

Taxonomic reassessment of *Parasesarma* (Crustacea: Brachyura: Decapoda: Sesarmidae) based on genetic and morphological comparisons, with the description of a new genus

ADNAN SHAHDADI^{1,*}, SARA FRATINI² and CHRISTOPH D. SCHUBART³

¹Department of Marine Biology, Faculty of Marine Sciences and Technology, University of Hormozgan, Bandar Abbas, Iran

²Department of Biology, University of Florence, via Madonna del Piano 6, 50019 Sesto Fiorentino, Italy

³Zoologie & Evolutionsbiologie, Universität Regensburg, Regensburg 93040, Germany

Received 19 October 2019; revised 6 February 2020; accepted for publication 27 February 2020

Parasesarma is a species-rich genus whose representatives are common in wetlands and mangroves of the Indo-Pacific. Morphologically, the genus is heterogeneous and has been postulated to constitute a polyphyletic taxon. In the present study, most species of *Parasesarma* are re-evaluated phylogenetically, using mitochondrial and nuclear molecular markers. The results show that the majority of the examined species cluster consistently with the type species *Parasesarma plicatum*. However, some species, among them the tree-climbing *Parasesarma leptosoma*, are clearly separated from this main clade of *Parasesarma*, forming a second stable monophyletic group, distinct from other known genera. Based on these results, and with additional support by morphological diagnoses highlighting consistent differences between the two species groups, we propose a new genus for the species clustering around *P. leptosoma*, proposing the new name ***Leptarma* gen. nov.**

ADDITIONAL KEYWORDS: molecular markers – new genus – *Leptarma* – phylogeny – sesarmid crabs – systematics.

INTRODUCTION

The brachyuran crab family Sesarmidae Dana, 1851, with 35 genera and > 250 species (Ng *et al.*, 2008, 2019; De Grave *et al.*, 2009; Naruse & Ng, 2012; Brösing *et al.*, 2014; Shahdadi & Schubart, 2017), is the most species-rich family in the subsection Thoracotremata Guinot, 1977. Although the family is a stable monophyletic taxon (see Schubart *et al.*, 2006), it nevertheless has a complex taxonomic history (Guerao *et al.*, 2004). For a long time, most of the sesarmid species were included in *Sesarma* Say, 1817 *s.l.* Later, this genus was split or subdivided into more genera and subgenera by De Man (1892, 1895), Tesch (1917) and Tweedie (1950). Serène & Soh (1970) introduced a large number of new genera and established the taxonomic system that is

mostly valid today (see Ng *et al.*, 2008). However, even after several recent revisionary studies (e.g. Davie, 1992, 1994, 2012; Schubart *et al.*, 2009), there are still many ambiguities and taxonomic problems at different levels in the family, calling for further studies (see Ng *et al.*, 2008).

Parasesarma De Man, 1895 was originally defined as a subgenus of *Sesarma* for nine species that were characterized by two or more rows of pectinated crests on the male chelar palm and lack of an epibranchial carapace tooth (see De Man, 1895: 181–217). Based on the same morphological characteristics, Ng *et al.* (2008) listed *Parasesarma* as a full genus, at that time with ≤ 28 recognized species. Species of *Parasesarma* are among the most common Indo-Pacific Sesarmidae. They mostly inhabit estuarine wetlands, including mangrove swamps (Tan & Ng, 1994; Shahdadi *et al.*, 2018a), where they play an important role in nutrient cycling (Lee, 1998; Guerao *et al.*, 2004; Cannicci *et al.*, 2008; Lee, 2015). The genus was recently redefined and enlarged (Shahdadi & Schubart, 2017), because of the

*Corresponding author. E-mail: adnan1361@gmail.com
[Version of record, published online 25 April 2020; <http://zoobank.org/> urn:lsid:zoobank.org:pub:43B9C712-8FB3-4606-8381-4ED90091D0A8]

additions and redescriptions of several species, and now comprises 71 recognized species (Rahayu & Ng, 2010; Ng *et al.*, 2016; Cannicci *et al.*, 2017; Shahdadi & Schubart, 2017; Li *et al.*, 2018, 2019; Shahdadi *et al.*, 2018a, b, 2019a; Fratini *et al.*, 2019; Shih, *et al.*, 2019). This makes it the most species-rich genus of the family Sesamidae. However, it still includes poorly known species (Rahayu & Ng, 2010; Rahayu & Li, 2013; Shahdadi *et al.*, 2018b; Fratini *et al.*, 2019) and its phylogeny has not been resolved fully (Shahdadi & Schubart, 2017).

Previous molecular phylogenetic studies on *Parasesarma* have detected and indicated the possibly polyphyletic status of the genus. For example, *Parasesarma leptosoma* (Hilgendorf, 1869) did not group with other included species of *Parasesarma* in a phylogenetic tree based on the mitochondrial 16S and 12S ribosomal RNA genes in the study by Schubart *et al.* (2006). Cannicci *et al.* (2017) found that *P. leptosoma* grouped closely together with *Parasesarma gazi* Cannicci, Innocenti, Fratini, 2017 in both mitochondrial and nuclear trees, but both were still separated from other congeners. Morphological heterogeneity among species of *Parasesarma* was also noticed by Rahayu & Ng (2009), who identified two morphological groups according to length proportions of the ambulatory legs, i.e. short vs. long legs. Among the long-legged species, *P. leptosoma* is arguably the most distinctive (Li *et al.*, 2018). Overall, these and other lines of evidence reported by Shahdadi & Schubart (2017) indicate that the species currently assigned to *Parasesarma* belong to more than one clade and that their phylogeny and taxonomy need to be re-evaluated.

