What is *Sesarmops impressus* (H. Milne Edwards, 1837) (Crustacea: Brachyura: Sesarmidae)?

Peter K. L. Ng¹, Jheng-Jhang Li²,³, and Hsi-Te Shih⁴,⁎

¹Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Republic of Singapore.
   E-mail: peterng@nus.edu.sg
²Department of Marine Biotechnology and Resources, National Sun Yat-sen University, 70, Lianhai Road, Kaohsiung 80424, Taiwan.
   E-mail: epigrapsus@gmail.com
³East Peak Ecological Consultants, Inc., 22, Wanggong Road, Linyuan Dist., Kaohsiung 83249, Taiwan
⁴Department of Life Science and Research Center for Global Change Biology, National Chung Hsing University, 250, Kuo Kuang Road, Taichung 402, Taiwan. *Correspondence: E-mail: htshih@dragon.nchu.edu.tw (Shih)

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The identity of the widely distributed mangrove and riverine sesarmid crab *Sesarmops impressus* (H. Milne Edwards, 1837) is clarified. The species has been reported from Madagascar to the South Pacific, but its taxonomy was previously confused. On the basis of morphological characters and available molecular evidence (using 16S rDNA and cytochrome oxidase subunit I), *Sesarmops impressus* is restricted to the western Indian Ocean and *S. frontale* A. Milne-Edwards, 1869 is confirmed to be its junior synonym. *Sesarmops similis* (Hess, 1865), long synonymised under *S. impressus*, is here recognised as a separate species and a neotype from Samoa is designated. The identity of the poorly known *S. atrorubens* (Hess, 1865), which has often been confused with *S. impressus*, is also clarified, and a neotype is selected from Fiji. Specimens from the eastern Indian Ocean and western Pacific are here identified as two new species, *S. indicus* sp. nov. and *S. imperator* sp. nov.

**Key words:** Taxonomy, New species, *Sesarmops impressus*, *S. indicus*, *S. imperator*, *S. atrorubens*, *S. similis*, Morphology, Mitochondrial 16S rDNA, Cytochrome oxidase subunit I.

**BACKGROUND**

Serène and Soh (1970) established a new genus, *Sesarmops*, for six Indo-West Pacific sesarmid species: *S. atrorubens* (Hess, 1865), *S. impressus* (H. Milne Edwards, 1837) (designated as type species), *S. intermedius* (De Haan, 1835), *S. mindanaoensis* (Rathbun, 1914), *S. sinensis* (H. Milne Edwards, 1853) and *S. weberi* (De Man, 1892). In doing so, they expressed doubts about *S. intermedius* (De Haan, 1835) and *S. sinensis* (H. Milne Edwards, 1853), noting that they may need to be moved elsewhere in the future. Ng et al. (2008: 223) recognised six species in *Sesarmops*, commenting that the placement of *S. intermedius*, *S. sinensis* and *S. weberi* were provisional and they actually belonged to other genera. Paulay and Starmer (2011) subsequently transferred another species, *Sesarma angustifrons* A. Milne-Edwards, 1869, to the genus.

Serène and Soh (1970: 400) defined *Sesarmops* as follows: carapace as long or longer than the width measured at the external orbital teeth, the frontal margin has a deep median concavity, the postfrontal lobes are prominent, the external orbital tooth is clearly separated from the rest of the lateral margin by a distinct cleft, with the gastric and cardiac regions well defined. In their key to the genera, in which they also cited the taxa as separate, Serène and Soh (1970: 391) had *Sesarmops* grouped with *Pseudosesarma* Serène & Soh, 1970, and
Bresedium Serène & Soh, 1970. Bresedium supposedly has the male telson deeply inserted into the distal margin of somite 6 and the chitinous distal part of the male first gonopod is distinctly elongate. Pseudoserasma and Sesarmops do not have these characters. The problem is that the type species of Sesarmops, S. impressus, actually has the male telson also inserted into the distal margin of somite 6 and the chitinous distal part of the male first gonopod is also long.

The composition of Sesarmops and its close affinities with Bresedium Serène & Soh, 1970 have been discussed at length by several authors (Ng et al. 2008; Li et al. 2020; Schubart and Ng 2020), but until a complete revision is done, not much can be said. Schubart and Ng (2020) formally transferred S. intermedius and S. sinensis to a new genus with several other species previously placed in Chiromantes Gistel, 1848. Li et al. (2020) also noted that S. mindanaoensis (Rathbun, 1914) is not a member of Sesarmops as it has a very different male thoracic sternum, pleon and male first gonopod, and is also genetically distinct (see also Schubart and Ng 2020). The same situation exists for S. angustifrons which is genetically more allied with S. mindanaoensis than other Sesarmops species (Schubart and Ng 2020; unpublished data). In their revision of Labuanium Serène & Soh, 1970, Naruse and Ng (2020) treated S. weberi which Ng et al. (2008) believed was close to Labuanium trapezoideum (H. Milne Edwards, 1837). Naruse and Ng (2020) showed that S. weberi and L. trapezoideum are unlikely to be related but deferred to a decision about where to place S. weberi until a revision of the genus could be done.

Christoph Schubart and his colleagues are now revising Sesarmops and Bresedium and will recognise more taxa in their ongoing attempts to derive a more monophyletic classification of sesarmid genera. Until this can be done, any revised diagnosis for Sesarmops would not be helpful. As such, the broad concept of Sesarmops used by Serène and Soh (1970) (see above) is followed in this study. One problem, however, that needs to be resolved here is with regards to the identity of the type species, Sesarma impressa H. Milne Edwards, 1837, whose type locality is unknown. Two species, Sesarma similis Hess, 1865 (from “Sydney”), and Sesarma frontale A. Milne-Edwards, 1869 (from Madagascar), are currently regarded as junior synonyms of this species (see De Man 1887; Crosnier 1965; Ng et al. 2008). Sesarmops impressus is one of the more common sesarmids inhabiting mangrove and fresh water habitats from Madagascar to the western Pacific and has often been reported in the literature. The first author has suspected there was a problem with the taxonomy of this species, as the life colours of the material from Madagascar, Comoros and Mayotte (e.g., Bouchard et al. 2013) is very different from those from the Philippines, Taiwan and Japan (e.g., Lee 2001; Liu 2009; Liu and Wang 2010; Li and Chiou 2013; W.-J. Chen and Lo 2014). Bouchard et al. (2013: 24) commented that “Sesarmops impressus is part of a species complex with at least two forms in the IWP [Indo-West Pacific]. The Indian Ocean population generally has white chela and a yellowish-white carapace. This is probably the real Sesarmops impressus. The ‘Sesarmops impressus’ reported from the East [sic] Pacific (e.g., Taiwan, China, Japan, Philippines, New Guinea, and eastern Indonesia) has dark brown carapaces with deep red chela. Their gonopods also differ.” The genetic study by Li et al. (2020) supports this observation. A revision of the species was also compounded by the uncertainty over the identity of Sesarmops atrorubens (Hess, 1865), which superficially resembles S. impressus.

One of the problems with the genus is associated with the identities of the two species described by Hess (1865) ostensibly from “Sydney” – S. atrorubens and S. similis. Both species were described based on one specimen each and only briefly, with only S. atrorubens figured. The material was supposed to be deposited in Göttingen University. De Man (1887) re-examined Hess’ material, reidentified the species, and discussed at length the various taxonomic problems associated with his specimens. He managed to compare the types of S. atrorubens and S. similis with the type and other specimens of Sesarma impressa from Madagascar. He decided that S. atrorubens is a valid species while S. similis is synonymous with S. impressa. Although De Man’s (1887) discussion is detailed, he had few specimens available and did not provide any figures. Neither species has been reported in recent years, nor have they been described to modern standards, with the important male pleonal and gonopodal characters not known.

The provenance of the two types is also not known. The extant decapod crustacean material of Hess (1865) is known to be deposited in the Senckenberg Museum, which incorporated the Göttingen University material as part of its collections (see Ahyong and Ng 2007; Ng 2012; K. Sakai and Türkay 2013; Naruse and Ng 2020). Some material is in The Naturalis Biodiversity Institute and was obtained by exchange (Fransen et al. 1997). The Swedish Museum of Natural History in Stockholm also has some hermit crab material (see Sandberg and McLaughlin 1993; Komai and Mishima 2003). A search of these museums with the help of the various curators failed to find the type of S. similis or S. atrorubens. The types must thus have been lost since 1887. As discussed by Ng (2012: 269), the reason why “Sydney” may have been indicated as the type locality is simply because it was the main port of call for many European vessels.
trading in the European territories in that period, with collections actually originating from the South Pacific Islands. In the present work, neotypes were selected from the South Pacific islands to stabilise the taxonomy of these species.

The authors examined the types of H. Milne Edwards and A. Milne-Edwards in Paris, as well as a good series of what has been traditionally called “Sesarmops impressus” from various parts of the Indo-West Pacific. Molecular evidence from the mitochondrial 16S rDNA and cytochrome c oxidase subunit I (COI) (see Li et al. 2019 2020; Shih et al. 2019a) was also used to support the morphological observations as far as possible. Material from the eastern Indian Ocean is also shown here to be different from S. impressus, and is referred to a new species. Most of the material from Southeast Asia and the western Pacific previously referred to as “Sesarmops impressus” is also considered a new species. The types of the two species described by Hess are lost. Fresh specimens matching Hess’ original description and figures of S. aitorubens were obtained from Fiji and the species is redescribed with the selection of a neotype. Sesarma similis is here recognised as a distinct species, a neotype is selected and the generic affinities are discussed.

