0	2	4.2	0.4
p3 propodus spines	14	12.1	2.1	21	10.7	2.3	9	9.0	1.3
p4 propodus spines	15	11.3	1.5	21	10.0	2.1	9	8.8	1.6
p5 propodus spines	15	10.2	1.7	21	8.7	2.0	2	8.1	1.2
p3 merus spines	12	2.0	0.0	18	1.7	0.5	9	1.5	0.7
p4 merus spines	12	2.0	0.0	18	1.9	0.5	9	2.0	0.0
p5 merus spines	12	1.9	0.3	20	1.6	0.5	2	2.0	0.0
Dorsal male	10	3.0	0.0	39	3.0	1.2	N/A	N/A	N/A
Dorsal female	7	2.9	0.4	27	2.7	0.9	N/A	N/A	N/A
Ventral male	11	6.3	0.9	39	6.3	0.6	N/A	N/A	N/A
Ventral female	7	6.7	0.5	28	6.1	0.5	N/A	N/A	N/A

Abbreviations of characters as detailed in the Materials and methods. Taxon names follow the taxonomy proposed in this study. Dorsal and ventral refers to rostrum teeth. **Abbreviations**: **SD**, standard deviation; **N/A**, not available; **p**, pereiopod.

package (v.0.9-38; Hothorn et al., 2015). All statistical tests were conducted in R v.4.0.3 (R Core Team, 2020).

Results

Molecular analyses

The phylogenetic results of the ML and BI analyses for both the *16S* and *COX1* markers show similar topologies and confirm the phylogenetic distinctiveness of the genus *Saron* for each marker (Figs 1–2). The phylogenetic analyses place the five Israeli specimens, sampled from both the Red Sea (*16S* only) and the Mediterranean Sea, within the genus. In both phylogenetic trees, *Saron* is divided into lineages, although not all nodes are well supported. For each marker and analysis, the Israeli specimens form a distinct clade. In the *16S* tree (Fig. 1), five major lineages were recovered: four representing *S. marmoratus* and one representing *S. neglectus*. Four of the five clades are from the Indo-West Pacific region (i.e., Madagascar, Australia, Papua New Guinea, Taiwan, New Caledonia, French Polynesia, and Hawaii), and the fifth comprises specimens from Israel's Red Sea and Mediterranean coasts. In the *COX1* tree (Fig. 2), the Israeli specimens cluster with a sample from Saudi Arabia (Red Sea) and are sister to two samples from Hawaii, although this latter relationship lacks support. The specimen from the pet shop, reportedly collected from Indonesia (SMNHTAU:Ar.29994), clusters with other Indo-West

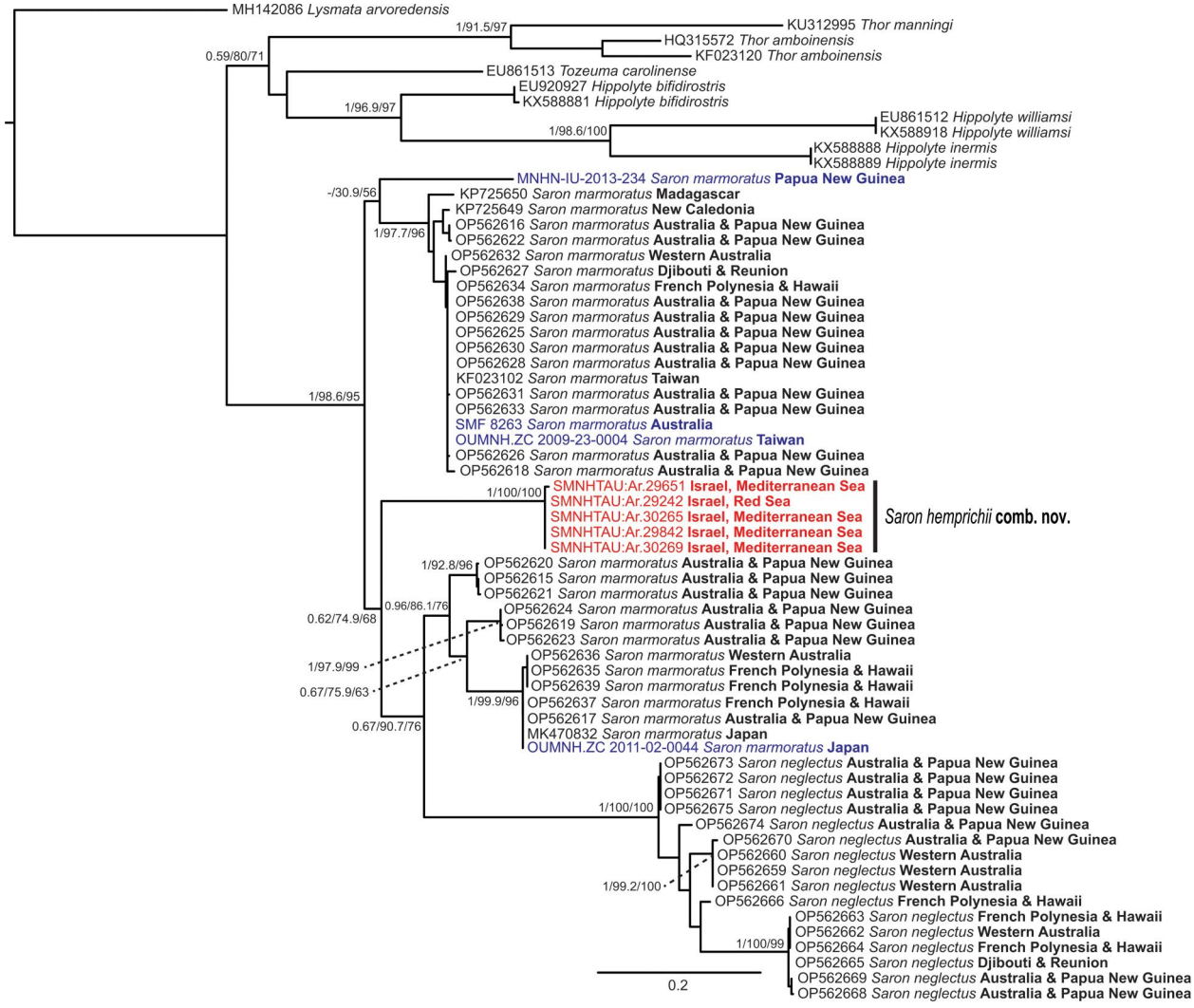

Fig. 1. Phylogenetic tree reconstructed from the ML analysis of *16S* mitochondrial marker dataset. Branch support is near each node in the following order: Bayesian posterior probabilities, SH-aLRT, and UFBoot. Coloured samples represent sequences generated in this study (Red, from Israel; Blue, from the Indo-West Pacific region). Taxon names correspond to changes proposed in this paper. Sample information is detailed in Supplemental Table S1.