For the present study, we examined almost all species of *Parasesarma* morphologically and genetically (with mitochondrial and nuclear molecular markers), with the following aims: (1) to investigate their phylogenetic relationships; (2) to reassess their taxonomy accordingly; and (3) to present new morphological diagnoses for newly defined taxa. This is the most extensive review carried out for the genus *Parasesarma* and solves taxonomically the deep phylogenetic divergence found among the members of the genus as so far described.

MATERIAL AND METHODS

MATERIAL EXAMINED AND MORPHOLOGICAL ANALYSES

Specimens were borrowed from or examined in the following museums: the Australian Museum (AM), Sydney, NSW, Australia; Queensland Museum (QM), Brisbane, Queensland, Australia; Western Australian Museum (WAM), Perth, WA, Australia; Museum Zoologi Bogor (MZB), Indonesian Institute of Sciences, Jakarta, Indonesia; National Museum of

Marine Biology and Aquarium (Crustacea Decapoda) (NMMBCD), Pingtung, Taiwan ROC; Natural History Museum and Institute (CBM), Chiba, Japan; Ryukyu University Museum (RUMF), Fujukan, Okinawa, Japan; Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore; US National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA; Academy of Natural Sciences of Drexel University (NASP), Philadelphia, PA, USA; Florida Museum of Natural History (UF), Gainesville, FL, USA; Forschungsinstitut und Museum Senckenberg (SMF), Frankfurt am Main, Germany [including material that was incorporated from the Zoologisches Museum der Universität Göttingen (ZMG)]; Zoologisches Museum Berlin (ZMB), Berlin, Germany; Zoologische Staatssammlung (ZSMA), Munich, Germany; Natural History Museum of the University of Florence (MZUF), Florence, Italy; Naturhistorisches Museum Wien (NHMW), Vienna, Austria; Naturalis Biodiversity Center (ex Rijksmuseum van Natuurlijke Historie; RMNH), Leiden, The Netherlands; Muséum National d'Histoire Naturelle (MNHN), Paris, France; Natural History Museum (NHM), London, UK. The holotype of *Parasesarma palauense* Takeda, 1971 was borrowed from Kitakyushu Museum of Natural History and Human History, Fukuoka, Japan (this specimen was formerly deposited in the Zoological Laboratory Kyushu University, ZLKU).

Except for *Parasesarma exquisitum* Dai & Song, 1986 (for which no material was available) and *Parasesarma aurifrons* Li, Shih & Ng, 2019, all species of *Parasesarma* were examined for the present paper (Table 1). The specimens were examined and described using a stereomicroscope (Leica S4E or Leica Wild Heerbrugg M8), and details of the male gonopods and female gonopores were examined with a photographic microscope (Keyence VHX500FXX). Maximum carapace widths and carapace lengths (in millimetres) were measured for all specimens (Table 1). The ratio of eyestalk length (esl; from the base of the posterior projection of the cornea to the base of the eyestalk) to maximum eyestalk width (esw) and the ratio of the length of the fourth pereopod (P4) to carapace width (cw) were calculated for selected specimens only (Table 1). The measurements for the eyestalk morphometry were obtained using the program tpsDig 2.10 (Rohlf, 2006) from digital photographs (Fig. 1A). Morphometric measurements of the carapace and the pereopod were obtained with digital callipers (Fig. 1B, C).

Data analyses and graphs were performed using IBM SPSS Statistics v.21. Photographs of the paratypes of *P. exquisitum* (catalogue number CB03317) and

Table 1. Material examined for this study (in alphabetical order), with sex, size [carapace width × length (cw×cl); in millimetres], locality of collection, museum catalogue number and, for some specimens, the ratio of eyestalk length to width (esl/esw) and ratio of pereopod 4 length to carapace width (P4/cw)

Species	Sex, cw×cl	Locality	Catalogue no.	esl/esw	P4/cw
<i>Parasesarma affine</i> (De Haan, 1837)	M, 19.4 × 15.4	Japan	RMNH 129 lectotype	–	1.76
	M, 24.0 × 19.4	Hong Kong: Mai Po mangrove	ZSM-A20171197	1.37	–
	M, NA*	Taiwan: mangroves near Hsinchu	ZRC 2000.1851	–	–
	M, 7.9 × 6.3*	Anambas Island	ZRC 2003.0726 paratype	1.23	1.89
<i>Parasesarma anambas</i> Yeo, Rahayu & Ng, 2004	M, 18.7 × 15.5	Nicobar Islands	NHMW10408 syntype	–	–
	M, 18.6 × 15.5	Nicobar Islands	NHMW10408 syntype	–	–
	M, 16.0 × 13.1*	India: Tamil Nadu	ZRC 2001.0851	–	–
	F, 13.3 × 10.2	India: Tamil Nadu	ZRC 2001.0851	1.22	–
<i>Parasesarma austrawati</i> Shahdadi, Davie & Schubart, 2019	M, 16.0 × 13.0	India: Tamil Nadu	ZRC 2001.0851	–	–
	M, 22.2 × 18.0	Australia: Northern Territory: Arrla Creek	AM-P.99000 holotype	–	1.62
	M, 17.2 × 13.1*	Australia: Northern Territory: Arrla Creek	AM-P.99003 paratype	–	–
	M, 15.7 × 13.9	Indonesia: Java: Jakarta	RMNH.CRUS.D1201 holotype	–	1.89
<i>Parasesarma batavianum</i> (De Man, 1890)	M, 12.6 × 10.3	Singapore	ZSM-A20171181	–	–
	M, 10.2 × 8.1*	Singapore: Bulon	ZSM-A20171184	1.24	–
	M, 19.1 × 16.2	Seri Lanka: Galle	QM-W26687 paratype	–	–
	M, 19.4 × 16.4*	Thailand: Phuket	SMF 49919	1.15	1.56
	M, 14.8 × 12.7	Thailand, Phuket	SMF 49919	–	–
	M, 8.89 × 7.40	Thailand: Phuket	CBM ZC6065	–	–
	M, 12.7 × 10.7	Seri Lanka: Bentota	SMF 32735	–	–
	M, 15.2 × 12.4	Thailand: Thap Lamu	NA	–	–
	F, 19.7 × 16.5	Thailand: Phuket	SMF 49919	–	–
	M, 25.2 × 21.7	Japan	RMNH.CRUS.D.145 holotype	1.39	1.62
<i>Parasesarma bidens</i> (De Haan, 1835)	M, 20.2 × 16.7*	Japan: Nagasaki	RUMF-ZC-1337	–	–
	F, 18.8 × 15.5	Japan: Iriomote	RUMF-ZC-1232	–	–
	M, 19.8 × 16.6	Australia: Queensland: Innisfail	QM-W2459 paratype	1.23	1.63
	M, 16.4 × 13.4*	Australia: Queensland: Cardwell	QM-W8270	–	–
<i>Parasesarma calypso</i> (De Man, 1895)	M, 17.2 × 14.6	Indonesia: Sumatra: Aceh	RMNH.CRUS.D102652 lectotype	–	1.90
	M, 14.9 × 12.3*	Indonesia: Sumatra: Aceh	RMNH.CRUS.D1514 paratype	–	–
	F, 15.2 × 12.1	Indonesia: Sumatra: Aceh	RMNH.CRUS.D1514 paratype	1.22	–
	M, 21.2 × 17.8	South Africa	ZRC 2017.0164	1.18	1.83
<i>Parasesarma capensis</i> Fratini, Innocenti & Cannicci, 2019	M, NA*	South Africa: Natal: Umlazi Lagoon	SMF 31131	–	–