**MATERIALS AND METHODS**

Specimens examined are deposited in the Muséum national d’Histoire naturelle, Paris (MNHN); Nationaal Natuurhistorisch Museum—Naturalis, Leiden (previously Rijksmuseum van Natuurlijke Historie, RMNH); Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOD); Senckenberg Museum und Forschungsinstitut, Frankfurt am Main (SMF); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum (previously Raffles Museum of Biodiversity Research), National University of Singapore (ZRC). Measurements provided, in millimetres, are of the carapace width and length, respectively. The abbreviations G1 and G2 are used for the male first and second gonopods, respectively. The terminology used follows Davie et al. (2015).

Part of the sequences of the mitochondrial 16S rDNA and COI in Li et al. (2020) were used, including the sequences of two clades of S. impressus. In addition, we tried to sequence the specimens from India (ZRC 2015.0344a–c), Fiji (ZRC 2019.1070) and Samoa (ZRC 2017.0008) by following the method described by Shih et al. (2016). The sequencing for specimens from India and Samoa failed, probably because the specimens were too old or had previously been preserved in formalin. The sequences of the Fijian specimen and additional specimen from Mayotte (ZRC 2011.0005) have been deposited in the DNA Data Bank of Japan (DDBJ), under accession numbers LC547017-LC547020.

For the combined 16S and COI dataset, the best-fitting models for sequence evolution of individual datasets were determined by PartitionFinder (vers. 2.1.1, Lanfear et al. 2017), selected by the Bayesian information criterion (BIC). The best models obtained were both GTR + I + G and were subsequently applied to the partitioned Bayesian inference (BI) analysis. The BI was performed with MrBayes (vers. 3.2.6, Ronquist et al. 2012). The search was run with four chains for 10 million generations and four independent runs, with trees sampled every 1000 generations. The convergence of chains was determined by the average standard deviation of split frequency values below the recommended 0.01 (Ronquist et al. 2005) and the first 600 trees were discarded as burnin. The maximum likelihood (ML) analysis was conducted in RAxML (vers. 7.2.6; Stamatakis 2006). Because RAxML does not accept the GTR + I model, the second-best model, GTR + G (i.e., GTRGAMMA), was used with 100 runs, and the best ML tree was found by comparing the likelihood scores. The robustness of the ML tree was evaluated by 1000 bootstrap pseudoreplicates under the model GTRGAMMA. Basepair (bp) differences and pairwise estimates of Kimura 2-parameter (K2P) distances (Kimura, 1980) for genetic diversities of COI between specimens were calculated with MEGA (vers. 10.0.5, Kumar et al. 2018).

**RESULTS**

**TAXONOMY**

**Family Sesarmidae Dana, 1851**

**Genus Sesarmops Serène & Soh, 1970**

*Type species:* *Sesarma impressa* H. Milne Edwards, 1837, by original designation; gender masculine.

**Sesarmops impressus** (H. Milne Edwards, 1837)  
(Figs. 1–6, 13A–D, 14A–C, 15A–G, 16A–G, N–P)

*Sesarma impressa* H. Milne Edwards, 1837: 74 (no locality); H. Milne Edwards 1853: 186 (no locality); De Man 1887: 653, 671 (Madagascar); Lenz 1905: 370 (Zanzibar).

*Sesarma frontale* A. Milne-Edwards, 1869: 27 (Madagascar).

*Sesarma frontalis* – De Man 1887: 649 (Madagascar).

*Sesarma nodulifera* – Lenz 1910: 562 (Comoros).

*Sesarma impressa* – Lenz 1910: 561 (Madagascar).
Material examined: Lectotype: female (40.6 × 38.0 mm) (MNHN-IU-2000-3959 = MNHN-B3959) [dried], no locality. 1 male (28.1 × 26.0 mm) (MNHN-IU-2000-3667 = MNHN-B3667) [dried, lectotype of Sesarma frontale A. Milne-Edwards, 1869], Nosy Bé, coll. Boivin (lectotype of Sesarma frontale A. Milne-Edwards, 1869); 1 male (29.7 × 25.6 mm), 1 female (26.0 × 22.1 mm) (MNHN-IU-2000-10929 = MNHN-B10929) [dried, paralectotypes of Sesarma frontale A. Milne-Edwards, 1869], same data as lectotype.


Diagnosis: Male: Carapace almost quadrate; external orbital tooth with outer margin convex, especially along posterior part, separated from lateral margin by distinct cleft (Figs. 2A, 3A, 4, 6A, B, 13A–D); epibranchial tooth short but distinct, sometimes with low lobe posterior to it, never dentiform, sometimes undiscernible (Figs. 13A–D, 14A); outer surface of chela covered with numerous smooth rounded granules; inner surface granulated, with strong transverse median ridge on proximal part, lined with 7–11 tubercles and granules; dorsal margin of dactylar finger with randomly arranged granules, no trace of stridulatory row (Figs. 2C, 5F–I); ambulatory merus relatively short, wide, propodus and dactylus relatively short, wide (Figs. 3A, D, 4, 5A–C, 6A, B, 14B); male pleon transversely wide, somite 6 subtruncate, much wider than long with convex lateral margins; telson wider than long, distinctly inserted into concave distal margin of somite 6 (Figs. 3C, 5A–C, 14C); G1 relatively slender, elongate, distal half of stem expanded, inner margin with gentle but obvious subdistal hump, subdistal part of outer margin gently sloping with chitinous distal part long, gently curved to angle of ca. 60° from longitudinal axis (Figs. 15A–G, 16A–G, N–P). Female: telson inserted into distal margin of somite 6, lateral margins of somite 6 gently convex (Figs. 2B, 6C); vulvae anterior half of sternite 6, just touching margin with sternite 5, posterior edge forming bilobed sternal vulval cover, operculum low, non-protruding (Fig. 6D).

Description of male: Carapace almost quadrate, widest point at edge of external orbital tooth posterolateral margin near base of third ambulatory legs (Figs. 2A, 3A, 4, 13A–D); dorsal surface rugose, small flattened granules and striae, regions clearly defined with distinct grooves, with only scattered short stiff setae on margins; not inflated in frontal view (Figs. 3A, B, D, 5D); surface adjacent lateral margins with distinct oblique striae; median gastro-cardiac groove distinct (Figs. 3A, B, D–E, 4). Front deflexed downwards, margin sinuous, bilobed, lobes separated by wide concavity, margin sinuous to gently convex (Figs. 3A, B, D, E, 4, 5D). Supraorbital margin separated from frontal margin by low angle, no lateral tooth, margin entire,
strongly convex, confluent with acutely triangular external orbital tooth, outer margin convex, especially along posterior part, separated from lateral margin by distinct cleft, sometimes deep; epibranchial tooth short but distinct, sometimes with low lobe posterior to it, never dentiform, sometimes undiscernible (Figs. 3A, D, 4). Antero- and posterolateral margins not demarcated, posterolateral area indicated only by presence of stronger striae, margin entire, gently sinuous to almost straight, gently divergent (sometimes subparallel) towards almost straight posterior carapace margin (Figs. 3A, D, 4). Epistome relatively narrow, transversely subtruncate, posterior margin with obtuse low median triangular tooth, lateral margins gently concave (Figs. 3B, E, 5D). Antennule large, transversely ovate, separated from base of antenna by low tooth, with distinct hiatus between them. Antenna relatively short; basal article subovate; flagellum entering orbit.

Third maxilliped slender; ischium shorter than merus, with oblique submedian sulcus; merus subovate with distinct median ridge extending to anteroexternal angle of ischium; exopod slender, reaching to mid-length of merus, with long flagellum, longer than width of merus (Fig. 5E).

Chelipeds subequal, stout in adults (Figs. 3A, D, 4). Basis, ischium separated by distinct suture; inner margin with clusters of sharp granules (Fig. 5A–C). Inner margin of merus lined with sharp granules of varying sizes with distal one largest; margins not lamelliform; outer margin gently convex, granulated; inner surface with oblique row of stiff setae (Fig. 5A–C). Outer surface of carpus distinctly squamiform; inner distal angle weakly or not produced, lined with short tubercles or relatively long spines (especially in smaller specimens) (Figs. 3A, B, E, 4, 5A–C). Adult chela high, outer surface prominently covered with numerous smooth rounded granules; inner surface granulated, with strong transverse median ridge on proximal part, lined with 7–11 tubercles and granules (Figs. 3A–E, 4, 5A–C, F–I); dorsal margin of palm granulated (Figs. 3A–C, 4, 5F, H); ventral margin with median part concave, granulated (Figs. 5F–I, 3C, E); fingers as long as palm, slightly gaping when closed (Figs. 3E, 5F–I); propodal finger gently curved, cutting margin with 3–5 large teeth on proximal half, usually with 1 subdistal tooth (Figs. 3E, 5F–I); dactylar finger curved, more slender, dorsal
margin distinctly granulated along proximal third, remaining margin with low granules to almost smooth, granules not arranged in stridulatory row (Figs. 3E, 5F–I); tips of both fingers chitinised, gently excavated on inner surface (Figs. 3E, 5F–I).

Ambulatory legs relatively short, stout, second pair longest (Figs. 3A, D, 4). Outer surfaces of merus, with distinct striae; outer surface of carpus and propodus smooth except for ridges (Figs. 3A, D, 4). Meri laterally flattened, dorsal margin gently cristate, gently serrate, with sharp, subdistal dorsal spine (Figs. 3A, D, 4). Outer surface of carpus of first to third legs with 2 low carinae; that of fourth leg with distinct carina (Figs. 3A, D, 4). Propodi of first to third legs with long, simple setae that partially obscures margins, that on third leg least setose; ventral margin of first propodus with very dense mat of short setae, absent on propodi of other legs; surface of fourth propodus almost glabrous except for scattered short setae (Figs. 3C, 4, 5A–C). Dactylopropodal lock not distinct. Inner surface of coxae of first to third ambulatory legs without tufts of dense short setae, with scattered short setae at most.