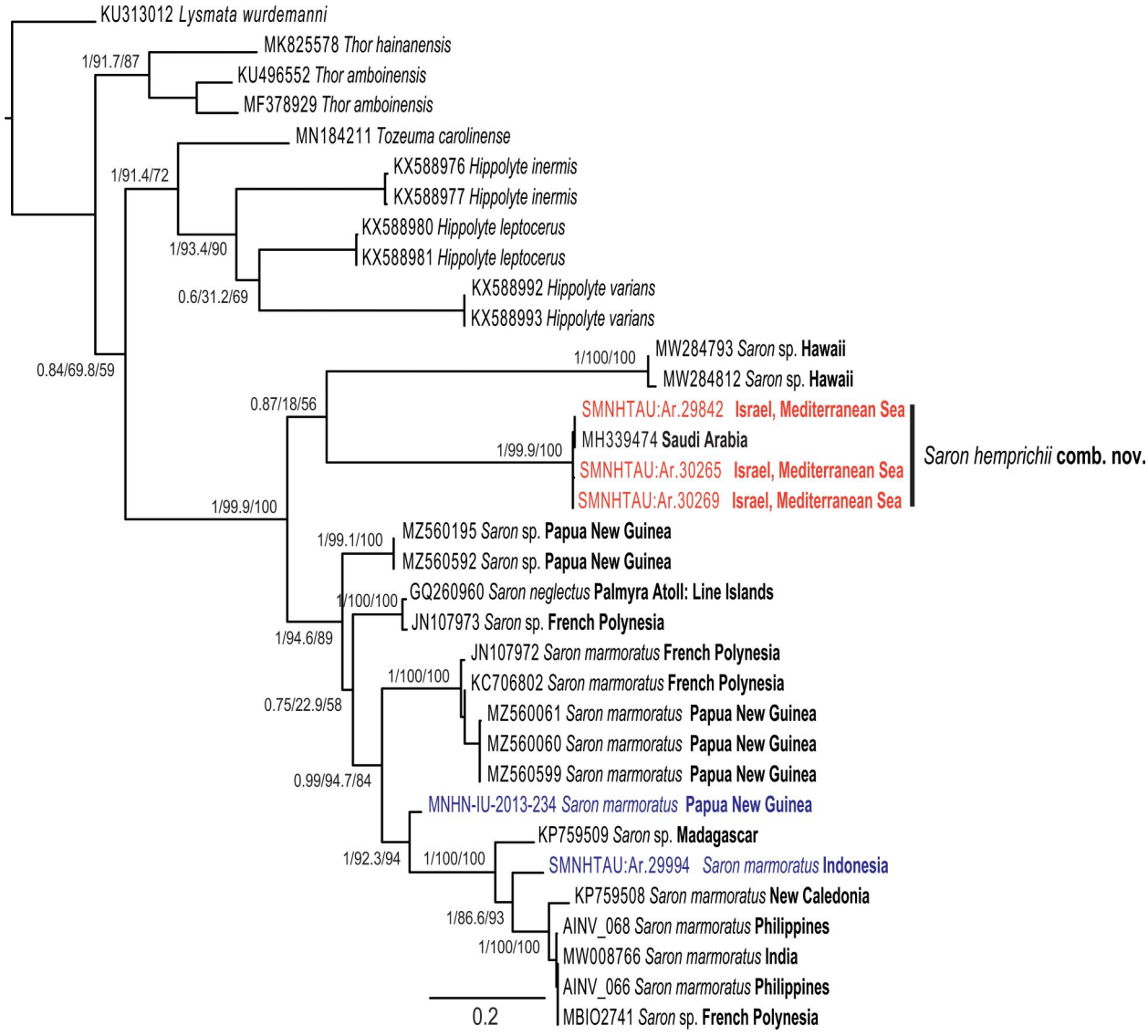

Fig. 2. Phylogenetic tree reconstructed from the ML analysis of *COX1* mitochondrial marker dataset. Branch support is near each node in the following order: Bayesian posterior probabilities, SH-aLRT, and UFBoot. Coloured samples represent sequences generated in this study (Red, from Israel; Blue, from the Indo-West Pacific region). Taxon names correspond to changes proposed in this paper. Sample information is detailed in Supplemental Table S1.

Pacific samples and is distinct from the Israeli specimens (Fig. 2). The mPTP species delimitation analyses based on the individual *16S* and *COX1* datasets resulted in nine and six distinct entities within *Saron*, respectively (Supplemental Fig. S1). In each analysis, the Mediterranean and Red Sea samples were grouped as one entity, whereas Indo-West Pacific specimens represented the other entities.

Genetic distances between the Israeli *Saron* specimens and other *Saron* samples ranged from 23–32% for *COX1* and 13–24% for *16S* (Supplemental Table S4). In both datasets, genetic distances among specimens from the Mediterranean and Red Sea range from 0 to 0.6%. For the *16S* dataset, genetic divergence of the Israeli specimens from samples identified as *S. marmoratus* ranged mostly from 13–18%, and from samples identified as *S. neglectus* from 19–24%. Genetic distances between *S. marmoratus* and *S. neglectus* ranged mostly from 17–22%. For the *COX1* dataset, genetic distances of the Israeli specimens from samples identified as *S. marmoratus* ranged from 23–28%, from samples identified as *Saron* sp. from 25–32%, and from one sample identified as *S. neglectus*

(specimen UF 10773, sequence GQ260960, from Palmyra Atoll, Line Islands in the Pacific Ocean) from 25–26%. Genetic distances between *S. marmoratus* and *S. neglectus* ranged mostly from 13–22%.

Morphological comparisons

The morphological dataset of *Saron* specimens included 18 specimens from the Mediterranean and Red Seas, and 34 specimens from the Indo-West Pacific region (Supplemental Table S3). The examined material from the Mediterranean Sea and Red Sea differs from the Indo-West Pacific specimens by the base structure of the first pair of pereiopods in males, which is jagged and not smoothly curved (Fig. 3), and by the structure of thoracic and abdominal sternites of both males and females (Figs 4–5) (compared to examined material and to Tirmizi & Kazmi, 1971). In males, from the former population, the notch of the fifth thoracic sternite is rounder and not narrow and pointed (Fig. 4A–C); the first three abdominal sternite spines are narrow and sharp, creating a quadrangular base (Fig. 5.1A–C) compared to more triangular spines and a rounder base (Fig. 5.1D); the fourth and fifth spines are triangular (Fig. 5.2A–D), though less distinguished, the sixth small spine is narrower (Fig. 5.3A–D) compared to the straighter and narrower fourth and fifth spines (Fig. 5.2E–F), and triangular sixth spine of the Pacific specimens (Fig. 5.3E). In females from the Mediterranean and Red Sea, the fifth thoracic sternite forms a deep concave notch (Fig. 4E–F) compared to very short spines and obscured notch (Fig. 4G), and the sixth abdominal sternite spine is triangular (Fig. 5.3F) compared to the pointed spine of the Pacific specimens (Fig. 5.3G).

Although the average number of segments in the carpus of the second pair of pereiopods and spines of the ambulatory pereiopods in the Mediterranean Sea and Red Sea populations was equal to or higher than in Indo-West Pacific populations (except for the merus in the fifth pair; Table 1), the results are inconclusive due to the small sample size and lack of statistical significance. One exception was found for the propodus in the third pair of pereiopods, where adding habitat as a factor increased the likelihood of a significant intercept-only model (LRT, $\chi^2[-2] = 6.21$, $p < 0.05$). However, this result is inconsequential due to the small sample size and non-significant GLM tests. Tirmizi and Kazmi (1971) noted differences in the number of rostral teeth between males and females in their Arabian Sea material. The Mediterranean and Red Sea populations examined here, as well as previous Indian Ocean records,

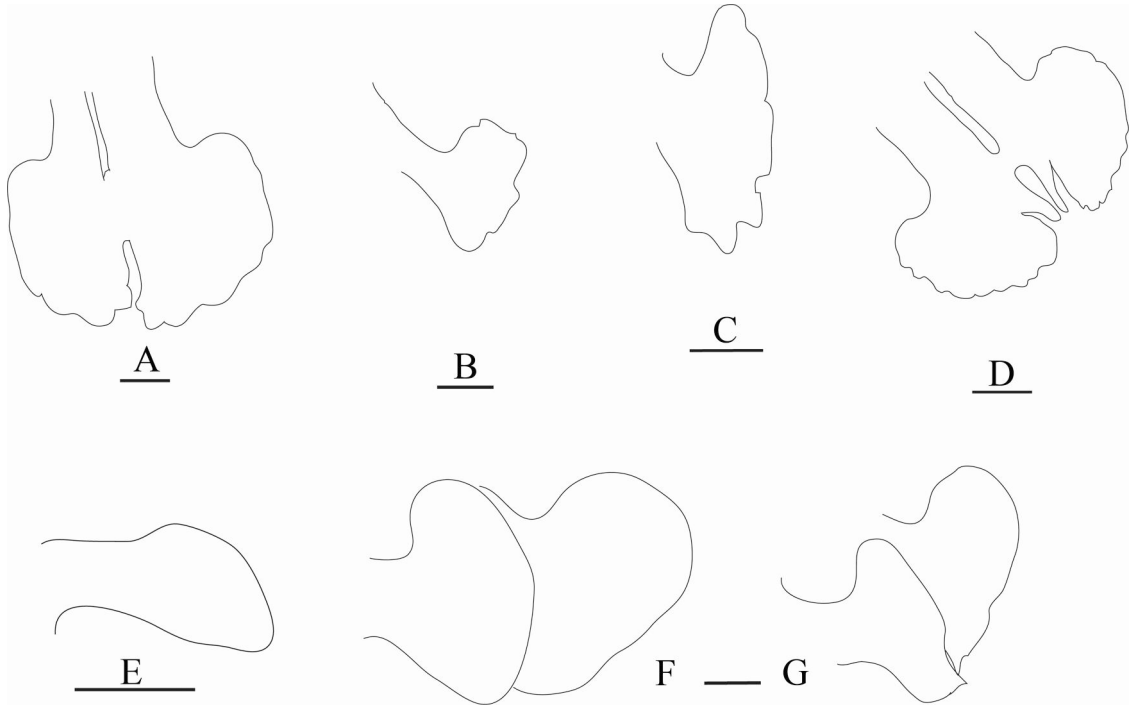

Fig. 3. Base of first pair of pereiopods in males: **A–D.** *Saron hemprichii* comb. nov.; **E–G.** *Saron marmoratus*. **A.** SMNHTAU:Ar.27936, cl. 15.6 mm, ventral view; **B.** SMNHTAU:Ar.29995, cl. 13.1 mm, lateral view; **C.** SMNHTAU:Ar.29651, cl. 11.2 mm, lateral view; **D.** SMNHTAU:Ar.29842, cl. 13.0 mm, ventral view; **E.** SMNHTAU:Ar.29994, cl. 7.6 mm, lateral view; **F.** SMF 8263, cl. 10.7 mm, lateral view; **G.** SMF 8263, cl. 1.8 mm, lateral view. Scale bars: 0.5 mm.