Table 1. Continued

Species	Sex, cw×cl	Locality	Catalogue no.	esl/esw	P4/cw
<i>Parasesarma carolinense</i> (Rathbun, 1907)	M, 9.5 × 7.0	Carolines: Kusaie	USNM 32861 holotype	1.10	1.49
<i>Parasesarma catenatum</i> (Ortmann, 1897)	M, 18.6 × 14.7*	South Africa: Durban Bay; Salisbury Island	RMNH.CRUS.D. 3252	1.28	1.56
	M, 12.2 × 9.5	South Africa: Durban Bay; Salisbury Island	RMNH.CRUS.D. 3252	–	–
	M, 24.5 × 19.0	See Remarks in Material examined section	ANSP CA2943 holotype	–	–
<i>Parasesarma charis</i> Rahayu & Ng, 2005	M, 8.9 × 6.8*	Indonesia: Irian Jaya: Kamora	ZRC 2002.0594 paratype	1.26	1.51
	F, 8.8 × 6.6	Indonesia: Irian Jaya: Kamora	ZRC 2002.0594 paratype	–	–
<i>Parasesarma corallicum</i> Ng, Davie & Li, 2016	M, 10.3 × 7.6*	Taiwan: Pingtung: Kenting	NMBCD4698 paratype	–	–
	M, 6.3 × 4.6	Taiwan: Pingtung: Kenting	ZRC 2016.0294 paratype	–	1.63
	F, 6.6 × 5.0	Taiwan: Pingtung: Kenting	ZRC 2016.0294 paratype	1.10	–
<i>Parasesarma cricotum</i> (Rahayu & Davie, 2002)	M, 15.1 × 13.4	Indonesia: Irian Jaya: Kamora River	SMF 49920	–	–
	M, 14.5 × 12.3	Indonesia: Irian Jaya: Kamora River	ZRC 2016.0522	–	–
	M, 22.6 × 18.9	Indonesia: Sulawesi	ZRC 2000.1727	1.43	1.74
	F, 12.6 × 10.6	Indonesia: Irian Jaya: Kamora River	SMF 49920	–	–
	F, 14.3 × 12.2*	Indonesia: Irian Jaya: Kamora River	ZRC 2016.0522	–	–
<i>Parasesarma darwinense</i> (Campbell, 1967)	M, 13.3 × 10.6	Australia: Northern Territory: Darwin Island	QM-W2443, paratype	1.27	1.82
	M, 12.2 × 10.2*	Australia: Northern Territory: Darwin Island	SMF 49921	–	–
	M, 9.0 × 7.5	Australia: Northern Territory: Darwin Island	SMF 49921	–	–
<i>Parasesarma dumacense</i> (Rathbun, 1914)	M, 20.4 × 17.0*	Philippines: Cebu: Kawasam waterfall	ZRC 2008.0833	1.17	1.66
	M, 18.6 × 14.9	Philippines: Cebu: Ronda Argao	ZSM-A20171177	–	–
	M, 18.7 × 15.7	Philippines: Cebu: Kawasam waterfall	ZRC 2008.0833	–	–
	F, 18.1 × 14.5	Philippines: Cebu: Kawasam waterfall	ZRC 2008.0833	–	–
<i>Parasesarma ellenae</i> (Pretzmann, 1968)	M, 8.3 × 7.0	New Caledonia, Tiouva	NHMW3271 holotype	1.10	–
	M, NA	New Caledonia	ZMB 4250	–	–
	M, 18.5 × 15.5	Vanuato Island	ZRC 2019.1329	–	–
	M, 20.0 × 16.3*	Vanuato Island	ZRC 2019.1328	–	1.81
<i>Parasesarma erythodactyla</i> (Hess, 1865)	M, 16.2 × 13.3	Australia: New South Wales: Sydney: Broken Bay	RMNH.CRUS.D.10595	1.17	–
	M, 13.5 × 11.1	Australia: New South Wales: Sydney: Broken Bay	RMNH.CRUS.D.10595	–	–
	M, 18.1 × 14.5	Australia: New South Wales: Sydney: Port Jackson Bay	MNH-IU-2013-14892	–	1.75
<i>Parasesarma eumolpe</i> (De Man, 1895)	M, 17.4 × 14.7	Malaysia: Penang	ZRC 2018.0249 neotype	–	–
	M, 18.6 × 15.7*	China: Hainan: Wenchang	SMF 49922	1.32	1.61
	M, 24.0 × 20.6	China: Hainan: Wenchang	SMF 49922	–	–