Surface, margins of anterior thoracic sternites setose. Sternites 1, 2 completely fused, forming triangular structure (Figs. 3C, 5C), separated from sternite 3 by suture, median part shallow, concave toward buccal cavity; sternites 3, 4 fused but demarcated by low transverse setose groove (Fig. 5C). No visible pleonal locking tubercle on sternite 5, locking mechanism formed by enlarged rim-like anterior edge of sternopleonal cavity on sternite 4. Sternites 4/5, 5/6, 6/7, 7/8 medially interrupted, with median longitudinal

![Fig. 2. Sesarmops impressus (H. Milne Edwards, 1837), lectotype female (40.6 × 38.0 mm) (MNHN-IU-2000-3959), no locality. A, overall dorsal view; B, ventral view of cephalothorax; C, outer view of left chela.](image-url)
Fig. 3. *Sesarmops impressus* (H. Milne Edwards, 1837). A–C, male (28.1 × 26.0 mm) (MNHN-IU-2000-3667) (dried, lectotype of *Sesarma frontale* A. Milne-Edwards, 1869), Madagascar; D–F, female (26.0 × 22.1 mm) (MNHN-IU-2000-10929) (dried, paralecotype of *Sesarma frontale* A. Milne-Edwards, 1869), Nosy Be, Madagascar. A, D, overall dorsal view; B, E, F, frontal view of cephalothorax and chelae; C, ventral view of cephalothorax.
Fig. 4. *Sesarmops impressus* (H. Milne Edwards, 1837), overall dorsal view. A, male (30.2 × 27.8 mm) (MNHN-IU-2019-4517), Madagascar; B, male (31.3 × 29.2 mm) (MNHN-IU-2019-45212), Madagascar; C, male (39.6 × 36.5 mm) (MNHN-IU-2009-953), Mayotte.
groove on sternites 7 and 8. Sternopleonal cavity deep, reaching to just before margin of fused sternites 3, 4, to imaginary line joining anterior edges of coxae of chelipeds (Fig. 5A–C). Penis long, curved, partially chitinised.

Pleon transversely wide, subtriangular; all somites, telson free (Figs. 3C, 5A–C). Somites 1–3 widest; somites 4, 5 transversely trapezoidal; somite

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**Fig. 5. Sesarmops impressus** (H. Milne Edwards, 1837). A, D, E, male (30.2 × 27.8 mm) (MNHN-IU-2019-4517), Madagascar; B, F, G, male (31.3 × 29.2 mm) (MNHN-IU-2019-45212), Madagascar; C, H, I, male (39.6 × 36.5 mm) (MNHN-IU-2009-953), Mayotte. A–C, ventral view of cephalothorax; D, frontal view of cephalothorax; E, right third maxilliped; F, H, outer view of left chela; G, I, inner view of left chela.
6 subtruncate, distinctly wider than long with convex lateral margins; telson wider than long with rounded tip, distinctly inserted into concave distal margin of somite 6 (Figs. 3C, 5A–C).

G1 relatively slender, elongate, distal half of stem expanded, inner margin with gentle but obvious subdistal hump, subdistal part of outer margin gently sloping with chitinous distal part long, gently curved to angle of ca. 60° from longitudinal axis (Figs. 15A–C, E, F, 16A, B, C, E). G2 short, about quarter length of G1, without flagellum (Fig. 16G).

Females: Female specimens are similar to males in most non-sexual characters (Figs. 2A, 6A, B), the major difference being in the form of the chelae. Female chelae are proportionately much smaller and not swollen, and the fingers not gaping when closed (Figs. 2C, 6A, B). In smaller specimens, the surfaces are generally smoother, the granules being more scattered, smaller and less distinct, and the fingers not gaping when closed (Fig. 3F). The pleon covers most of the thoracic sternum and the telson is inserted into the distal margin of somite 6 which has the lateral margins gently convex (Figs. 2B, 6C). The vulvae are on the anterior half of sternite 6, just touching the margin with sternite 5, with low, non-protruding operculum, and the anterior and posterior edges forming a bilobed sternal vulval cover with the posterior lobe more developed (Fig. 6D).

Colour: Carapace bicoloured, anterior half of carapace white or yellowish to dirty white, posterior half dark brown to almost black; chelipeds white to yellowish-brown; ambulatory legs dark brown to almost black; ventral surfaces dirty white with margins purplish (Fig. 1).

Remarks: Henri Milne Edwards (1837: 74) described S. impressus only briefly: “Bords latéraux de la carapace armés de trois dents (dont la postérieure à peine distincte), droits, un peu diversgents postérieurement et se terminant en dessus des pates de la quatrième paire. Front moins large que dans les espèces précédentes, ne dépassant pas notablement le troisième article des antennes externes, presque vertical et profondément quadrilobé en dessus. Deuxième article des pates-mâchoires externes marqué d’une dépression semi lunaire longitudinale. Pinces fortes, surtout du coté gauche. Ressemble beaucoup à la S. tétragone. Longueur, 18 lignes.” [Lateral edges of the carapace armed with three teeth (including the posterior which is barely distinct), straight, a little divergent posteriorly and ending above the legs of the fourth pair. Front less wide than in the preceding species, not exceeding the third section of the external antennae, almost vertical and deeply quadrilobed. Second

![Fig. 6. Sesarmops impressus (H. Milne Edwards, 1837). A, C, D, female (22.1 × 20.8 mm) (ZRC 2010.302), Madagascar; B, female (28.5 × 25.7 mm) (ZRC 2009.896), Seychelles. A, B, overall dorsal view; C, pleon; D, sternopleonal cavity and vulvae.](image-url)
article of third maxilliped marked with a semi-lunar longitudinal depression. Strong chelae, especially on the left side. Very similar to Sesarma tetragonona. Length, 18 lines (= 40.5 mm.) The single measurement provided suggests he may only have had one specimen, and it matches the width of the present specimen very well (although he cited it as carapace length). As for Sesarma frontale, which is clearly a junior synonym of S. impressa, A. Milne-Edwards (1869: 27) described the species briefly, providing the measurements for one specimen (25.0 × 22.0 mm) from western Madagascar but without recording its sex. He did not indicate how many specimens he had. MNHN has three dried type specimens, all of which should be regarded as syntypes. The measurements of the syntypes do not exactly match those of the MNHN specimens but the differences are not substantial and probably due to how accurately they were measured then. We here select the best male specimen (28.1 × 26.0 mm, MNHN-IU-2000-3667) to be the lectotype of Sesarma frontale. The selection of lectotypes for S. impressa and Sesarma frontale will stabilise the taxonomy of the species involved.

Serène and Soh (1970: pl. 7 figs. A, B) figured two specimens from MNHN and the Natural History Museum in London but did not state where they were from. The carapaces of the two specimens closely match that of S. impressus s. str. So it is likely both were from the western Indian Ocean.

Crosnier (1965: 63) noted that Lenz’s (1910) record of “Sesarma nodulifera” from the Comoros is actually S. impressus, and probably also his record of the latter species from Madagascar.

Ecology: Sesarmops impressus is primarily a mangrove species although it can be found further upstream in more freshwater habitats (Keith et al. 2006; Bouchard 2009). Bouchard et al. (2013: 24) observed that “It lives generally in the upper part of the Mangrove, in cultivated fields and/or in meadows.”

Distribution: Madagascar, Mayotte, Comoros and adjacent areas in the western Indian Ocean.

Sesarmops indicus sp. nov.
(Figs. 7, 8, 14D–F, 15H–M, 16H–M)
urn:lsid:zoobank.org:act:70D65351-90DD-4E32-8630-D3270E9D10F1

Sesarma (Episesarma) frontalis – De Man 1895: 172 (Atjeh, northern Sumatra).
Sesarma (Sesarma) impressa – Nobili 1900: 507 (Mentawei Islands, west coast Sumatra).
Sesarma (Sesarma) frontalis – Nobili 1900: 509 (Engano, west coast Sumatra).

Material examined: Holotype: male (22.7 × 22.0 mm) (ZRC 2015.344a), hill streams, evergreen and semi-evergreen forest, Mt. Harriet, South Andaman Islands, 11°42′05”–11°51′45”N, 92°43′41”–92°48′13”E, ca. 300–400 m asl, coll. I. Das, 20–30 August 1997. Paratypes: male (19.7 × 18.1 mm), 2 females (10.4 × 9.6 mm, 21.5 × 19.5 mm) (ZRC 2019.1829), same data as holotype; 1 male (16.0 × 14.4 mm) (ZRC 2015.345), Saddle Peak, Dumor Nalla, North Andamans, India, coll. P. Biswas, 8 June 1998.

Diagnosis: Male: carapace almost quadrate; external orbital tooth with outer margin convex, especially along posterior part, separated from lateral margin by distinct cleft (Fig. 7A); epibranchial tooth short but distinct, no visible low lobe posterior to it (Fig. 14D); outer surface of chela covered with numerous smooth rounded granules; inner surface granulated, with transverse median ridge on proximal part, lined with 8–10 tubercles and granules; dorsal margin of dactylar finger with randomly arranged granules, no trace of stridulatory row (Fig. 7C, D); ambulatory merus relatively longer, more slender, propodus and dactylus long (Fig. 14E); male pleon transversely narrower, somite 6 subtruncate, just wider than long with strongly convex lateral margins; telson as long as wide, not inserted into straight distal margin of somite 6 (Figs. 7B, 14F); G1 relatively slender, elongate, stem straight with no obvious expansion along entire length, without subdistal hump along inner margin, subdistal part of outer margin with distinct angular hump, chitinous distal part long, straight, bent at angle of about 45° from longitudinal axis, relatively longer, gently tapering when viewed laterally, with base shorter (Figs. 15H–M, 16H–M). Female: telson inserted into distal margin of somite 6, lateral margins of somite 6 margins of somite 6 more strongly convex, appears proportionately wider (Fig. 8C); vulvae anterior half of sternite 6, just touching margin with sternite 5, posterior edge forming weakly bilobed sternal vulval cover, operculum low, non-protruding (Fig. 8D).