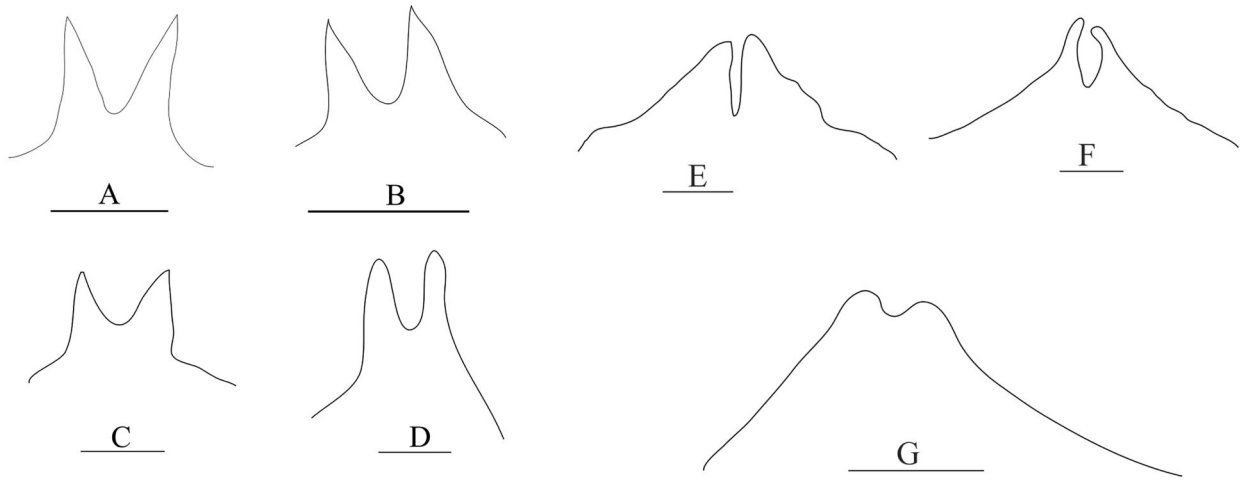

Fig. 4. Fifth thoracic sternite in males (A–D) and females (E–G), ventral view. **A–C, E–F.** *Saron hemprichii* comb. nov.; **D, G.** *Saron marmoratus*. **A.** Holotype, NHMW-CR1029, male, cl. 5.2 mm; **B.** Paratype, NHMW-CR1029, male, cl. 4.0 mm; **C.** SMNHTAU:Ar.27936, male, cl. 15.6 mm; **D.** SMNHTAU:Ar.29994, male, cl. 7.6 mm. **E.** SMNHTAU:Ar.27936, ovigerous-female, cl. 10 mm; **F.** SMNHTAU:Ar.29650, ovigerous-female, cl. 11.6 mm; **G.** SMNHTAU:Ar.29994, female, cl. 8.1 mm. Scale bars: A = 1 mm; B–G = 0.5 mm.

showed no significant differences between males and females in average dorsal and ventral rostral teeth numbers (Table 1). Kemp (1914) noted other sexual characters in the first pair of pereiopods and third pair of maxillipeds. In this study, these appendages were enlarged in several of the largest males but proportional in females and smaller males, consistent with Miyake and Hayashi (1966). Boone (1935) described unequal chelae in the first pair of pereiopods of the female specimen from the Marquesas Islands (French Polynesia) and a second pair larger than the first. In the current study, one male from the Mediterranean Sea (SMNHTAU:Ar.29651) and another from the pet shop (supposedly from Indonesia; SMNHTAU:Ar.29994) had unequal chelae. Most examined material had a longer second pair of pereiopods, except in a few of the largest males (cl. > 11.2 mm), though not all.

Taxonomic account

The results of this study present clear molecular distinctiveness of *Saron* specimens from the Mediterranean Sea and the Red Sea across the two mitochondrial gene fragments analysed. This genetic distinctiveness is further corroborated by morphological differences relative to other congeners, including type material of *S. inermis*, *S. rectirostris*, and *S. neglectus*, as well as the Indo-West Pacific populations of *S. marmoratus* (including material from Australia, its type locality). These findings support the recognition of the Mediterranean and Red Sea *Saron* specimens as a distinct species, separate from the marbled shrimp *S. marmoratus*, to which they have previously been assigned. Within the Mediterranean marine fauna, this taxon represents an alien species. A morphologically similar shrimp, *Hippolyte hemprichii*, was originally described from the Red Sea by Heller (1861a), subsequently synonymized with *S. marmoratus* by Holthuis (1947). Our comparative analyses reveal close morphological similarities between the syntypes of *H. hemprichii* and the specimens examined from both the Mediterranean and Red Sea. Accordingly, we herein resurrect and re-describe *H. hemprichii* as a valid species distinct from *S. marmoratus*, with an established alien population in the Mediterranean Sea.

Family HIPPOLYTIDAE
Saron Thallwitz, 1891
Saron marmoratus (Olivier, 1811)
(Table 1; Figs 1, 2, 3E–G, 4D, G, 5.1D, 5.2E–F, 5.3E, G, 6A–B; Supplemental Tables S1, S3, S4)

Holotype. Collected by Perron from Shark Bay, New Holland (Australia), not recovered in the collections of the Muséum national d'Histoire naturelle in Paris (MNHN-IU) (Baeza et al., 2023).

Other material examined. SMNHTAU:Ar.29994, four males and three females (cl. 7.6–8.8 mm), bought at a pet shop (Tel-Aviv, Israel) on January 2015, reportedly collected from Indonesia; MNHN-IU-2013-16, one juvenile (cl. 2.6 mm), collected on 5 November 2012, from Papua New Guinea, 05°11.3′S, 145°49.4'E; MNHN-IU-2013-13129, one juvenile (cl. 1.9 mm), collected on 5 November 2012 by T. Y. Chan, from Papua

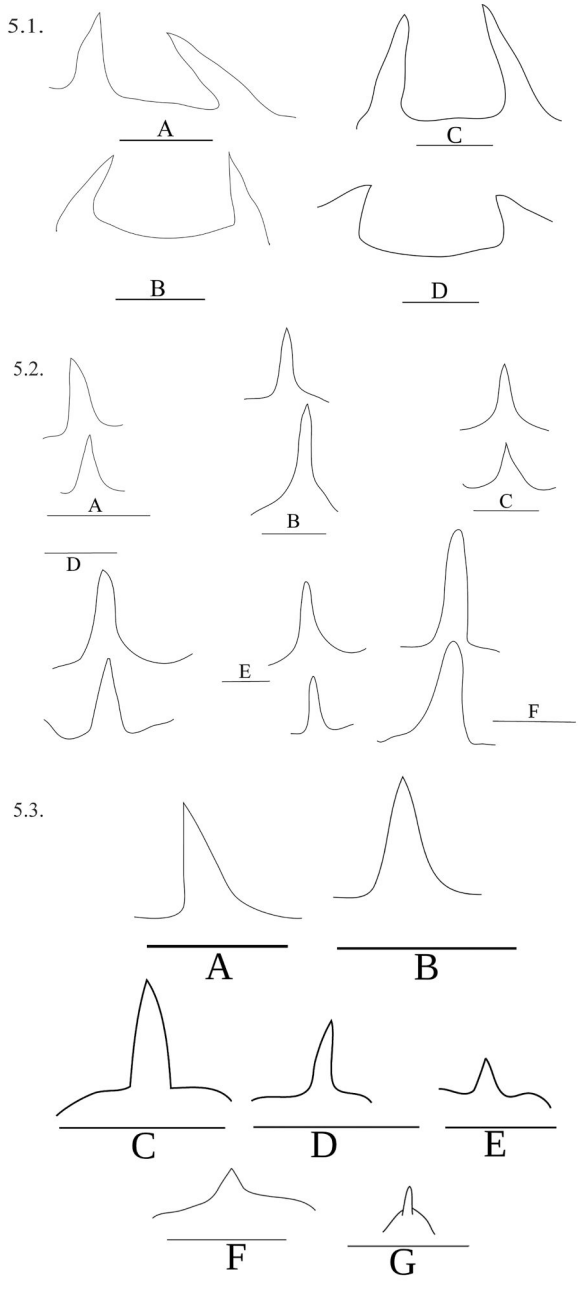

Fig. 5. Third–sixth abdominal sternites, ventral view. **5.1.** Third abdominal sternites in males. **A–C.** *Saron hemprichii* comb. nov.; **D.** *Saron marmoratus*. **A.** Holotype, NHMW-CR1029, cl. 5.2 mm; **B.** Paratype, NHMW-CR1029, cl. 4.0 mm; **C.** SMNHTAU:Ar.29995, cl. 13.1 mm; **D.** SMNHTAU:Ar.29994, cl. 7.6 mm. Scale bars: A–B = 0.5 mm; C–D = 1 mm. **5.2.** Fourth–fifth abdominal sternites in males. **A–D.** *Saron hemprichii* comb. nov.; **E–F.** *Saron marmoratus*. **A.** Holotype, NHMW-CR1029, cl. 5.2 mm; **B.** Paratype, NHMW-CR1029, cl. 4.0 mm; **C.** SMNHTAU:Ar.29650, cl. 14.7 mm; **D.** SMNHTAU:Ar.29995, cl. 13.1 mm; **E.** SMNHTAU:Ar.29994, cl. 7.6 mm; **F.** SMF 8263, cl. 1.8 mm. Scale bars: A–B, E = 0.5 mm; C–D, F = 1 mm. **5.3.** Sixth abdominal sternites in males (A–E) and females (F–G). **A–D, F.** *Saron hemprichii* comb. nov.; **E, G.** *Saron marmoratus*. **A.** Holotype, NHMW-CR1029, male, cl. 5.2 mm; B. Paratype, NHMW-CR1029, male, cl. 4.0 mm; **C.** SMNHTAU:Ar.29650, male, cl. 14.7 mm; **D.** SMNHTAU:Ar.29995, male, cl. 13.1 mm; **E.** SMNHTAU:Ar.29994, male, cl. 7.6 mm. **F.** SMNHTAU:Ar.29650, ovigerous-female, cl. 11.6 mm, **G.** SMNHTAU:Ar.29994, female, cl. 8.1 mm. Scale bars: A–B, E–G = 0.5 mm; C–D = 1 mm.