Table 1. Continued

Species	Sex, cw×cl	Locality	Catalogue no.	esl/esw	P4/cw
<i>Parasesarma foresti</i> (Rahayu & Davie, 2002)	M, 17.0 × 13.7 M, 16.6 × 14.5* M, 17.3 × 14.9 M, 17.1 × 14.5 F, 14.2 × 11.5 F, 14.2 × 11.8 M, 15.5 × 13.1	Malaysia: Chukai Indonesia: Irian Jaya: Kamora Indonesia: Irian Jaya: Kamora Indonesia: Irian Jaya: Ajkwa River Indonesia: Irian Jaya: Kamora Indonesia: Irian Jaya: Ajkwa River Kenya: Gazi Bay	MNHN-B-21854 ZRC 2003.0481 paratype ZRC 2000.1818 SMF 49923 ZRC 2016.0523 SMF 49923 MZUF 3671 paratype	– 1.10 – – – – –	– – – – – – 1.87
<i>Parasesarma gazi</i> Cannicci, Innocenti & Fratini, 2017	M, 16.9 × 13.8* F, 12.6 × 10.3 M, NA soft carapace F, NA soft carapace M, 12.2 × 10.1 M, 15.8 × 14.3* M, 14.9 × 13.3 F, 14.2 × 12.8 M, 11.9 × 10.1* M, 14.2 × 12.0* M, NA	Kenya: Gazi Bay Kenya: Gazi Bay Madagascar: Tulear Madagascar: Tulear Europa Island Japan: Okinawa Island: Awase Japan: Iriomote Japan: Iriomote Philippines: Cebu Indonesia: Irian Jaya: Kamora Zanzibar	MZUF 3670 MZUF 3673 MNHN-B16698 MNHN-B16698 MNHN- IU-2012-660 RUMF-ZC-4710 holotype UF 48137 UF 48137 NA ZRC 2000.1883 MNHN-B3949 holotype	– 0.94 – – – 0.9 – – – – 0.74 –	– – – – – 2.2 – – – – 1.99 –
<i>Parasesarma gecko</i> Li, Rahayu & Ng, 2018	M, 16.0 × 13.5* M, 22.4 × 18.1 F, 18.7 × 15.0 M, 28.7 × 22.7* M, 29.4 × 22.7	Kenya: Gazi Eritrea: Massawa Kenya: Gazi Australia: Western Australia: Onslow Australia: Western Australia: Uendo creek	SMF 49924 RMNH.CRUS.D.25027 SMF 49924 QM-W28879 paratype WAM-C59485	– 1.40 – 1.29 –	– – – 1.70 –
<i>Parasesarma hartogi</i> Davie & Pabriks, 2010	M, 18.6 × 14.4 F, 16.1 × 12.6	Australia: Western Australia: Carnarvon Australia: Western Australia: Uendo creek	AM-P-39706 WAM-C59485	– –	– –
<i>Parasesarma hasswelli</i> (De Man, 1887)	M, 9.8 × 7.9 M, 19.2 × 16.2*	Myanmar: Mergui Archipelago Australia: Western Australia: Ashburton River	NHM1886.52 syntype QM-W28880 paratype	1.24 –	– 1.72
<i>Parasesarma holthuisi</i> (Davie, 2010)	M, 11.8 × 9.5 F, 17.0 × 13.8 M, 28.9 × 24.7* M, 27.9 × 23.9	Australia: Western Australia: Onslow Australia: Western Australia: Onslow Indonesia: Ambon Indonesia: Ambon	WAM-C42690 WAM-C4267 paratype RMNH.CRUS.D.141 lectotype RMNH.CRUS.D.19 paralecotype	1.22 – 1.42 –	– – – –