Colour: Not known.

Remarks: The present series of specimens from the Andamans are superficially similar to S. impressus s. str. and S. imperator sp. nov., but can easily be separated by the proportions of the ambulatory legs, as well as structures of the male pleons and gonopods (see DISCUSSION). Records of “Sesarma impressa” and “Sesarma frontalis” from northern Sumatra, Mentawai Islands and Engano Islands, all in the eastern Ocean, by De Man (1895) and Nobili (1900) are provisionally referred to this species until the specimens can be re-examined. This pattern of distribution is to be expected for an inland crab species which still have a dispersive phase via their planktonic larvae (see Ng and Shih 2014; Lai et al. 2017).

Ecology: Most of the type specimens were
Fig. 7. *Sesarmops indicus* sp. nov., holotype male (22.7 × 22.0 mm) (ZRC 2015.344), Andamans. A, overall dorsal view; B, ventral view of cephalothorax; C, outer view of left chela; D, inner view of left chela.
collected from an altitude of 300–400 m asl in freshwater streams in good forest. There are streams flowing to the Indian Ocean, most of which are only 500–1000 m from the sea. Nothing else is known about its ecology. Another freshwater sesarmid, *Geosesarma thelxinoe* (De Man, 1908), was found with *Sesarmops indicus* (see Naruse and Ng 2020). For the ecology and other fauna known from this site, see Das (1997 1998) and Chandramouli et al. (2016).

**Distribution:** Known only from the Andamans but probably also present in other parts of the eastern Indian Ocean.

*Sesarmops imperator* sp. nov.
(Figs. 9–12, 13E, F, 14G–I, 15N–S, 16Q–S, 17)
urn:lsid:zoobank.org:act:6D28BF5B-4BC8-47AC-85AF-F19BE67266B7

*Sesarma atrorubens* – De Man 1887: 653, 676, 678 (part) (Timor, Ambon and Soela Besi [Moluccas], Sanghir [northern Sulawesi]).

*Sesarma impressa* – De Man 1892: 330 (Timor); Bürger 1893: 620, pl. 21 figs. 4, 5 (Philippines; Palau Islands); Schenkel 1902: 546 (Sulawesi). (not *Sesarma impressa* H. Milne Edwards, 1837)

*Sesarma frontalis* – De Man 1892: 334, pl. 19 fig. 13 (Flores). (not *Sesarma frontale* A. Milne-Edwards, 1869).

*Sesarma (Sesarma) impressa* – Nobili 1900: 507 (Timor).

*Sesarma (Sesarma) impressa* – De Man 1902: 527 (Ternate, Batjan, Halmahera); Tesch 1917: 158 (Halmahera, Sulawesi, Nias, Papua New Guinea); Balss 1922: 155 (southern Taiwan); Sakai 1939: 685, pl. 110 fig. 1 (Danshuei, Taiwan); Horikawa 1940: 30 (Taiwan; list); Sakai 1940: 32 (Taiwan; list); Lin 1949: 30 (southern Taiwan; no new specimens); Chen and Dai 1964: 136, 1 unnumbered fig. (Hainan, China). (not *Sesarma impressa* H. Milne Edwards, 1837).

*Sesarma (Sesarma) atrorubens* – Tesch 1917: 131 (part) (Timor, Ambon and Soela Besi [Moluccas], Sanghir [northern Sulawesi]).

*Sesarma (Parasesarma) impressa* – Miyake 1939: 226, 244 (Palau). (not *Sesarma impressa* H. Milne Edwards, 1837).

*Sesarma (Sesarmops) impressus* – Dai et al. 1986: 493, pl. 69(7), text fig. 178(1–3) (Taiwan); Dai and Yang 1991: 540, pl. 69(7), text fig. 178(1–3) (Taiwan). (not *Sesarma impressa* H. Milne Edwards, 1837).

*Sesarma impressus* – Serène and Soh 1970: 401, 406 (part), pl. 7 figs. A, B (no locality data); Sakai 1976: 660, text fig. 360 (Taiwan); Wang and Liu 1996: 123, figs. 161–162 (Taiwan); Liu 1999: 88 (Taiwan); Cai and Ng 2001: 691, fig. 19 (Halmahera, Indonesia); Lee 2001: 134, 2 unnumbered figs. (Taiwan); Ng et al. 2001: 43 (Taiwan); C.-H. Jeng and M.-F. Wang 2002: 85, 2 unnumbered figs. (Taiwan); Ho 2003: 9, 34, 2 unnumbered figs. (Taiwan). Liu 2009: 57, fig. 18 (Taiwan); Li and Chiu 2013: 56, 3 unnumbered figs. (Taiwan); Li and Chiu 2019a: 89; Li and Chiu 2019b: 45 (Taiwan); Ng et al. 2017: 106; Shao et al. 2007: 207, 1 unnumbered fig. (not *Sesarma impressa* H. Milne Edwards, 1837).

*Parasesarma pictum* – Y.-H. Chen 2001: 222, 1 unnumbered fig. [lower]. (not *Grapsus (Pachysoma) pictus* De Haan, 1835)

*Sesarma impressum* – W.-J. Chen and Lo 2014: 144, 2 unnumbered figs. (Taiwan). (not *Sesarma impressa* H. Milne Edwards, 1837)

*Sesarmops impressus* – Fukui et al. 1989: 230 (Taiwan); Yu et al.

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**Fig. 8.** *Sesarmops indicus* sp. nov. A, paratype male (19.7 × 18.1 mm) (ZRC 2019.1829), Andamans; B–D, paratype female (21.5 × 19.5 mm) (ZRC 2019.1829), Andamans. A, B, overall dorsal view; C, pleon; D, sternopleonal cavity and vulvae.
Fig. 9. Colour in life. Sesarmops imperator sp. nov. A, B, male (38.0 × 36.3 mm) (NCHUZOOL 15870), Pingtung, Taiwan; C, female, Pingtung, Taiwan (specimen not collected); D, male, Pingtung, Taiwan (specimen not collected; photograph: H.-C. Liu); E–H, male (34.8 × 32.7 mm) (ZRC 2016.252), Manado, Sulawesi.
1996: 15, figs. 75–76 (Taiwan); Jeng 1997: 18 (Taiwan); Jeng 1998: lower image on p. 81, upper image on p. 82 (Taiwan); Ng et al. 2008: 223 (part); C.-H. Jeng et al. 2010: 72, 5 unnumbered figs. (Taiwan); Li et al. 2010: 6 (Taiwan); Liu and Wang 2010: 61, 3 unnumbered figs. (Taiwan); Maenosono and Naruse 2016: 7 (Ryukyus, Japan; Lanyu, Taiwan); Maenosono and Saeki 2016: 9 (Ryukyus, Japan). (not Sesarma impressa H. Milne Edwards, 1837).

Sesarmops impressus 2 – Li et al. 2010: fig. 22 (Taiwan; Philippines; Sulawesi, Indonesia).

**Material examined:** Holotype: male (37.7 × 36.3 mm) (NCHUZOOL 15068), Beiguan Tidal Park, outside Beiguan Crab Museum, 24°54′42.0″N, 121°52′38.0″E, Dasi, Yilan, coll. P.K.L. Ng, 4 June 2009. Paratypes: Taiwan: 2 males (32.3 × 31.4 mm, 34.9 × 35.0 mm) (ZRC 2009.670), same data as holotype; 1 male (ZRC 2009.694), Siangjiaowan, Hengchun, Pingtung, coll. P.K.L. Ng, June 2009; 1 male (38.0 × 36.3 mm), 1 female (36.7 × 34.8 mm), 1 ovig. female (36.1 × 35.7 mm) (NCHUZOOL 15870), Gangkou R. estuary, Manjhou, Pingtung, coll. H.-T. Shih, 2 July 2009.

Fig. 10. Sesarmops imperator sp. nov., holotype male (37.7 × 36.3 mm) (NTOU), Taiwan. A, overall dorsal view; B, frontal view of cephalothorax; C, ventral view of cephalothorax; D, outer view of left chela; E, inner view of left chela.
Fig. 11. *Sesarmops imperator* sp. nov. A, C, male (24.7 × 23.4 mm) (ZRC 2019.1816), Sulawesi; B, D–F, male (41.8 × 41.1 mm) (ZRC 2001.307), Philippines. A, overall dorsal view; C, D, ventral view of cephalothorax; E, outer view of left chela; F, inner view of left chela.
2001; 2 males (37.6 × 33.7 mm, 35.4 × 32.3 mm), 1 female (23.0 × 20.7 mm) (NCHUZOOL 15069), lower reaches of Gangkou R., Manjhou, Pingtung, coll. J.-J. Li, 6 July 2017; 1 male (46.9 × 43.1 mm) (NCHUZOOL 15070), lower reaches of Gangkou R., Manjhou, Pingtung, coll. J.-J. Li, 4 April 2018; 2 females (29.0 × 26.3 mm, 28.9 × 26.8 mm) (NCHUZOOL 15071), lower reaches of Gangkou R., Manjhou, Pingtung, coll. J.-J. Li, 18 May 2019; 1 male (40.1 × 38.0 mm) (ZRC 2001.32), Kenting National Park, Pingtung, coll. P.K.L. Ng, 7 November 2000; 1 male (ZRC 1998.400), Hengchun Peninsula, Pingtung, coll. H.-C. Liu, 19 May 1998; 1 male (ZRC 2000.1858), Lanyu Island, Taitung, coll. C.D. Schubart et al., 20 September 1999; 1 male (35.2 × 34.6 mm) (NCHUZOOL 15869), Lanyu, Taitung, 7 April 2002; 1 male (ZRC 1999.1276), near Nanliao Fishport, Lyudao (= Green Island), Taitung, coll. P.K.L. Ng, 6 June 1993; 1 female (ZRC 2002.427), at night, Changbin, Taitung, 23°18′22″N, 121°24′14″E, coll. P.K.L. Ng and H.-C. Liu, 22 June 2002; 1 male (ZRC 2017.0984), near shore, along banks, Nioushan, Hualien, coll. J.-J. Li and P.Y.C. Ng, 14 June 2017; 5 males (13.7 × 12.7 mm, 15.5 × 14.8 mm, 18.2 × 17.3 mm, 20.3 × 19.4 mm, 30.3 × 29.6 mm), 4 females (12.6 × 11.4 mm, 13.1 × 12.0 mm, 21.8 × 20.8 mm, 31.6 × 30.4 mm) (NCHUZOOL 15868), Meilun R. estuary, Hualien, 29 July 2014; 8 males, 2 females (ZRC 2017.0985), near shore, along banks, Meilun River estuary, Hualien City, Hualien, coll. J.-J. Li and P.Y.C. Ng, 14 June 2017.