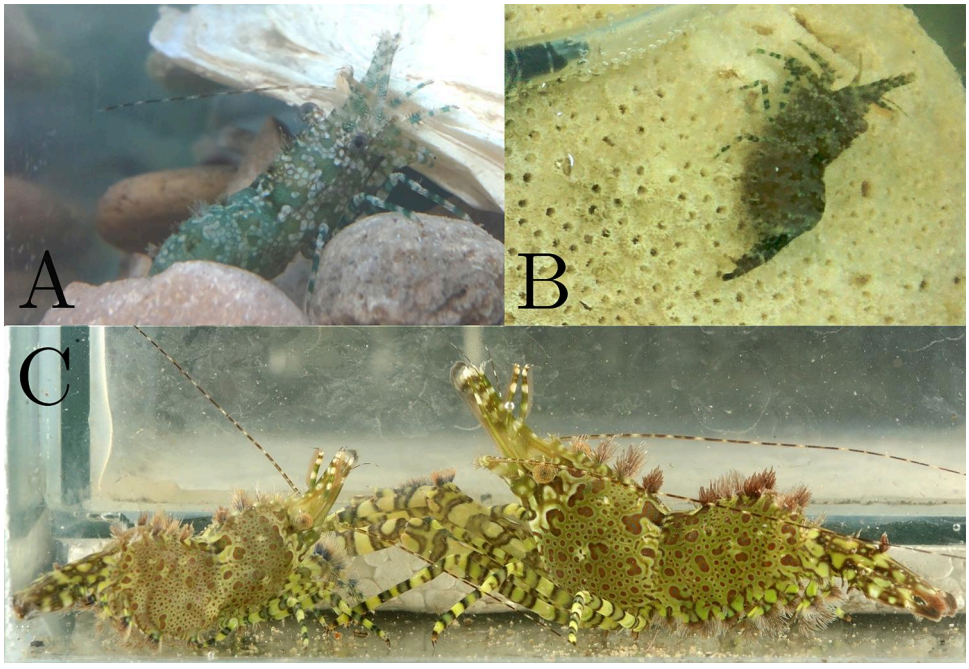

Fig. 6. Colour pattern types of *Saron* specimens in the laboratory. **A–B.** *Saron marmoratus*, during a laboratory experiment, reportedly collected from Indonesia, Photos by Ya'arit Levitt-Barmats; **C.** *Saron hemprichii* comb. nov., SMNHTAU:Ar.29650; male, cl. 14.7 mm, on the right; ovigerous-female, cl. 11.6 mm, on the left; lateral view. Photo by Oz Rittner.

New Guinea, 05°11.3′S, 145°49.4'E; MNHN-IU-2013-110, one male (cl. 4.1 mm), collected on 6 November 2012 by T. Y. Chan, from Papua New Guinea, 05°12.1'S, 145°49.3′E; MNHN-IU-2013-234, one male (cl. 7.3 mm), collected on 0 November 2012 by T. Y. Chan, from Papua New Guinea, 05°12'S, 145°48.1'E; MNHN-IU-2013-2052, one male (cl. 18.5 mm), from Papua New Guinea, 05°09.4'S, 145°49.9'E; MNHN-IU-2013-13126, one juvenile (cl. 2.6 mm), collected by T. Y. Chan, from Papua New Guinea, 05°12.1'S, 145°49.3′E; MNHN-IU-2013-13127, one male (cl. 3.4 mm), collected by T. Y. Chan, from Papua New Guinea, 05°12.1'S, 145°49.3′E; MNHN-IU-2013-13128, two males (cl. 3.2 mm, second with broken rostrum), collected by T. Y. Chan, from Papua New Guinea, 04°59.1'S, 145°47.7'E; SMF 8263, two males (cl. 10.7, 1.8 mm), from Western border, Australia; ZMB 12149, one male and one female (cl. 6.1 and 7.3 mm, respectively), collected by Hildebrandt, from Madagascar, Africa, 19°S, 47°E; ZMB 15546, seven males and two females (cl. 5.9–13.7 mm), collected in 1909 by Wache, from Djibouti, Gulf of Aden, Africa, 11°35′N, 43°8'E.

Diagnosis. Rostrum longer than carapace, curved upward; dorsal margin with 5–6 (mostly 6) teeth of which 2 subdistal and 2–3 postorbital and 1 more posterior protrusion, teeth usually with tufts of plumose setae just in front; ventral margin with 4–7 (mostly 6–7) teeth; tri-dentate tip. In males, the structure of base of the first pair of pereiopods is smoothly curved (Fig. 3E–G); the spines on the fifth thoracic sternite are relatively broad and distally rounded, forming a narrow and pointed notch (Fig. 4D); the spines on the first three abdominal sternites are triangular, creating a relatively rectangular-shaped base (Fig. 5.1D); the spines on the fourth and fifth abdominal sternites are narrow and distally rounded (Fig. 5.2E–F); the spine on the sixth abdominal sternite is triangular with a relatively broad base (Fig. 5.3E). In females, the spines on the fifth thoracic sternite are very short, with obscured notch (Fig. 4G); the spine on the sixth abdominal sternite is pointed (Fig. 5.3G). The body colour is diverse, background may vary from red to grey-blue, with numerous spots in different sizes; rostrum and appendages with encircled-stripes (e.g., Fig. 6A–B).

Distribution. *Saron marmoratus* is a coral reef species found down to 50 m depth along Indo-West Pacific coasts, including East Africa, Australia, French Polynesia, Japan, and Hawaii (Anker & De Grave, 2016; De Grave et al., 2012). Reports of this species from the Mediterranean Sea and Red Sea may represent the reinstated synonym *Hippolyte hemprichii*, redescribed below, although further investigation is needed to clarify their identifications.

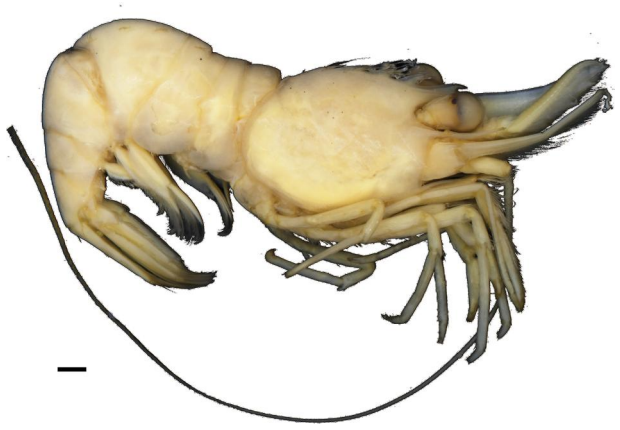

Fig. 7. *Saron hemprichii* comb. nov., holotype, NHMW-CR1029, male, cl. 5.2 mm; lateral view. Scale bar: 0.1 mm. Photo by Martin Schwentner.

Saron hemprichii (Heller, 1861) comb. nov.
(Table 1; Figs 1, 2, 3A–D, 4A–C, E–F, 5.1A–C, 5.2A–D, 5.3A–D, F, 6C, 7–11; Supplemental Tables S1, S3, S4)

Holotype. NHMW-CR1029, male (cl. 5.2 mm), collected in 1855 by Frauenfeld from "Rothes Meer" (the Red Sea) (Fig. 7).
Paratype. NHMW-CR1029, male (cl. 4.0 mm), collected in 1855 by Frauenfeld from "Rothes Meer" (the Red Sea).