Table 1. Continued

Species	Sex, cw×cl	Locality	Catalogue no.	esl/esw	P4/cw
<i>Parasesarma jamelense</i> (Rathbun, 1914)	M, 11.5 × 10.0 F, 10.6 × 9.1	Philippines: Luzon	USNM 45917 holotype	0.85	1.86
<i>Parasesarma kuekenthali</i> (De Man, 1902)	M, 9.5 × 7.6	Philippines: Luzon	USNM 120524 paratype	–	–
	M, 16.7 × 14.0	Indonesia: Mulukken: Halamahara	KauSMF 2020 (ZMG) syntype	–	–
	M, 13.4 × 10.8*	Indonesia: Mulukken: Halamahara	KauSMF 2022 (ZMG) syntype	–	–
<i>Parasesarma kui</i> Li, Rahayu & Ng, 2018	M, 13.8 × 11.0	Philippines: Cebu: Kawasan	ZSM-A20171201	–	–
	F, 20.2 × 16.7	Indonesia: Sulawesi: Manado	RMNH.CRUS.D.40869	1.11	–
	M, 13.1 × 12.1	Indonesia: Mulukken: Halamahara	KauSMF 2021 (ZMG) syntype	–	–
<i>Parasesarma lanchesteri</i> (Tweedie, 1936)	M, 13.0 × 11.6*	Taiwan: Pingtung	ZRC 2018.0792	0.87	2.14
	M, 20.8 × 16.2	Philippines: Cebu	UF48132	–	–
	M, 12.8 × 10.5	Singapore	NHM 1947.11.18.24 holotype	1.34	–
<i>Parasesarma lenzii</i> (De Man, 1895)	F, 24.8 × 18.8*	Singapore: Belok Besan	SMF 7139	–	–
	M, 13.3 × 11.3	Singapore	ZRC 1967.11.8.3	–	–
	M, 11.8 × 9.9*	Indonesia: Sumatra: Aceh	RMNH.CRUS.D.102653 syntype	–	–
<i>Parasesarma lepidum</i> (Tweedie, 1950)	M, 11.4 × 8.8	Cocos (Keeling) island	ZRC 2018.1373	0.88	1.81
	M, 10.3 × 8.1	East Malaysia: North Borneo: Labuan	NHM 1951.2.15.5-6 cotype	–	–
	M, 10.4 × 7.8	East Malaysia: North Borneo: Labuan	ZRC 1964.9.3.466-487 paratype	–	–
<i>Parasesarma leptosoma</i> (Hilgendorf, 1869)	M, 6.4 × 5.3	East Malaysia: North Borneo: Labuan	ZRC 1964.9.3.466-487 paratype	–	1.84
	F, 10.1 × 8.3	Brunei, Sangol Bunga	ZRC 2016.0398	–	–
	F, 17.0 × 16.0	East Malaysia: North Borneo: Labuan	ZRC 1964.9.3.466-487 paratype	1.15	–
<i>Parasesarma liho</i> Koller, Liu & Schubart, 2010	M, 17.7 × 16.5*	Zanzibar	ZMB 3181 holotype	–	–
	M, 14.3 × 13.2	Kenya: Mida Creek	MZUF 4977	–	–
	M, 19.0 × 17.5	Kenya: Mida Creek	MZUF 4976	0.91	–
	M, 17.9 × 16.0	Kenya: Mida Creek	MZUF 4978	–	1.88
	F, 16.5 × 15.6	Kenya: Mida Creek	MZUF 4978	–	–
	F, 20.8 × 17.8	Kenya: Mida Creek	MZUF 4976	–	–
	NA	Kenya: Mida Creek	MZUF 4977	–	–
	M, 13.8 × 12.5	Taiwan: Hualien city	MZUF 2547	–	–
	M, 13.1 × 11.8*	Taiwan: Hualien city	SMF 36266 holotype	–	–
	M, 13.0 × 11.6	Taiwan: Pingtung: Kankou	ZSM-A20100040 paratype	0.92	–
	F, 9.6 × 8.7	Taiwan: Hualien city	ZRC 2013.1757	–	2.0
<i>Parasesarma limbense</i> (Rathbun, 1914)	M, 7.6 × 6.9	Taiwan: Hualien city	ZSM-A20100041 paratype	–	–
	F, 12.8 × 11.5	Indonesia: Sulawesi: Lembeh Island	USNM 45920 holotype	0.88	2.14
	M, 26.4 × 22.2	Indonesia: Sulawesi: Lembeh Island	USNM 120523 paratype	–	–
<i>Parasesarma lividum</i> (A. Milne-Edwards, 1869)		New Caledonia	MNHN-B3634 holotype	–	–

Table 1. Continued

Species	Sex, cw×cl	Locality	Catalogue no.	esl/esw	P4/cw
<i>Parasesarma longicristatum</i> (Campbell, 1967)	M, 17.8 × 15.2* M, 23.9 × 20.3 F, 17.2 × 14.2 M, 18.5 × 14.9*	New Caledonia New Caledonia New Caledonia Australia: Queensland: Port Alma	QM-W24243 QM-W24243 QM-W24243 QM-W2464 paratype	1.46 — — —	— — — —
<i>Parasesarma luomi</i> Serène, 1982	M, 17.6 × 14.6 M, 13.9 × 11.3 M, 13.5 × 10.8*	Australia: Queensland: Moreton Bay Vietnam: Nha Trang Bay Vietnam	QM-W19924 ZRC 1967.11.18.2-4 MNHN-B16721	— — —	— — 1.60
<i>Parasesarma macaco</i> Li, Rahayu & Ng, 2018	M, 13.6 × 10.2	Vietnam: Nha Trang Bay	MNHN-B7282	1.32	—
<i>Parasesarma maipoense</i> (Soh, 1978)	M, 12.3 × 11.8 M, 27.7 × 21.0 M, 25.3 × 19.6*	Taiwan: Pingtung Hong Kong: Mai Po marshes Vietnam: Red River	ZRC 2018.0788 NHM 1976.106 holotype ZRC 2009.0800	0.98 — 1.71	2.14 — 1.62
<i>Parasesarma melissa</i> (De Man, 1887)	M, 12.5 × 10.7 M, 10.8 × 9.3 M, 13.8 × 11.4* M, 12.9 × 10.6	Singapore: Mandai mangroves Singapore: Buloh mangroves Singapore Singapore: Lim Chu Kang	ZRC 1993.257-258 ZSM-A20171188 MZUF 2597 ZRC 2000.1955	1.40 — — —	1.84 — — —
<i>Parasesarma messa</i> (Campbell, 1967)	M, 18.8 × 16.0 M, 17.6 × 14.4	Australia: Queensland: Flying Fish Point Australia: Queensland: Flying Fish Point	QM-W2452 paratype QM-W2452 paratype	— —	— —
<i>Parasesarma moluccense</i> (De Man, 1892)	M, 19.3 × 16.7* M, 18.5 × 16.0 M, 14.6 × 13.6	Australia: Queensland: Brisbane: Redland Australia: Queensland: Townsville Indonesia: Flores	ZRC 1999.0650 QM-W2446 paratype RMNH.CRUS.D.102590 lectotype	— 1.27 0.91	— 1.92 1.86
<i>Parasesarma obliquifrons</i> (Rathbun, 1924)	M, 12.3 × 10.9 M, 13.2 × 11.8* M, 12.7 × 11.1* M, 12.1 × 10.2 F, 11.4 × 10.0 M, 23.9 × 19.3* M, 22.4 × 18.7	Indonesia: Flores Indonesia: Moluccas Samoa: Pago Pago Samoa: Pago Pago Samoa: Pago Pago Singapore Malaysia: Penang	RMNH.CRUS.D.102591 paralectotype RMNH.CRUS.D.40911 USNM 45913 holotype USNM 45913 paratype USNM 45913 paratype ZRC 2000.1490 SMF 49925	— — 0.87 — — 1.64 —	— — — 2.0 — 1.69 —
<i>Parasesarma palauense</i> (Takeda, 1971)	M, 9.42 × 7.6	Palau Island	ZLKH 3380 holotype	—	1.86
<i>Parasesarma pangauranense</i> (Rathbun, 1914)	F, 6.0 × 4.9	Philippines: Busuanga Island: Pangauran River	USNM 45909 holotype	1.48	—
<i>Parasesarma parvulum</i> Li, Rahayu & Ng, 2018	M, 9.8 × 8.2*	Mindoro, Philippines	ZRC 2020.0136	0.9	2.15
<i>Parasesarma paucitorum</i> Rahayu & Ng, 2009	M, 19.9 × 18.8* F, 19.3 × 17.6*	Indonesia: Sulawesi: Manado Indonesia: Sulawesi: Manado	MZB.cru.2243 holotype ZRC 2008.0869, paratype	0.82 —	2.02 —