Fig. 12. *Sesarmops imperator* sp. nov. A, C, D, ovigerous female (30.1 × 27.8 mm) (ZRC 2001.307), Philippines; B, ovigerous female (26.0 × 24.0 mm) (ZRC 2001.307), Philippines. A, B, overall dorsal view; C, pleon; D, sternopleonal cavity and vulvae.
Fig. 13. Carapaces. A, *Sesarmops impressus* (H. Milne Edwards, 1837), lectotype female (40.6 × 38.0 mm) (MNHN-IU-2000-3959), no locality; B, *S. impressus* (H. Milne Edwards, 1837), male (39.6 × 36.5 mm) (MNHN-IU-2009-953), Mayotte; C, *S. impressus* (H. Milne Edwards, 1837), male (36.1 × 33.1 mm) (ZRC 2011.5), Comoros; D, *S. impressus* (H. Milne Edwards, 1837), male (30.2 × 27.8 mm) (MNHN-IU-2019-4517), Madagascar; E, *Sesarmops imperator* sp. nov., male (34.8 × 32.7 mm) (ZRC 2016.252), Sulawesi; F, *S. imperator* sp. nov., male (35.9 × 34.7 mm) (ZRC 2017.477), Philippines.

Fig. 14. A–C, Sesarmops impressus (H. Milne Edwards, 1837), male (24.8 × 22.3 mm) (MNHN-IU-2019-4517), Madagascar; C, S. impressus (H. Milne Edwards, 1837), male (21.7 × 19.9 mm) (MNHN-IU-2019.4519), Madagascar; D–F, S. indicus sp. nov., holotype male (22.7 × 22.0 mm) (ZRC 2015.344), Andamans; G–I, S. imperator sp. nov., paratype male (22.8 × 21.6 mm) (ZRC 2001.307), Philippines. A, D, G, right side of carapace; B, E, H, right fourth ambulatory leg; C, F, I, male pleonal somites 5, 6 and telson.
Fig. 15. Right G1. A–G, *Sesarmops impressus* (H. Milne Edwards, 1837), male (30.2 × 27.8 mm) (MNHN-IU-2019-4517), Madagascar; H–M, *S. indicus* sp. nov., holotype male (22.7 × 22.0 mm) (ZRC 2015.344), Andamans; N–S, *S. imperator* sp. nov., holotype male (37.7 × 36.3 mm) (NTOU), Taiwan. A, H, N, left G1 (dorsal view); B, I, O, left G1 (ventral view); C, J, P, distal part of left G1 (dorsal view); D, K, Q, distal part of left G1 (ventromesial view); E, L, R, distal part of left G1 (ventral view); F, G, M, S, distal part of left G1 (dorsomesial views).
Fig. 16. Right gonopods. A–G, *Sesarmops impressus* (H. Milne Edwards, 1837), male (30.2 × 27.8 mm) (MNHN-IU-2019-4517), Madagascar; H–M, *S. indicus* sp. nov., holotype male (22.7 × 22.0 mm) (ZRC 2015.344), Andamans; N–P, *S. impressus*, male (24.8 × 22.3 mm) (MNHN-IU-2019-4517), Madagascar; Q–S, *S. imperator* sp. nov., male (22.8 × 21.6 mm) (ZRC 2001.307), Philippines. A, H, N, Q, left G1 (dorsal view); B, left G1 (ventral view); C, I, O, R, distal part of left G1 (dorsal view); D, J, distal part of left G1 (ventromesial view); E, K, P, S, distal part of left G1 (ventral view); F, L, distal part of left G1 (dorsomesial view); G, M, left G2. Scale bars: A, B, H, M, N, Q = 1.0 mm; C–F, I–L, O, P, R, S = 0.5 mm.
Deharveng and A. Bedos, 17 September 2006.

**Diagnosis:** Male: carapace subtrapezoidal, longer than wide in adults; external orbital tooth with outer margin gently convex to almost straight, separated from lateral margin by cleft (Figs. 10A, 11A, B, 13E, F); epibranchial tooth short, may possess barely discernible very low lobe posterior to it but never distinct or dentiform (Figs. 13, E, F, 14G); outer surface of chela covered with numerous smooth rounded granules; inner surface granulated, with strong transverse median ridge on proximal part, lined with 7–11 tubercles and granules; dorsal margin of dactylar finger with randomly arranged granules, no trace of stridulatory row (Figs. 10D, E, 11E, F); ambulatory merus relatively short, wide, propodus and dactylus relatively short, wide (Fig. 14H); male pleon transversely wide, somite

**Fig. 17.** Right gonopods. *Sesarmops imperator* sp. nov. A–E, holotype male (37.7 × 36.3 mm) (NTOU), Taiwan; F–K, male (41.8 × 41.1 mm) (ZRC 2001.307), Philippines. A, F, left G1 (dorsal view); B, G, distal part of left G1 (dorsal view); C, H, distal part of left G1 (ventromesial view); D, I, distal part of left G1 (ventral view); J, distal part of left G1 (dorsomesial view); E, K, left G2. Scale bars: A, E, F, K = 1.0 mm; B–D, G–J = 0.5 mm.
6 subtruncate, much wider than long with convex lateral margins; telson wider than long, distinctly inserted into concave distal margin of somite 6 (Figs. 10C, 11C, D, 14I); G1 relatively slender, elongate, stem straight with no obvious expansion along entire length, without subdistal hump along inner margin, subdistal part of outer margin with distinct angular hump, chitinous distal part long, straight, bent at angle of about 45° from longitudinal axis, relatively shorter, proximal and distal parts subequal in width when viewed laterally, with base longer (Figs. 15N–S, 16Q–S). Female: telson inserted into distal margin of somite 6, lateral margins of somite 6 more strongly convex, structure appears proportionately wider (Fig. 12C); vulvae anterior half of sternite 6, intrudes into margin with sternite 5, posterior edge forming weakly bilobed sternal vulval cover, operculum low, non-protruding (Fig. 12D).

**Colour**:
Carapace reddish-brown to purplish-brown, lateral and frontal margins yellow to orange; chelipeds usually purple, sometimes dark red, with tubercles white; ambulatory legs light brown; ventral surfaces dirty white (Fig. 9). This species (as *Sesarma impressus* or *S. impressum*) has been well figured in many Taiwanese books (e.g., Lee 2001: 134; Liu and Wang 2010: 61; Li and Chiu 2019a: 89; Li and Chiu 2019b: 45).

**Etymology**:
The name is derived from the Latin for emperor, with which the colour purple has always been associated in European culture. The name alludes to the colour of the species as well as the relatively large size when compared to the other sesarmids that occur in its habitat. The name is used as a noun.

**Remarks**:
The species is superficially similar to *S. impressus* s. str. with which it has long been confused. The differences, notably in the G1, however, are marked and leave no doubt it is a distinct species (see DISCUSSION).

On the basis of the specimens examined, *S. imperator* sp. nov., has a very wide range from Sundaic Southeast Asia to the Ryukyus and Vanuatu in the western Pacific. We have also examined photographs of specimens from various parts of the Indonesian Moluccas and Papua New Guinea, and they are all *S. imperator*. On the basis of the distribution, we provisionally refer old records of “*S. impressus*”, “*S. frontalis*” and “*S. atrorubens*” from Flores and Timor by De Man (1887 1892), Nobili (1900) and Tesch (1917) to *S. imperator* as well.

**Ecology**:
*Sesarmops imperator* is a freshwater species, typically found among rocky areas in riverine habitats, usually with clean faster flowing water, often at the bases of waterfalls. They can be found near the shore where there is tidal influence all the way to several kilometres inland, even in highland sites (see also Liu 2009; Li et al. 2010; Liu and Wang 2010; Li and Chiu 2013; personal observations). In the central Philippines in particular, it can be found with two other species, *S. mindanaoensis* and *S. mora* Li, Shih & Ng, 2020. They have also been found near limestone caves in the Philippines (unpublished data), and one specimen (ZRC 2019.1817) from Riorua in Vanuatu was collected from next to a cave (see Lips et al. 2011). They are not known from mangroves.

**Distribution**:
Southeast Asia to Taiwan and Japan (Ryukyus), Palau, Indonesia (Moluccas, Lesser Sunda Islands, Sulawesi), Papua New Guinea and Vanuatu. Surprisingly, not yet known from Guam, other Mariana Islands and New Caledonia (cf. Paulay et al. 2003; Ng and Richer de Forges 2007).