Other material examined. SMNHTAU:Ar.29650, one male and one female (cl. 14.7 and 11.6 mm, respectively), collected on 5 June 2016 by M. Ilan, from Akhziv, coast of Israel, 33°3′20.37′′N, 35°6'7.76′'E, 0.5 m (Fig. 6C); SMNHTAU:Ar.29651, one male (cl. 11.2 mm), collected on 18 June 2016 by O. Klein, from Nahariyya, coast of Israel, 26 m; SMNHTAU:Ar.30265, one female (cl. 16.5 mm), collected in August 2017 by R. Gevili, from Ashdod, coast of Israel, 0–1 m; SMNHTAU:Ar.29842, two males (cl. 13.0 and 15.9 mm), collected on 19 June 2017 by N. Shenkar, from Akhziv, coast of Israel, 33°3′20.37′′N, 35°6'7.76′'E, 0–1 m; SMNHTAU:Ar.27936, one male and one ovigerous-female (cl. 15.6 and 10.0 mm, respectively), collected on 18 July 2017 by G. Vered, from Akhziv, coast of Israel, 33°3′20.37′′N, 35°6'7.76′'E, 0–1 m; SMNHTAU: Ar.29995, one male (cl. 13.1 mm), collected on 7 November 2019 by I. Kain, from Nahariyya, coast of Israel: 0–1 m; SMNHTAU:Ar.30269, one male (cl. 11.6 mm), collected on 30 May 2022 by T. Feldstein, from Akhziv, coast of Israel, 0.5 m; SMNHTAU:Ar.27059, one male and one female (cl. 13.1 and 10.1 mm, respectively), collected on 1 February 1987 by E. Shpanier, from Ras Gara (At Tur), Gulf of Suez, coast of Egypt; SMNHTAU:Ar.29242, one female (cl. 11.3 mm), collected on 21 May 2014 by Kopolovitz G. and Levitt-Barmats Y., from Elat, Gulf of Aqaba, coast of Israel, 29°32'49″N, 34°57'14″E, 10 m; ZMB 18239, three males (cl. 3.1–5.7 mm), collected in 1901–1902 by Hartmeyer, from Red Sea, Gulf of Suez.

Diagnosis. The referred species belonging to the genus *Saron*, is characterized by the following characters: (1) its curved upward rostrum with three-dentate tip, longer than carapace, with 5–6 dorsal teeth and 5–8 ventral teeth; (2) the antennular peduncle third segment with a dorsal horizontal tooth; (3) the carpus of the second pair of pereiopods with 9–15 articles; (4) in males, the first pair of pereiopods base is jagged, the fifth thoracic sternite spines are fused at the base and bifurcate distally, the first three abdominal sternites have a pair of long, narrow, and sharp spines, the fourth and fifth abdominal sternites have one large, acute triangular-shaped spine, the sixth abdominal sternite has a narrow acute spine; (5) in females, the chelae of the first pair of pereiopods have 2 small spines with dark tips on each side of the dactyl and scattered setae, the fifth thoracic sternite spines are forming a deep and narrow concave notch with distally rounded projections, the sixth abdominal sternite has a small acute, triangular-shaped spine.

Differential diagnosis. *Saron hemprichii* comb. nov. can be differentiated from *S. marmoratus* mostly based on sexual differences displayed in the thoracic and abdominal sternites. In males, the structure of the first pair of pereiopods base is jagged; the fifth thoracic sternite spines are fused in the base but bifurcate distally, forming a deep notch; the first three abdominal sternites have a pair of long, narrow, acute spines, with a quadrangular-shaped base, the fourth and fifth abdominal sternites have 1 large, acute triangular-shaped spine; and though this is a less distinguished character, the spine of the sixth abdominal sternite is acute and small. In females, the fifth thoracic sternite has a deep and narrow notch; the sixth abdominal sternite is triangular-shaped.

Saron hemprichii comb. nov. differs from *S. neglectus* by (1) the entire orbital margin (versus orbital margin with postorbital ridge in *S. neglectus*), (2) cutting edge of the second pereiopod's movable finger entire (versus minutely denticulate in *S. neglectus*), and (3) the horizontal orientation of the dorsal tooth on the third segment of the antennular peduncle (versus conspicuously upstanding in *S. neglectus*).

Saron hemprichii comb. nov. differs from *S. inermis* and *S. rectirostris* by (1) the slender rostrum which is longer than the carapace (versus the deep rostrum being shorter than the carapace in *S. inermis* and *S. rectirostris*) and (2) the presence of 2 spines on the merus of the fifth pereiopods (versus the absence of these spines in *S. inermis* and *S. rectirostris*).

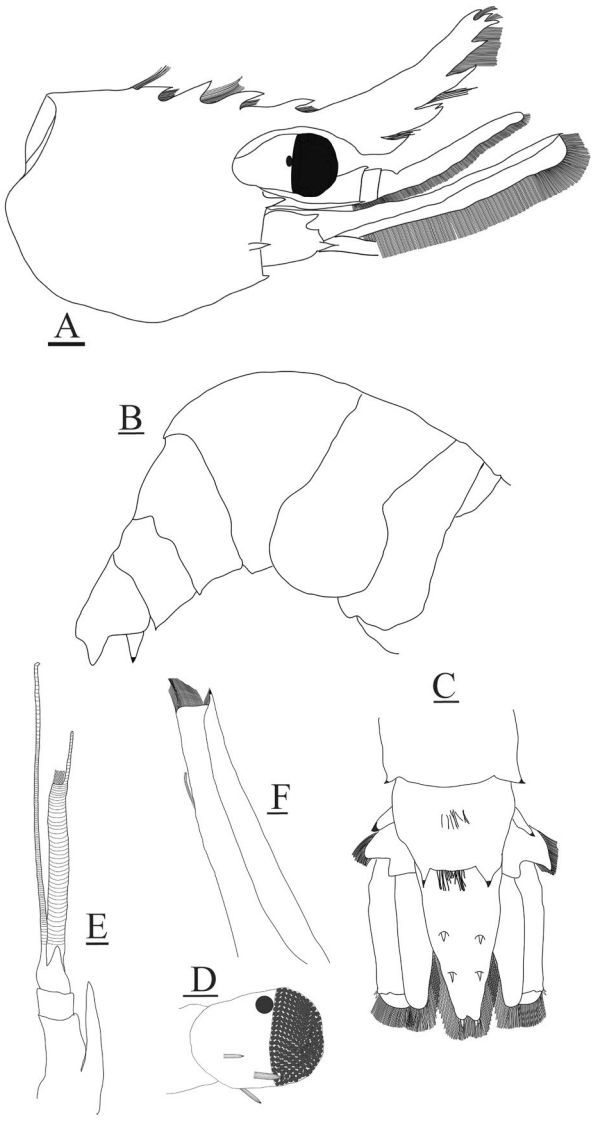

Fig. 8. *Saron hemprichii* comb. nov. males. **A–C.** holotype, NHMW-CR1029, cl. 5.2 mm; **D–F.** SMNHTAU:Ar.29650, cl. 14.7 mm. **A.** carapace, lateral view; **B.** abdomen, lateral view; **C.** telson and uropods, dorsal view; **D.** right eye, lateral view; **E.** antennula, lateral view; **F.** scaphocerite, dorsal view. Scale bars: 1 mm.

Description of the holotype. NHMW-CR1029. Adult male, in poor state of preservation. Rostrum longer than carapace, curved upward (Fig. 8A); dorsal margin with 5 teeth of which 1 subdistal and 3 postorbital and 1 more posterior protrusion, with tufts of plumose setae submedially at base of teeth; ventral margin with 5 teeth, with rows of plumose setae in between. Carapace with tufts of plumose setae submedially at base of teeth (Fig. 8A); antennal spine robust, branchiostegal and pterygostomian spines small (Fig. 8A).

Abdomen smooth; pleura of first and second pleonite ventrally rounded, of third angular posteroventrally, of fourth and fifth with small but distinct posteroventral tooth, sixth pleonite with ventrally articulating, triangular, posteroventrally acute flap, with pleura with acute tooth posterolaterally (Fig. 8B). The first three abdominal sternites with narrow and sharp spines, creating a quadrangular base (Fig. 5.1A); fourth and fifth sternites with triangular spines (Fig. 5.2A); sixth sternite with small narrow spine (Fig. 5.3A).

Telson approximately 1.5 times as long as sixth pleonite, leaf-like in shape; distal margin with slightly concave notch and two pairs of spines, lateral spines shorter and more robust than median ones, dense cover of setae along the tip and distolateral margins; two pairs of distinct dorsolateral spines, distal pair half-way between proximal pair and distal margin (Fig. 8C).

Eyes are relatively large with hemispherical cornea; short eyestalks with some scattered setae and small dorsal circular ocellus (Fig. 8A).

Antennular peduncle about half of rostrum length (Fig. 8A); first segment long, dorsally concave, with ventromedial forward directed tooth; stylocerite long, acute, reaching third segment of antennular peduncle; second segment of antennular peduncle rectangular; third segment of antennular peduncle very short, dorsal margin with short, broad, triangular-shaped, horizontally orientated distal process; outer flagellum much broader than inner flagellum, fused basal part composed of 36 segments, with dense cover of aesthetascs ventrolaterally, shorter free ramus obsolete, longer free ramus slender, just reaching distal tip of rostrum; inner flagellum slender, overreaching outer flagellum with more than 50 segments.

Antennal basicerite with 2 acute spines, distodorsal spine long, distolateral spine smaller (Fig. 8A); scaphocerite almost as long as rostrum, with long median ridge proximally; distal margin of blade blunt; distolateral tooth well-developed, exceeding blade (Fig. 8A).

Endopod of third pair of maxillipeds is three-segmented; ultimate with short simple setae and 5 scattered spines with dark tips, diverse in shape on distal margin, ultimate median and proximal margins with long plumose setae; penultimate segment with long plumose setae and large spine; antepenultimate segment with short and dense tufts of grooming setae digitate scale setules and 2 distinct spines on distal margin; exopod simple, reaching more than half of antepenultimate segment (Fig. 9A).