Table 1. Continued

Species	Sex, cw x cl	Locality	Catalogue no.	esl/esw	P4/cw
<i>Parasesarma peninsulare</i> Shahdadi, Ng & Schubart, 2018	M, 25.5 × 22.2	Singapore: Mandai mangroves	ZRC 2017.1075 holotype	–	1.7
<i>Parasesarma persicum</i> Naderloo & Schubart, 2010	M, 24.4 × 20.6*	Singapore: Besar mangroves	ZRC 2012.0260 paratype	1.33	–
	M, 24.3 × 19.0*	Persian Gulf: Iran: Nayband Bay	ZSM-A20171193	1.35	1.65
<i>Parasesarma pictum</i> (De Haan, 1835)	F, 19.6 × 14.6	Persian Gulf: Iran: Nayband Bay	ZSM-A20171194	–	–
	M, 19.8 × 17.6*	Japan: Hiroshima: Kamo River	ZSM-A20171191	1.39	1.96
	F, 21.40 × 18.2	Japan: Hiroshima: Kamo River	ZSM-A20171192	–	–
	M, 23.1 × 20.1	Japan: Kanagawa: Sagami Bay	RMNH.CRUS.D.26954	–	–
	M, 20.4 × 17.0*	Thailand: Phuket	ZRC 2000.1913	–	–
<i>Parasesarma plicatum</i> (Latreille, 1803)	M, 21.7 × 17.4	Sri Lanka	SMF 49926	–	–
	M, 17.6 × 14.1	Sri Lanka	NHMW 1637	–	–
	M, 22.4 × 17.8	Thailand: Phuket	SMF 49918	1.21	–
	F, 17.4 × 13.9	Thailand: Phuket	SMF 49927	–	–
	M, 10.7 × 8.8*	Thailand: Phuket	CBM ZC 6068	1.22	–
<i>Parasesarma prashadi</i> (Chopra & Das, 1937)	F, 8.8 × 7.2	Thailand: Phuket	CBM ZC 6068	–	–
	M, 13.0 × 11.5*	Malaysia: Tioman	ZRC 1017.1240	0.85	2.11
<i>Parasesarma purpureum</i> Li, Rahayu & Ng, 2018	F, 12.2/10.6	Malaysia: Tioman	ZRC 1017.1240	–	–
<i>Parasesarma raouli</i> Rahayu & Ng, 2009	M, 6.8 × 5.9	Peninsular Malaysia: Johor: Sungai Melayu	ZRC 1967.11.14.5 paratype	–	–
	M, 9.5 × 7.1*	Singapore: Lim Chu Kans	ZSM-A20171190	1.48	–
<i>Parasesarma rutilimanum</i> (Tweedie, 1936)	F, 6.9 × 5.5	Peninsular Malaysia: Johor: Sungai Melayu	ZRC 1967.11.14.3 paratype	–	–
	M, 10.7 × 8.8	Singapore: Pulau Senang:	NHM 1947.11.18.35-36 syn-type	–	–
<i>Parasesarma samawati</i> (Gillikin & Schubart, 2004)	M, NA	Singapore: Pulau Tekong	ZRC NA	–	–
	M, 8.5 × 6.6	Malaysia: Labuan	ZRC 1973.11.3.15-88	–	1.89
	M, 9.0 × 8.0	Malaysia: Labuan	ZRC 1973.11.3.15-88	1.26	–
	F, 10.6 × 7.9	Malaysia: Labuan	ZRC 1973.11.3.15-88	–	–
	M, 23.7 × 20.5*	Kenya: Watamu	SMF 29333 holotype	–	–
<i>Parasesarma sanguimanus</i> Li, Shih & Ng, 2019	M, 28.6 × 23.9	Kenya: Watamu	SMF 29334 paratype	1.23	–
	M, 17.9 × 15.3	Seychelles	MZUF 2938	–	–
	M, 14.5 × 11.6*	Philippines: Bohol	NA	–	–
<i>Parasesarma semperi</i> (Bürger, 1893)	M, 17.0 × 13.1	Philippines: Bohol	SMF 625 (ZMG) lectotype	–	–
	M, 12.2 × 9.6	Indonesia: Irian Jaya: Ajkwa	SMF 49928	–	–
	F, 13.7 × 11.4*	Indonesia: Irian Jaya: Tipoeika	ZRC 2016.0524	–	–
	F, 14.4 × 11.7	Indonesia: Irian Jaya: Tipoeika	ZRC 2016.0524	1.24	–