*Sesarmops atrorubens* (Hess, 1865)  
(Figs. 18–21, 23A–G, 24A–F)

*Sesarma atrorubens* Hess, 1865: 149; pl. 6 fig. 12 (Sydney); Haswell 1882: 108 (list); De Man 1887: 653, 676, 678 (part) (Sydney); De Man 1890: 95 (Fiji); Ortmann 1894: 724 (Fiji).  
*Sesarma (Sesarma) atrorubens* – Tesch 1917: 131 (part) (Fiji).


*Sesarma atrorubens* – Ng et al. 2008: 223 (part; list). (not *Sesarma impressa* H. Milne Edwards, 1837).

**Material examined**: Neotype (here designated):  
male (31.9 × 32.4 mm) (ZRC 2019.1069), fast flowing stream with large boulder rocks, stream of Twin waterfall, near Naba Village along Lavena Coastal Walk, Taveuni Island, 16°52′15.3″S, 179°54′06.6″W, Fiji, coll. B.Y. Lee, et al., 24 July 2019.


**Diagnosis**:
Male: carapace subtrapezoidal, longer than wide in adults; external orbital tooth with outer margin convex, especially along posterior part, separated from lateral margin by distinct cleft (Figs. 19A, 20A, B); epibranchial tooth short, may possess barely discernible very low lobe posterior to it but never distinct or dentiform (Fig. 20B); outer surface of chela covered with small number of large round tubercles; inner surface with several large rounded granules, that on subdorsal surface largest, without transverse median ridge; dorsal margin of dactylar finger lined with striuladatory row of 26–30 granules, most transversely rectangular with median transverse depression, proximal ones more rounded, similar to surrounding rounded granules, distal ones low, poorly formed (Figs.
19C, 20F–I); ambulatory merus relatively longer, more slender, propodus and dactylus long (Figs. 19, 20A); male pleon transversely narrower, somite 6 subtruncate, just wider than long with gently convex lateral margins; telson as long as wide, not inserted into straight distal margin of somite 6 (Figs. 19B, 20E); G1 relatively short, stout, stem with distal part distinctly wider than median parts, outer margin distinctly concave, with subdistal hump along inner margin, subdistal part of outer margin with distinct angular hump, chitinous distal part short, straight, subtruncate, spatuliform, bent at angle of about 45° from longitudinal axis (Figs. 23A–

G, 24A–F). Female: telson inserted into distal margin of somite 6, lateral margins of somite 6 convex (Fig. 21B); vulvae anterior half of sternite 6, distinctly intrudes into margin with sternite 5, posterior edge forming low bilobed sternal vulval cover with prominent, protruding operculum (Fig. 21C).

**Colour**: McLay and Ryan (1990: 110) noted that in life, the “Dorsal surface of carapace and limbs dark purple, ventral surface pale creamy yellow. Fingers and tubercles on outer face of cheliped propodus pale yellow against a dark purple background.” The present specimens agree in general with this description, though we would add the following: the lateral margins of the carapace are white, the ventral margins of the ambulatory meri are white, the palm of the chela is evenly purple except for the white tubercles, with the pollex completely white to pale yellow, the dactylar finger has the upper part of the proximal third purple with white tubercles, the carpus of the cheliped is dark purple with white granules, the ventral surfaces are dirty white to pale yellow, and the eyes bright yellow (Figs. 18, 19). The two sexes do not differ in colour.

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**Fig. 19.** Colour in life. *Sesarmops atrorubens* (Hess, 1865), neotype male (31.9 × 32.4 mm) (ZRC 2019.1069), Fiji. A, overall dorsal view; B, ventral view of cephalothorax; C, outer view of right chela. (photographs: B. Y. Lee).
Fig. 20. *Sesarmops atrorubens* (Hess, 1865), neotype male (31.9 × 32.4 mm) (ZRC 2019.1069), Fiji. A, overall dorsal view; B, dorsal view of carapace; C, right third maxilliped; D, frontal view of cephalothorax; E, anterior thoracic sternum and pleon; F, outer view of right chela; G, inner view of right chela; H, I, dorsal views of dactylus of right chela.
Remarks: Hess (1865: 149) described the species relatively briefly as follows: “Der Cephalothorax ist fast quadratisch, die Seiten fast grade mit drei Zähnen bewaffnet, von denen der letzte nur sehr klein ist. Die senkrecht nach abwärts gerichtete Stirn ist ausgeschweift und von vier sehr stark geschiedenen Loben fast überragt. Die Ischia sind gekörnelt und ziemlich lang, die übrigen Fussglieder büschelförmig behaart, besonders stark am oberen und unteren Rande. Die Klauenglieder sind grade und scharf zugespitzt. Der Carpus ist gross, gekörnelt, die Hand mit grossen Tuberkeln bedeckt. Die Finger sind am Innenrande stark gezähnt. Am Daumen befinden sich drei, am Zeigefinger zwei grössere Zähne. Der Aussenrand des Zeigefingers ist glatt, der des Daumens gerippt. Länge 3.8 Cm., Breite 3.5 Cm. Farbe dunkelviolet.” [The carapace is almost square, the sides almost armed with three teeth, the last of which is very small. The front, which is directed vertically downwards, is swept out and almost obscured by four very strongly separated ridges. The meri are granular and fairly long, the rest of the segments hairy, being particularly strong on the upper and lower edges. The dactyli are straight and sharply pointed. The carpus is large, granular, the hand covered with large tubercles. The fingers are heavily serrated on the inner edge. There are three larger teeth on the pollex and two larger teeth on the dactylyar finger. The outer edge of the dactylyar finger is smooth, that of the pollex is ribbed. Length 3.8 cm, Width 3.5 cm. Dark purple colour.] A figure of the overall specimen was provided (Hess 1865: pl. 6 fig. 12).

Davie (2002: 226) commented that the syntypes in the Göttingen University “appear to be lost as they were not found when collection was transferred to SMF”. We have since confirmed this but note that Hess (1865) only had one male specimen anyway. The type locality for S. atrorubens is wrong, and has already been shown for several of Hess’ (1865) species (see also Ng 2012). Davie (2002: 226) noted that “the Australian distribution for this species is based on the type locality of ‘Sydney’, and this is certainly in error; extensive field collecting across northern Australia has so far failed to recollect S. atrorubens; most probably it was collected from the islands of the south-west Pacific and sent to Hess via Sydney; however, as the northern coast of Australia is within the latitudinal range of the species, I will not yet exclude its possible occurrence.”

De Man’s (1887: 671–675) examined the type male and his detailed comparisons leave no doubt that the present material of S. atrorubens from Fiji is identical with the type male. Most significantly, De Man (1887: 675) notes that “Die nahe verwandte

**Fig. 21.** *Sesarmops atrorubens* (Hess, 1865), female (26.8 × 26.5 mm) (ZRC 2019.1070), Fiji. A, overall dorsal view; B, pleon; C, sternopleonal cavity and vulvae.
Sesarma atrorubens Hess lässt sich von der impressa leicht durch ihre schmälere, mehr hervorragende Stirn sowie durch den Bau der Scheerenfüße und ihre schlankeren Lauffüße unterscheiden, indem die Scheeren des Männchens an der Aussenseite nur mit einer beschränkten Zahl grosser Tuberkeln besetzt sind, während der bewegliche Finger auf seinem Oberrande eine Längs reihe von 25–30 kleinen, glatten Querrrippchen trägt. ” [The closely related Sesarma atrorubens Hess can be differentiated from impressa easily by its narrower, more pronounced front as well as the structure of the chelae, with the male palm slimmer and fewer large tubercles while the upper margin of the dactylar finger has a longitudinal row of 25–30 small, smooth transverse tubercles.] His observations agree completely with the specimens of the two species on hand.

De Man (1887: 678) commented that S. atrorubens was close to Sesarma trapezoidea H. Milne Edwards, 1837 (at present in Labuanium Serène & Soh, 1970), noting they differed only in the proportions of the carapace that is also more convex dorsally, and the relatively longer ambulatory legs. Both species have the distinctive pattern of transverse tubercles on the dactylar finger of the male chela (see also Jeng et al. 2003). The similarities are indeed marked, and the G1 of L. trapezoideum, although longer and slenderer than that of S. atrorubens, has the same general shape (cf. Jeng et al. 2003: fig. 4H, I), including the distinctive bulge on the distal part of the subterminal segment (Figs. 23A–D, F, 24A, B, D). Although both occur in freshwater habitats, their habits are quite different, with L. trapezoideum known to be a climber, occurring on steep walls, while S. atrorubens lives on the forest floor.

De Man (1887: 678) also reported specimens of S. atrorubens from Timor, Ambon and Xulla Besi in the Moluccas, as well as Sanghir in northern Sulawesi, but this material needs to be re-examined. The only species known from this area thus far is S. imperator sp. nov., and as such, his records from these sites are provisionally referred there. This also applies to Tesch’s (1917) record who lists De Man’s (1887 1890) material (spelling Xulla Besi as Soela Besi instead). It is also possible that De Man (1887) confused his material from these areas with another species, Sesarmops weberi which was described only later by himself (De Man 1892) (see Naruse and Ng 2020, for redescription of types). Sesarmops weberi and S. atrorubens have similar carapace features and longer proportions of the ambulatory legs and have the same pattern of transverse tubercles on the dactylar finger of the male chela; although their G1s are very different in structure (see Naruse and Ng 2020, for redescription of types). Interestingly, when De Man (1892: 338–341) described S. weberi, he compared it at length with Labuanium trapezoideum but not with S. atrorubens although he said they were very close a few years earlier (De Man 1887: 678).