First pair of pereiopods shorter than third maxilliped, both not overreaching scaphocerite; left and right chelae equal in size and form, spatulated fingers with dense cover of stiff setae on inner margins (Fig. 9B), with one

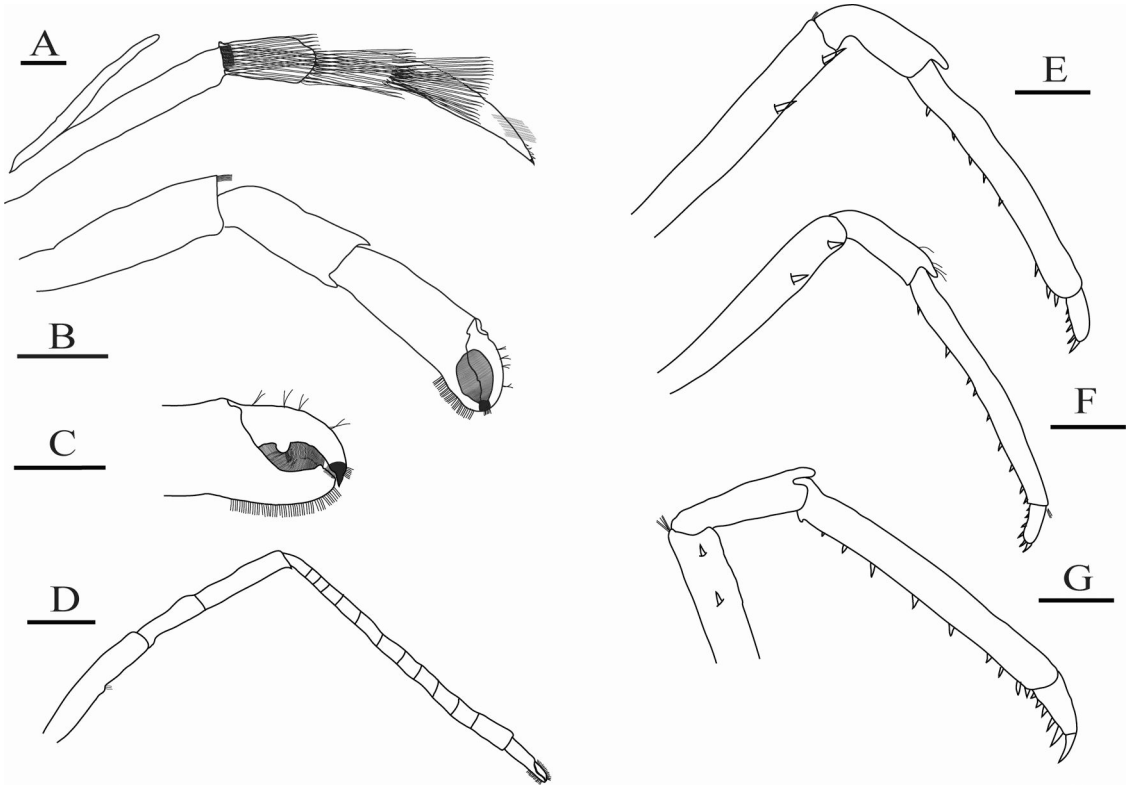

Fig. 9. *Saron hemprichii* comb. nov., holotype, NHMW-CR1029, male, cl. 5.2 mm. **A.** third maxilliped, lateral view; **B.** first pereiopod, lateral view; **C.** chela, first pereiopod; **D.** second pereiopod; **E.** third pereiopod; **F.** fourth pereiopod; **G.** fifth pereiopod. Scale bars: A = 0.5 mm; B–G = 1 mm.

distinct protuberance on inner side of movable finger and small protuberance on the inner side of the fixed finger (Fig. 9C); dactylar finger with a few scattered serrate setae; propodus with many serrate setae on distal margin; structure of pereiopods base is curved, relatively coarse, not smooth.

Second pair of pereiopods longer than first pair; dactyls slender, about 0.3 times length of palm, fingers with short stiff setae; carpus with 12 articles, about 1.8 times longer than merus; ischium about 0.9 times merus length (Fig. 9D).

Ambulatory pereiopods slender. Dactylus of third pereiopod with 5 spines, carpus about three times as long as proximal width; propodus about four times longer than dactylus, about nine times as long as wide, with 2 distolateral spines and 8 spines along ventral margin; carpus 0.3 times propodus length, 2.1 times as long as distal width, unarmed; merus about 2.5 times carpus length, 5.3 times longer than central width, with 2 spines on distal half; ischium about 0.7 times merus length, 4.4 times longer than distal width; basis and coxa without special features (Fig. 9E). Dactylus of fourth pereiopod with 6 spines, carpus length about three times as long as proximal width; propodus about four times longer than dactylus, about nine times as long as wide, with 2 distolateral spines and 9 spines along ventral margin; carpus 0.3 times propodus length, twice as distal width, unarmed; merus about 3.3 times carpus length, 6.5 times longer than central width, with 2 spines on the distal half; ischium about 0.4 times merus length, 3.9 times longer than distal width; basis and coxa without special features (Fig. 9F). Dactylus of fifth pereiopod with 6 spines, carpus length about twice as proximal width; propodus about four times longer than dactylus, about eight times as long as wide, with 2 distolateral spines and 9 spines along ventral margin; carpus 0.3 times propodus length, twice as distal width, unarmed; merus about 2.5 times carpus length, about six times longer than central width, with 2 spines on the distal half; ischium about 0.7 times merus length, about four times longer than distal width; basis and coxa without special features (Fig. 9G).

Uropods slightly shorter than distal margin of telson, both exopod and endopod of equal length, about three times longer than wide, with subovate-shape and dense thick setae along tip and lateral margins; exopod with 2 spines on distolateral margin; protopodite with 2 strong and large spines (Fig. 8C).

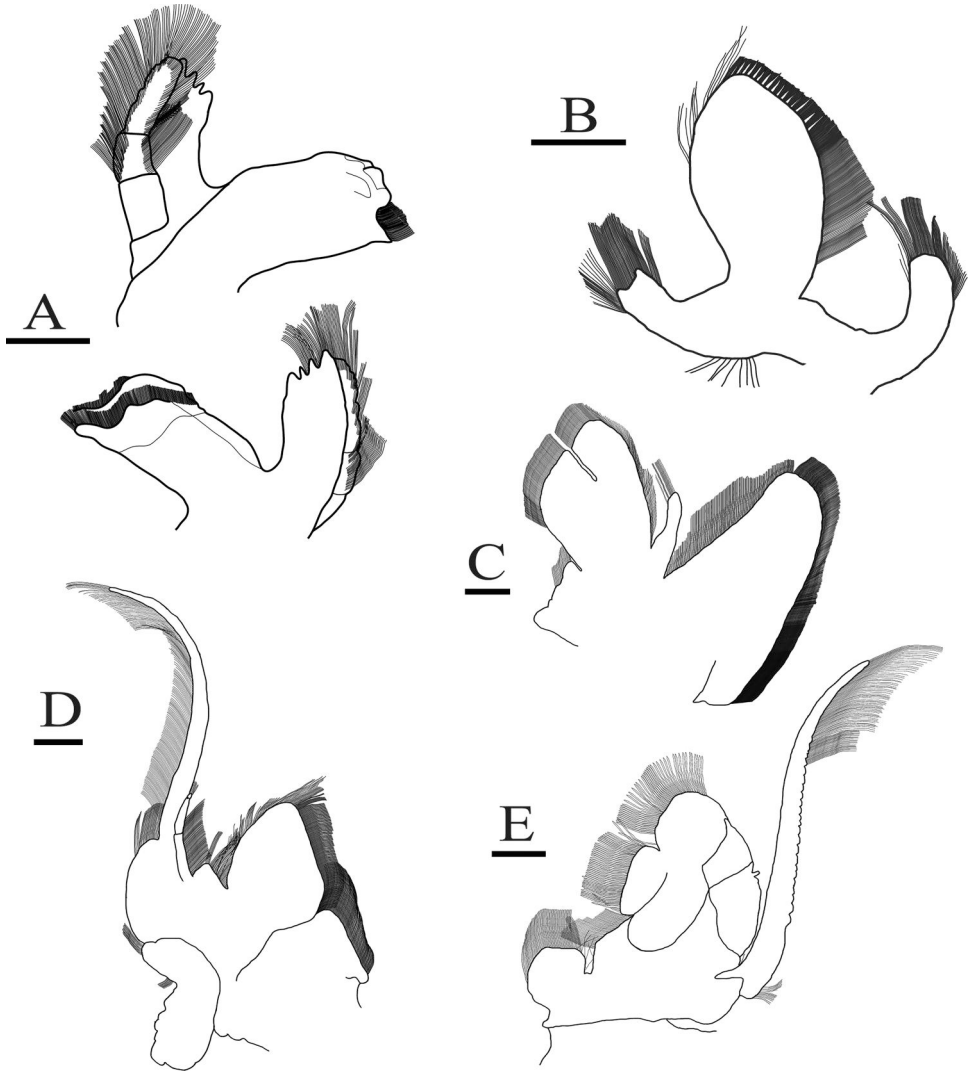

Fig. 10. *Saron hemprichii* comb. nov., SMNHTAU:Ar.29650, male, cl. 14.7 mm. **A.** left mandible, dorsal and ventral views; **B.** maxillule, ventral view; **C.** maxilla, ventral view; **D.** first maxilliped, ventral view; **E.** second maxilliped, ventral view. Scale bars: 1 mm.