Table 1. Continued

Species	Sex, cw×cl	Locality	Catalogue no.	esl/esw	P4/cw
<i>Parasesarma sigillatum</i> (Tweedie, 1950)	M, 10.7 × 7.6 M, 8.4 × 6.3 F, 10.4 × 7.5	Cocos (Keeling) Islands Cocos (Keeling) Islands Cocos (Keeling) Islands	NHM 1950.4.17.4 lectotype ZRC 2019.0418 NHM 1950.4.17.5 paralectotype	1.15 – –	– 1.5 –
<i>Parasesarma tarantula</i> Li, Rahayu & Ng, 2018	F, 11.0 × 7.8*	Cocos (Keeling) Islands	ZRC 1965.8.2.260–269	–	–
<i>Parasesarma tripectinis</i> (Shen, 1940)	M, 14.2 × 12.8* M, 12.6 × 10.9 M, 12.8 × 9.7 M, 9.9 × 8.0* M, 15.8/12.0 M, 28.2 × 24.0*	Indonesia: Sulawesi: Bunaken Island Indonesia: Sulawesi: Bitung Taiwan: Chunan Taiwan: Chunan China: Hong Kong: Remnant shore Vietnam: Tan Thoi Island: Cua Tieu River	ZSM-A20171205 ZRC170402 ZSM-A20171189 ZSM-A20171189 ZRC 1998.0340 QM-W28348 holotype	0.97 – 1.27 – – 1.5	– 2.02 – – 1.7 1.5
<i>Paraesarma tuerkayi</i> (Shahdadi, Davie & Schubart, 2017)	F, 25.3 × 21.2	Vietnam: Tan Thoi Island: Cua Tieu River	QM-W27002 paratype	–	–
<i>Paraesarma unguatum</i> (H. Milne Edwards, 1853)	M, 12.1 × 9.8	Indonesia: Sulawesi	MNHN-B3694	–	–
<i>Bresedium brevipes</i> (De Man, 1889)	M, 16.7 × 13.0* M, 18.8 × 14.8 F, 16.1 × 12.5 M, NA*	Indonesia: Irian Jaya: Ajkwa River Thailand: Chonburi Indonesia: Irian Jaya: Ajkwa River Australia: Queensland: Flame Tree Creek	ZRC 2008.0815 ZRC 1999.0566 ZRC 2008.0815 QM-W 22085	– 1.25 – –	– 1.57 – –
<i>Chiromantes dehaani</i> (H. Milne Edwards, 1853)	F, NA*	Japan: Satsuma Peninsula	ZRC 2002.0226	–	–
<i>Chiromantes haematocheir</i> (De Haan, 1833)	NA*	Japan: Wakayama: Samusaura	SMF 25989	–	–
<i>Eneosesarma azizi</i> Brösing, Spiridonov, Al-Aidaros & Türkay, 2014	M, 15.9 × 12.4*	Red Sea: Saudi Arabia: Jizan: Farasan Island	SMF 43475 paratype	–	–
<i>Perisesarma dusumieri</i> (H. Milne Edwards, 1853)	M, 25.2 × 21.8*	Thailand: Phuket	SMF 49930	–	–
<i>Sarmatium crassum</i> (Dana, 1851)	F, 22.5 × 19.3*	Kenya: Dabaso	MZUF 2545	–	–
<i>Selatium elongatum</i> (A. Milne-Edwards, 1869)	M, 36.3 × 36.3*	Kenya: Mida Creek	MZUF 2521	–	–

Abbreviations: F, female; M, male; NA, not applicable here for this study. See main text for museum abbreviations.

*Specimens used for molecular analyses.