McLay and Ryan (1990) recorded a female specimen from Taveuni Island in Fiji, redescribed the species and figured the carapace, cheliped, ambulatory leg and pleon. Their description as well as colour notes agree well with the present specimens.

As discussed earlier, the type of Sesarma atrorubens Hess, 1865, is no longer extant. We here select a freshly collected male (31.9 × 32.4 mm) (ZRC 2019.1069) from Fiji as the neotype of the species. This action will stabilise the name and allow for a more effective revision of the genera in Sesarmidae in the future.

Ecology: McLay and Ryan (1990: 110) observed that “This crab is known locally as the ‘blue’ land crab and the present specimen came from a dried creek bed, 1.5 km from the sea at an altitude of approx. 100 m. Here a crab was observed during the day sitting on a boulder in among mosses and ferns. On a previous occasion one of us (P.A.R.) observed a cast exoskeleton of S. (S.) impressum in a creek bed in Taveuni rainforest at an altitude of approx. 1200 m. Clearly this crab is capable of living far from the sea.” The present specimens were collected only a few hundred metres from the sea and were hiding under rocks at the base of the waterfall (BY Lee, personal communication). The local communities protect the crab from over exploitation as its popular with tourists and locals.

Distribution: Known for certain only from Fiji.

Sesarmops similis (Hess, 1865)
(Figs. 22, 23H–Q, 24G–L)


Material examined: Neotype (here designated): male (32.5 × 30.0 mm) (ZRC 2017.8), Upolu, Samoa, coll. Wroblewsky (Museum Goddefroy), 1800s.

Diagnosis: Male: carapace almost quadrate; external orbital tooth with outer margin convex, separated from lateral margin by distinct cleft (Fig. 22A, B); epibranchial tooth short but distinct, sometimes without lobe posterior to it (Fig. 22B); outer surface of chela covered with numerous smooth rounded granules; inner surface granulated, with transverse median ridge on proximal part, lined with 17 tubercles and granules; dorsal margin of dactylar finger with randomly arranged granules, no trace of striulatory row (Fig. 22G, H); ambulatory merus relatively short, wide, propodus and
Fig. 22. *Sesarmops similis* (Hess, 1865), neotype male (32.5 × 30.0 mm) (ZRC 2017.8), Samoa. A, overall dorsal view; B, dorsal view of carapace; C, frontal view of cephalothorax; D, right third maxilliped; E, pleon; F, ventral view of cephalothorax; G, outer view of left chela; H, inner view of left chela.
Fig. 23. Gonopods. A–G, *Sesarmops atrorubens* (Hess, 1865), neotype male (31.9 × 32.4 mm) (ZRC 2019.1069), Fiji; H–Q, *S. similis* (Hess, 1865), holotype male (32.5 × 30.0 mm) (ZRC 2017.8), Samoa. A, left G1 (dorsal view); B, left G1 (dorsal view); C, left G1 (dorsomesial view); D, distal part of left G1 (dorsal view); E, distal part of left G1 (ventromesial view); F, distal part of left G1 (ventral view); G, distal part of left G1 (dorsomesial view); H, right G1 (dorsal view); I, right G1 (ventromesial view); J, right G1 (ventral view); K, L, right G1 (dorsomesial views); M, distal part of right G1 (dorsal view); N, distal part of right G1 (ventromesial view); O, distal part of right G1 (ventral view); P, Q, distal part of right G1 (dorsomesial views).
dactylius relatively short, wide (Fig. 22A); male pleon transversely wide, somite 6 subtruncate, wider than long with gently convex lateral margins; telson slightly longer than wide, not inserted into straight distal margin of somite 6 (Fig. 22E); G1 short, stout, stem with distal part distinctly wider than median parts, outer margin distinctly concave, subdistal part of outer margin with rounded hump, chitinous distal part short, beak-like, very wide (Figs. 23H–Q, 24G–K). Female: not known.

**Colour:** The female holotype was described as “dark yellow-red” by Hess (1865: 150).

**Remarks:** Hess (1865: 150) described *Sesarma similis* as follows: “Der Cephalothorax ist wie bei *Ses. atrorubens*. Die Stirn ist gleichfalls in vier Loben getheilt, die jedoch nicht so weit vorragen. Die Beine wie bei der vorigen Species, nur sind die Ischia breiter und kürzer. Die Scheerenfüsse des Weibchens sind sehr klein. Die Hände sind nicht mit Tuberkeln besetzt. Jeder Finger trägt drei grössere Zähne. Länge 3.5 Cm., Breite 3.3 Cm. Farbe dunkelgelbroth.”, noting that

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**Fig. 24.** Gonopods. A–F, *Sesarmops atrorubens* (Hess, 1865), neotype male (31.9 × 32.4 mm) (ZRC 2019.1069), Fiji; G–K, *S. similis* (Hess, 1865), holotype male (32.5 × 30.0 mm) (ZRC 2017.8), Samoa. A, left G1 (dorsal view); B, distal part of left G1 (dorsal view); C, distal part of left G1 (ventromesial view); D, distal part of left G1 (ventral view); E, distal part of left G1 (dorsomesial view); F, left G2; G, right G1 (dorsal view); H, right G1 (dorsomesial view); I, distal part of right G1 (dorsal view); J, distal part of right G1 (ventromesial view); K, distal part of right G1 (ventral view); L, right G2. Scale bars: A, F, G–L = 1.0 mm; B–E, I–K = 0.5 mm.
“Vielleicht nur Weibchen des vorigen, war ich um so mehr vermuthe, da von den Exemplaren der Sammlung die ersteren nur Männchen, die letzteren nur Weibchen sind.” [The carapace is like Ses. atrorubens. The front is likewise divided into four ridges, which, however, does not protrude as far anteriorly. The legs as in the previous one species, only the meri are wider and shorter. The chelae of the female are very small. The palms are not covered with tubercles. Each finger carries three bigger teeth. Length 3.5 cm, Width 3.3 cm. Colour dark yellow-red... Maybe only females of the previous one {Ses. atrorubens}, which is likely, as from the collection, the former there are only males, the latter only females.] No figures were provided.

We do not agree with Hess that Sesarma similis is a female of S. atrorubens because we now have females of the latter, and its colour is like males (purple and white), the postfrontal lobes still protrude prominently anteriorly like males, the outer surface of the chelae is still covered with distinct large tubercles, and the ambulatory meri are not distinctly wider and shorter. As Hess specimen measures 33 mm in carapace width, it is quite large and not a juvenile.

The type locality for S. similis is probably incorrect (see above discussion for S. atrorubens). Davie (2002: 226) commented that “(the Australian distribution for this species is based on the type locality of ‘Sydney’ for Sesarma similis Hess, and this is certainly erroneous; extensive field collecting across northern Australia has so far failed to recollect S. impressus; most probably it was collected from the islands of the south-west Pacific and sent to Hess via Sydney; however, as the northern coast of Australia is within the latitudinal range of the species, I will not yet exclude its possible occurrence.)”

De Man’s (1887) comparisons of S. similis with S. impressus were made difficult by the fact that S. similis is known only from a female. On the basis of the present material we refer to these two species, we agree that they are superficially very similar. As noted by De Man, the carapaces are very close, with the shape, dorsal surface, lateral teeth, frontal margin and postfrontal lobes all similar. The ambulatory leg proportions, notably in the merus and dactylus, are also the same. Without a male of S. similis and relying only on carapace and pereopod features, it is not surprising De Man believed both species were synonymous. We believe; however, that they are separate species.

In the ZRC is an old specimen from Samoa which the late Raoul Serène in 1970 had labelled as a new species, “Sesarmops samoensis”. The name has never been published. The specimen is distinct species, with a very diagnostic G1 (Figs. 23H–Q, 24G–K). The specimen was the property or obtained by “Wroblewsky”, who is almost Johannes Julius Wroblewsky (or Wroblewski) (1820–1888). He was a Danish physician associated with several Danish zoologists such as Merck and Steenstrup (MacGregor 2008: 236, 237) and probably purchased the specimen from the Museum Godeffroy (see also Schleisner 1889: 19).

We here argue that Serène’s “Sesarmops samoensis” is the same taxon as what has been described as Sesarma similis Hess, 1865. The carapace and ambulatory characters match in all respects. More significantly, most Sesarmops species, even S. atrorubens, have the outer surface of the female chelae granulated. It is less prominently granulated compared to males but still distinct. Hess (1865) described the chela as smooth, and this is for a large adult specimen. Li et al. (2020) showed that only in adult female S. mindanaoensis are the outer surfaces of the female chelae almost smooth or with only few low granules. S. mindanaoensis (known from Philippines, Taiwan and Sulawesi), however, has distinctly more elongate ambulatory legs and a more slender G1 (see Li et al. 2020).

In recognizing the synonymy of S. similis with S. impressus, Davie (2002: 226) noted that the zoological collections of the Göttingen University had two female specimens (catalogue number ZMG 602) which have been transferred to Senckenberg Museum. A search in the Senckenberg collections failed to uncover this material. This is clearly incorrect data as Hess (1865) himself had only one female specimen. As the type of Sesarma similis Hess, 1865 is lost and no longer extant, we here select the present male (32.5 × 30.0 mm) (ZRC 2017.8) from Samoa to be the neotype of the species. This will stabilise the taxonomy of these species names and allow the necessary generic revisions to be done in the future (see DISCUSSION).

Ecology: Not known.

Distribution: Known for certain only from Samoa.