Body colour of the types is not described and is faded following preservation process (Fig. 7).

Variation. To avoid damaging the old and fragile type specimen some of the drawings were made only based on the recently collected material, all are similar to the holotype: right eye, lateral view (Fig. 8D); antennular peduncle, lateral view (Fig. 8E); scaphocerite, dorsal view (Fig. 8F); mandible (Fig. 10A); maxillule (Fig. 10B); maxilla (Fig. 10C); first pair of maxillipeds (Fig. 10D); second pair of maxillipeds (Fig. 10E); first pair of pleopods (Fig. 11A); second pair of pleopods (Fig. 11B); third pair of pleopods (Fig. 11C); fourth pair of pleopods (Fig. 11D).

Mandible with three-segmented palp; incisor process with 4 stout triangular-shaped teeth on distal margin, 2 exterior teeth with a broad base; molar process stout, with stiff dense setae (Fig. 10A). Maxillule with bilobed palp; upper lacinia large with relatively quadrangular-shaped with round margins, medial spines short, acute; lower lacinia slender, spines long, acute; both laciniae with simple setae (Fig. 10B). Maxilla with rounded, unsegmented palp; basal endite relatively quadrangular-shaped, bilobed, with dense cover of short setae along medial margins, distal lobe smaller than proximal lobe; coxal endite obsolete, with dense cover of setae along medial margin (Fig. 10C). First pair of maxillipeds with three-segmented palp, rounded distally; caridean lobe rather small, exopod long with fringe of setae; epipod bilobed; endites with distal quadrangular-shape (Fig. 10D). Second pair of maxillipeds with relatively broad

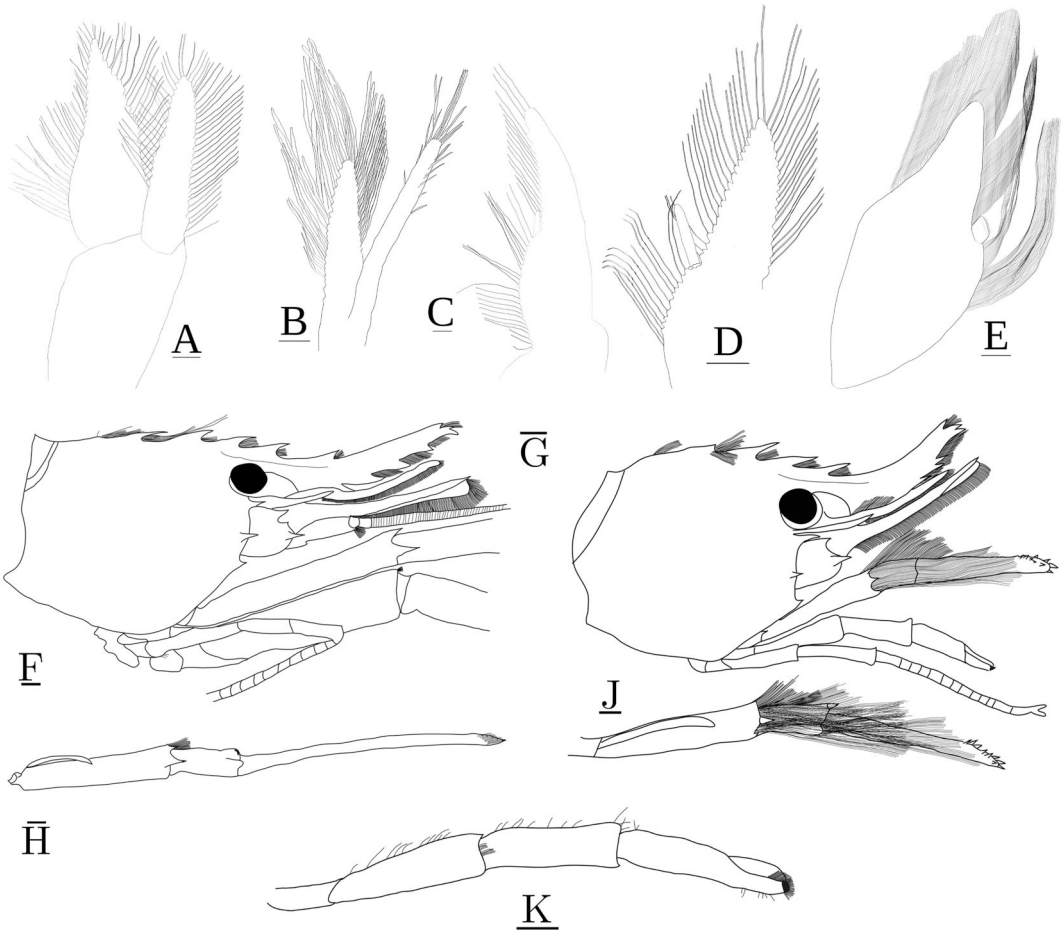

Fig. 11. *Saron hemprichii* comb. nov., SMNHTAU:Ar.29650. **A–D, F, H.** male, cl. 14.7 mm; **E, G, J–K**, ovigerous-female, cl. 11.6 mm. **A.** First pleopod; **B.** Endopod of the second pleopod and appendix masculine; **C.** Endopod of the third pleopod; **D.** Endopod of the fourth pleopod; **E.** Endopod of the second pleopod; **F.** carapace, lateral view; **G.** carapace, lateral view; **H.** third maxilliped, lateral view; **J.** third maxilliped, lateral view; **K.** first pereiopod, lateral view. Scale bars: A–E = 0.5 mm; F–K = 1 mm.

proximal segments; dactylus is broad with stout densely spaced spines along distal margin; propodus with broadly rounded distolateral margin (Fig. 10E).

First pair of pleopods with leaf-like shaped exopod; endopod long, distally relatively rounded, reaching 0.75 of exopod length; both with long plumose setae (Fig. 11A). Appendix masculina of second pair of pleopods overreaching distal margin appendix interna, with long serrate setae; appendix interna with terminal hooked setae (Fig. 11B).

Appendix interna of third pair of pleopods reduced; endopod with long plumose setae (Fig. 11C). Appendix interna of fourth pair of pleopods is reduced though a bit larger than that of the third pleopod; endopod with long plumose setae (Fig. 11D).

The species present diversity in some of the morphological characters and sexual differences between males and females. The rostral dorsal margin has 5–6 (mostly 6) teeth, the posterior protrusion on the carapace, usually beneath tufts of setae; the rostral ventral margin has 5–8 (mostly 6–7) teeth. The carapace and abdomen may have some tufts of plumose setae submedially along dorsal midline except for the first pleonite, especially in females (see Fig. 11F for male, 11G for female). The third pair of maxillipeds presents sexual and size differences; in the larger males (cl. 10 mm), ultimate segment with short and dense tufts of setae on distal margin, without long plumose on penultimate segment, 2–8 (mostly 6 and below) scattered dark tips spines diverse in shape, penultimate segment without setae, exopod short, reaching less than half of antepenultimate segment (Fig. 11H); in females ultimate and penultimate segments with long and dense tufts of setae, ultimate with 8–9 (mostly 8) scattered dark tips spines on distal margin (Fig. 11J).

The first pair of pereiopod chelae was found unequal in one specimen (SMNHTAU:Ar.29651); sexual dissimilarity is present; in males as described for the

holotype, in females the chelae have scattered setae and 2 small spines with dark tips on the fingers (Fig. 11K). In the largest males (SMNHTAU:Ar.27936, SMNHTAU:Ar.29842, SMNHTAU:Ar.29650) both first pair of pereiopods and third maxilliped overreaching scaphocerite. Second pair of pereiopods in larger males is usually shorter than the first pair (cl. more than 11.2 mm; SMNHTAU:Ar.27936, SMNHTAU:Ar.29650, SMNHTAU:Ar.29651, SMNHTAU:Ar. 29842, SMNHTAU:Ar.30269), but not all; in smaller males, two large males (more than 11.2 mm; SMNHTAU:Ar.27059, SMNHTAU:Ar.29995), and females the second pair is longer than the first; the carpus has 9–15 (mostly 12–13) articles. The ambulatory pereiopods dactyli have 5–7 (mostly 5–6) spines on the flexor margin, the propodus has 9–16 (mostly 10–12) ventral spines, and the merus has 1 or 2 (mostly 2) spines.

The fifth thoracic sternite and sixth abdominal sternite in males are the same as described for the holotype; in females, the fifth thoracic sternite forms a deep and narrow concave notch (Fig. 4E–F), the sixth abdominal sternite has a small sharp triangular-shaped spine (Fig. 5.3F).