Molecular analyses

A phylogenetic tree of the combined 16S and COI markers was reconstructed using BI and ML analyses (Fig. 25). Both Sesarmops imperator and S. impressus are well supported, and sister to each other, although the support values are low. The above two species, as well as Bresedium eurypleon Li, Shih & Ng, 2020 and B. brevipes (De Man, 1889), form a strongly supported clade, which is sister to S. mora Li, Shih & Ng, 2020. Both S. mindanaoensis and S. atrorubens are not closely related to the other species.

The mean pairwise nucleotide divergence of K2P distances and bp differences of haplotypes of the four closely related species, Sesarmops impressus,
Fig. 25. Bayesian inference (BI) tree for species of Sesarmidae used in this study based on combined 16S rDNA and cytochrome c oxidase subunit I (COI) genes. Probability values at nodes represent support values for BI and maximum likelihood (ML). Only support values higher than 50% are shown in the trees. The numbers before localities of the species refer to the corresponding GenBank/DDBJ accession numbers.

Table 1. Matrix of percentage pairwise nucleotide divergences with K2P distance (and value range) based on 658 bp of COI within and between four closely related species of *Sesarmops* and *Bresedium*. Lower-left values are K2P and upper-right ones are bp differences.
S. imperator, Bresedium eurypleon and B. brevipes, are shown in Table 1. The intraspecific nucleotide divergences of the four species were all ≤ 1.23% (8 bp difference). The interspecific divergences among the four species were all ≥ 2.65% (17 bp difference). The interspecific divergence was at least 2.7-fold greater than intraspecific values (between B. brevipes and B. eurypleon), supporting our hypothesis that the four species are distinct.

DISCUSSION

In this study, species confused with or allied to Sesarmops impressus are revised, and two new species were established. Although we could not obtain the sequences from S. indicus sp. nov., or S. similis, the morphological differences diagnosed for the other three species, S. impressus, S. imperator sp. nov., and S. atrorubens are well supported by mitochondrial 16S and COI (Fig. 25).

Sesarmops impressus s. str. is superficially similar to S. imperator and S. indicus in carapace features. The most reliable external way to distinguish S. imperator from S. impressus and S. indicus is the form of the external orbital tooth. In S. imperator, the outer margin of the external orbital tooth, is gently convex to almost straight (Figs. 13E, F, 14G). In S. impressus and S. indicus, the outer margin of the external orbital tooth is distinctly more convex, especially at the proximal part, with the cleft separating it from the lateral margin usually being more pronounced (Figs. 13A–D, 14A, D). In larger specimens, the carapace shapes are also slightly different, with that of S. impressus appearing more quadrate with the lateral margins slightly divergent to almost subparallel (Fig. 13A–D) while that of S. imperator tends to be more trapezoidal in shape (Fig. 13E, F). The lectotype of S. impressus is dried and slightly deformed, with the right side badly indented (Figs. 2A, 13A). The tips of the epibranchial teeth on both sides are also broken off (Fig. 13A) such that it appears lower.

The shape of the female pleon is also useful for separating the species, but only when it is fully formed. In S. impressus, the telson is inserted into the distal margin of somite 6, the lateral margins of which are gently convex (Fig. 6C). In S. indicus and S. imperator, the lateral margins of somite 6 are more strongly convex, such that the structure appears proportionately wider (Figs. 8C, 12C). The shape of the female pleon of the dried lectotype female of S. impressus (Fig. 2B) agrees very well with that here figured for more recent specimens of S. impressus (Fig. 6C), confirming our identification of the present material.

The present specimens of S. indicus are relatively smaller than those of S. impressus and S. imperator, but even when specimens of similar sizes are compared (Fig. 14), several major differences are observable. Externally, S. indicus can easily be separated from S. impressus and S. imperator by its proportionately longer ambulatory legs, notably in the merus and dactylus (Fig. 14E versus Fig. 14B, H). In addition, the male pleon of S. indicus is proportionately less broad (notably somite 6) when compared to those of S. impressus and S. imperator (somite 6 much broader with the telson distinctly inserted into the distal margin of somite 6) (Fig. 14F versus Fig. 14C, I) and the telson is not inserted into the distal margin of somite 6 (Fig. 14F). These differences are also valid for large specimens of S. impressus and S. imperator. The G1s of the three species are distinct and the differences are valid even for small males. In S. impressus, the G1 has the distal half of the stem expanded, such that the inner margin has a gentle but distinct subdistal hump, and the subdistal part of the outer margin is gently sloping, with the chitinous distal part gently curved to an angle of about 60° from the longitudinal axis (Figs. 15A–C, E, F, 16A, B, C, E). In S. indicus and S. imperator, the entire G1 stem is straight with no apparent expansion along its entire length, there is no subdistal hump along the inner margin, the subdistal part of the outer margin has a distinct angular hump, and the chitinous distal part is straight but bent to about 45° from the longitudinal axis (Figs. 15H–J, L, N–P, R, 16H, I, K). The G1 of S. indicus, however, differs from S. imperator in that its chitinous distal part is relatively long and gently tapers when viewed laterally, with its base shorter (Figs. 15H–J, L, M, 16H, I, K versus Figs. 15N–P, R, S, 16Q–S, 17A, B, D, F, G, I). The above differences are valid even for small specimens of S. impressus (Fig. 16N–P) and S. imperator (Fig. 16Q–S) examined.

Genetically, the identity of S. impressus and S. imperator are supported by the phylogenetic tree based on the combined 16S and COI markers, although their sister relationship is not strongly supported, and they form a larger clade including Bresedium brevipes and B. eurypleon (Fig. 25). With regards to the interspecific K2P distance of COI of the above four species, the values (≥ 2.65%) are larger than the minimum interspecific divergences among intertidal and terrestrial crabs (e.g., the families Dotillidae, Mictyridae, Ocyopodidae, Sesarmidae and Varunidae) (see Chu et al. 2015; N. K. Ng et al. 2018; Shih et al. 2018 2019a b 2020; Shih and Poupin 2020).

In this study, S. atrorubens and S. similis are retained in Sesarmops out of convenience, at least until the generic limits of the genus can be established. While the carapaces and general appearances of S. atrorubens
and S. similis superficially resemble S. impressus, there are major differences.

As discussed under the remarks for S. atrorubens, the species is unusual in that it possesses a row of stridulatory tubercles on the dorsal margin of the male cheliped dactylus (Fig. 20H, I), a feature shared with Sesarmops weberi and Labuanium trapezoideum but absent in S. impressus, S. indicus and S. imperator. In addition, the male telson is not inserted into the distal margin of somite 6 (Fig. 20E), the inner surface of the male chela does not have a transverse ridge of granules (Fig. 20G), and significantly, the G1 is proportionately shorter and stouter, with the chitinous distal part short (Figs. 12A–G, 13A–E). The distal part of the G1 is closer to that of S. mindanaoensis (see Li et al. 2020), but the G1 stem of the latter is proportionately more elongate. While the male pleon of S. mindanaoensis is similar to that of S. atrorubens, the dactylus of the chela does not have a row of stridulatory granules (cf. Li et al. 2020). The phylogenetic relationship of S. atrorubens also supports the unusual morphology (Fig. 25). As discussed earlier, S. mindanaoensis will probably need to be separated into its own genus in the future, and on the basis of the present data, S. atrorubens will need to be moved as well.

Sesarmops similis is another matter. The male telson is not inserted into somite 6 (Fig. 22E), the dactylus of the chela is not lined with stridulatory granules (Fig. 22G, H), and the G1 is unusually short and stout with a short and very wide chitinous distal part (Figs. 23H–Q, 24G–K). The relatively short and stout G1 structure resembles those of species of Pseudosesarma s. str. (cf. Ng and Schubart 2017; Schubart and Ng 2020), but the carapace of S. similis is different, with the external orbital tooth longer and more acutely triangular, the regions of the carapace clearly indicated with the dorsal surface rugose to granulose (external orbital tooth shorter with the carapace regions smooth and poorly indicated; cf. Ng and Schubart 2017; Schubart and Ng 2020). In addition, while Pseudosesarma species are known only from the Indian Ocean in Southeast Asia, S. similis is from some distance away from Samoa. There are no known Pseudosesarma species in the area between these sites. As such, for morphological and biogeographical reasons, it is perhaps not advisable to transfer S. similis to Pseudosesarma. Schubart and Ng (2020) established a new genus for three species (Sesarma (Sesarma) modesta De Man, 1902 [type species], and two new species from Indonesian Papua and Papua New Guinea), noting that it shares characters of Sesarmops, Bresedium and Pseudosesarma. The carapaces of these species are more similar to that of S. similis and the form of the male chela is also similar (Fig. 22G, H) (cf. Schubart and Ng 2020) but the G1 of the latter species is still much stouter and shorter, with the distal chitinous part too short and wide. Sesarmops similis may need to be transferred to this new genus at a later date.

The generic status of S. atrorubens and S. similis would preferably be decided after the positions of S. weberi, S. mindanaoensis and S. angustifrons are ascertained, and the limits of Bresedium s. str. with Sesarmops s. str. established. For the moment, keeping both taxa in Sesarmops seems to be in the best interest of stability.

The distribution of the species studied shows a common pattern observed for species occurring in the Indo-West Pacific, and this is probably because geographic barriers of land and/or currents affect larval dispersal. Sesarmops impressus is restricted to the western Indian Ocean, S. indicus to the eastern Indian Ocean, S. imperator in Southeast Asia and the western Pacific, S. atrorubens in Fiji, and S. similis in Samoa. Similar distributional patterns for Indo-West Pacific crabs, for example, can be found in fiddler crabs (Crane 1975; Shih et al. 2010 2016; Shih and Poupin in press) and gecarcinid land crabs (Lai et al. 2017; Ng and Shih 2014 2015). However, as the species of Sesarmops studied also mixed with species of Bresedium, further studies with more molecular markers and species will be necessary to clarify the issues of distribution and cladogenesis.

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