The pleopod of males are as described for the holotype; in females, the second pleopod has a miniature bulge-like appendix interna, with rows of hooks along its distal margin; the endopod has long plumose setae on the distal and lateral margins (Fig. 11E).

Body colour of present specimens is diverse, the carapace and abdomen are with yellowish-brown or light-brown background and numerous reddish-brown spots in different sizes, in the centre of the large spots there are small blue dots; rostrum and appendages are yellow with dark encircled-stripes, third pair of maxilliped and first pair of pereiopods, the stripes may be more flexible; the telson is also yellow with brown patterns; the carapace, abdomen and third pair of maxilliped, the dense tufts of setae is usually dark in the base and become more reddish-brown towards the edge (Fig. 6C).

Distribution. *Saron hemprichii* comb. nov. occurs on rocky bottoms within crevices, corals, and dead corals, sometimes near sea urchins, down to approximately 30 m depth along the Mediterranean and Red Sea coasts (Katsanevakis et al., 2020; Rothman et al., 2013; Vine, 1986; current study), including Israel's coastal shores. Other studies have reported *Saron* specimens from eastern Mediterranean coastal areas (i.e., Lebanon, Syria, Cyprus, and Turkey; Ammar & Raya, 2019; Bianchi et al., 2022; Ergüden et al., 2018; Langeneck et al., 2022). These records most likely represent *S. hemprichii* comb. nov. as well, although careful investigation is needed for proper identification.

Discussion

The progressive expansion of the Suez Canal over the years, connecting the Mediterranean and Red Sea, along with intensified human activities, such as shipping, aquaculture, and the marine aquarium trade, has facilitated the introduction of alien species into the Mediterranean (Galil, 2011; Galil et al., 2018; Ojaveer et al., 2018; Tsiamis et al., 2020). This increased invasive risk, combined with rising seawater temperatures, which facilitates the establishment of tropical species, underscores the need for systematic monitoring of Mediterranean marine biota to elucidate population changes, particularly along the warmer Levant Basin coasts. To date, over 200 alien crustacean species have been reported from the Mediterranean Sea, more than half are considered established (Zenetos et al., 2022).

In this study, we conducted morphological and phylogenetic analyses of *Saron* populations from the Mediterranean and Red Sea. Previous studies identified these populations as *S. marmoratus*, a species with a broad Indo-West Pacific distribution (Ammar & Raya, 2019; Bianchi et al., 2022; Ergüden et al., 2018; Katsanevakis et al., 2020; Langeneck et al., 2022; Rothman et al., 2013; Zenetos et al., 2015). Our morphological and molecular data reveal clear differentiation between Mediterranean/Red Sea populations and Indo-West Pacific *S. marmoratus* (including from the Australian type locality), thereby justifying reinstatement of *S. hemprichii* comb. nov., originally described from the Red Sea in 1861 and later synonymized with *S. marmoratus*.

Morphological differences between *S. hemprichii* comb. nov. and *S. marmoratus* were found in the basal structure of the first pair of male pereiopods and in the thoracic and abdominal sternites of both sexes. *Saron hemprichii* comb. nov. also differs morphologically from the other three species of the genus. Both *S. inermis* and *S. rectirostris* have a deep rostrum that is usually shorter than the carapace and lack spines on the merus of the fifth pereiopods (Chace, 1997; Hayashi, 1984, 1989). *Saron hemprichii* comb. nov. differs from the morphologically similar *S. neglectus* in the orbital margin, the shape of the second pereiopod's movable finger, and the orientation of the dorsal tooth on the third segment of the antennular peduncle (Chace, 1997; De Man, 1902). Colour pattern variation also distinguishes *Saron* species. Notably, ambulatory pereiopod colouration differs conspicuously between *S. hemprichii* comb. nov. and *S. neglectus* (Baeza et al., 2023). *Saron marmoratus* exhibits extensive body colour polymorphism, with certain patterns consistent across broad geographic ranges (Baeza et al., 2023; Anker & De Grave, 2016; Debelius, 2001; Minemizu, 2013). In Singapore, specimens display the *S. marmoratus* sensu stricto

pattern, characterized by a brownish-orange background with large brown spots (Anker & De Grave, 2016: fig. 62A). Live *S. marmoratus* specimens purchased in this study from an Indonesian source showed colour variation (Fig. 6A–B), predominantly reddish backgrounds, though some exhibited greyish-bluish backgrounds with white dots akin to Singaporean specimens (Anker & De Grave, 2016: fig. 62B–C). By contrast, live *S. hemprichii* comb. nov. specimens feature a yellowish-brown to light-brown background with small reddish-brown spots (Fig. 6C). Colour pattern similarity between Mediterranean and Red Sea specimens, as noted by Rothman et al. (2013), further corroborate their close phylogenetic affinities.

Molecular phylogenetic research on the genus *Saron* remains relatively limited, as most studies have included only one or a small number of individuals within broader systematic frameworks (e.g., Aznar-Cormano et al., 2015; De Grave et al., 2014; Wang et al., 2021). The first broad sampling of the Indo-West Pacific species *S. marmoratus* and *S. neglectus* in Baeza et al. (2023), coupled with morphological examinations, indicated that they likely represent cryptic species complexes, aligning with previous morphological hypotheses. None of these molecular studies, however, included Mediterranean or Red Sea specimens, leaving their phylogenetic position unresolved. Our phylogenetic reconstructions, using mitochondrial markers *16S* and *COX1*, yielded congruent topologies across analyses and marked genetic diversity within *Saron*. Our results support the genetic distinctiveness of Mediterranean or Red Sea populations relative to Indo-West Pacific populations (including those from Australia, the type locality of *S. marmoratus*). In all analyses, Mediterranean specimens clustered closely with Red Sea individuals, indicating strong phylogenetic affinity between the two regions. The pet shop specimen sampled in our study grouped with Indo-West Pacific populations, aligning with the seller's reported Indonesian provenance.

Rothman et al. (2013) provided the first record of *S. marmoratus* (now *S. hemprichii* comb. nov.) from the Levant Basin, prompting questions about potential introduction pathways. The authors proposed three possibilities: introduction via the marine aquarium trade by aquarists, transport in the hull fouling communities of slow-moving vessels from the Persian Gulf or the Indo-West Pacific, or introduction via the Suez Canal – deeming the latter the most likely given the species' established presence in the Gulf of Suez and Red Sea and its zoeal stage length. Our morphological and phylogenetic analyses reveal clear distinctiveness and strong affinities between Mediterranean and Red Sea populations, thereby supporting the Suez Canal pathway over the alternative scenarios. Notably, *S. marmoratus* specimens reported from the northern Levant Basin (Ammar & Raya, 2019; Ergüden et al., 2018; Langeneck et al., 2022; Zenetos et al., 2015) may instead represent the reinstated *S. hemprichii* comb. nov. Accurate taxonomic identification of these *Saron* specimens is essential for delineating their Mediterranean distribution and assessing ecological impacts on native biota.

In his comprehensive expedition monograph, Chace (1997) described the genus *Saron* as a "taxonomic nightmare". Baeza et al. (2023) suggested the existence of cryptic species within the broadly distributed *S. marmoratus* complex, advocating for future studies employing integrated methodologies. The reinstatement of *S. hemprichii* comb. nov. for Red Sea and Mediterranean populations in our study constitutes a significant step toward resolving the *S. marmoratus* species complex. Accordingly, further research, including broader sampling from additional Mediterranean localities in comparison with Israeli populations, is warranted.

Acknowledgements

This research could not have been carried out without the support and help of R. Ben-David Zaslow, the Chief Collections Manager, the Steinhardt Museum of Natural History, Israel National Centre for Biodiversity Studies, Tel Aviv University, along with N. Shenkar and her past lab members for collecting some of the material studied: L. Novak, G. Kopolovitz, M. Gewing, L. Raijman, G. Vered, Y. Shmuel, T. Gordon, and Y. Jacobi. We are grateful to M. Ilan, G. Kopolovitz, G. Vered, O. Klein, and I. Kain; S. Rothman, A. Ben-Dov Segal, Z. Yanai, R. Pickholtz, O. Ben-Zvi, and O. Rittner for their help and support in the lab and the field; M. Schwentner of the Natural History Museum, Vienna for sending and photographing the type specimens; L. Corbari of the Museum national d'Histoire naturelle, Paris; B. Trautwein of the Senckenberg Museum, Frankfurt-am-Main, Germany; O. Coleman of the Museum für Naturkunde, Berlin; and S. De Grave of the Oxford University Museum of Natural History, Oxford for sending and loaning us samples from the Indo-West Pacific Ocean. Special thanks to C. Fransen for his review and valuable comments on the taxonomic part of the paper; T. Feldstein-Farkash from the Steinhardt Museum of Natural History, Tel Aviv University for the help with the molecular work; and to H. Barmats for the help with the figures. We thank the two reviewers for their constructive comments.

Supplemental material

Supplemental material for this article can be accessed online here: https://doi.org/10.1080/14772000.2026.2684068.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This study was supported by the Israel Taxonomy Initiative PhD fellowship to YLB.

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