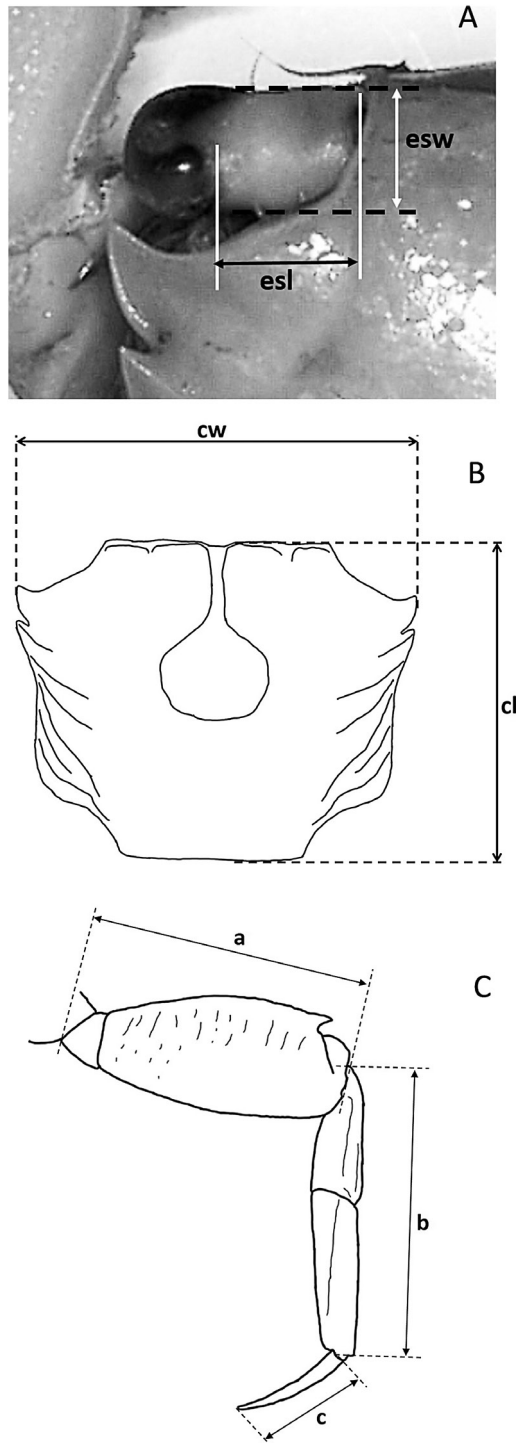


Figure 1. Diagrams of the morphometric characters used for this study. A, eyestalk. B, carapace: cw, carapace width, cl, carapace length. C, fourth pereiopod (P4): $a+b+c = P4$ length (ischium–dactylus).

Parasesarma tripectinis (Shen, 1940) (catalogue number CB03227-8; from Beijing Natural History Museum, Beijing, China) were kindly provided by our

colleagues Ngan Kee Ng and Peter K. L. Ng (National University of Singapore).

The following abbreviations are used in the text: cl, carapace length; cw, carapace width; esl, eye stalk length; esw, eye stalk width; G1, male first gonopod; P, pereiopod.

MOLECULAR ANALYSES

Genomic DNA was isolated using a modified Puregene method (Gentra Systems, Minneapolis, MN, USA) or Mollusc DNA kit (Omega Bio-tek D3373-02, Norcross, Georgia, USA) from muscular leg tissue or female pleopods, using the manufacturers' protocols. In cases of old specimens or those fixed in formalin, the muscle tissues were soaked in GTE buffer (Glucose/Tris/EDTA) overnight before starting the DNA extraction process (Shedlock *et al.*, 1997) with the Mollusc DNA kit. For nine species [*Parasesarma carolinense* Rathbun, 1907, *Parasesarma erythodactyla* (Hess, 1865), *Parasesarma hasswelli* (De Man, 1887), *Parasesarma jamelense* (Rathbun, 1914), *Parasesarma lepidum* (Tweedie, 1950), *Parasesarma limbense* (Rathbun, 1914), *P. palauense*, *Parasesarma panguaranense* (Rathbun, 1914) and *Parasesarma rutilimanum* (Tweedie, 1936)], DNA extraction was not successful, mainly because of DNA degradation of the available material.

Fragments of four genes, namely the mitochondrial protein-coding gene cytochrome *c* oxidase subunit I (*COX1*), the mitochondrial gene encoding the ribosomal RNA (rRNA) of the large ribosomal subunit (16S) and, for a subset of specimens, the nuclear protein-coding gene sodium-potassium ATPase alpha-subunit (*NaK*) and the nuclear gene encoding the rRNA of the large ribosomal subunit (28S), were amplified. For most of the examined species, DNA sequences of at least one genetic marker were used in the analyses (Table 2; Figs 2–4).

Polymerase chain reactions (PCRs) were performed using 1X reaction buffer, 250 μ M dNTPs, 2 mM $MgCl_2$, 0.5 μ M of each primer and 0.5 unit Go Taq polymerase (or U Taq for the few cases in which REDiant 2X PCR Master Mix, 1st BASE, Singapore was used), with the following profiles: initial denaturation step for 4 min at 94 °C; 40 cycles with 45 s at 95 °C for denaturing, 60 s at 48 °C (*COX1*, 16S and 28S) or 58 °C (*NaK*) for annealing, 60 s at 72 °C for extension and 5 min at 72 °C as a final extension step. To amplify a segment of ~604 bp of the *NaK* gene (including the primer regions), the primers NaK for-b2 (forward) and NaK rev3 (reverse) were used. For the 28S gene, the primer combination 28L4 (forward) and 28H4 (reverse) was used to amplify a segment of ~690 bp; if this combination did not work, the new primer 28H6 was used as a reverse primer to amplify a shorter

Table 2. List of species used for phylogenetic analyses along with their locality, GenBank accession numbers (*COXI*, 16S, *NaK* and 28S) and references

Species	Locality/localities	<i>COXI</i>	16S	<i>NaK</i>	28S	Reference(s)
<i>Parasesarma affine</i> (De Haan, 1833)	Taiwan: mangroves near Hsinchu	MT020717	MT021412	MT025970	NA	Present study
<i>Parasesarma anambas</i> Yeo, Rahayu & Ng, 2004	Anambas Island	LC510452*	MT021410	MT025969	NA	Li <i>et al.</i> (2019); present study
<i>Parasesarma asperum</i> (Heller, 1865)	India: Tamil Nadu	MT020712	MT021406	MT025967	NA	Present study
<i>Parasesarma aurifrons</i> Li, Shih & Ng, 2019	Taiwan: Pingtung	LC510454*	NA	NA	NA	Li <i>et al.</i> (2019)
<i>Parasesarma austrawati</i> Shahdadi, Davie & Schubart, 2019	Australia: Northern Territory: Arrla Creek	MH552902*	MH552897*	MH552920*	NA	Shahdadi <i>et al.</i> (2019a)
<i>Parasesarma batavianum</i> (De Man, 1890)	Singapore: Bulon	MT020718	MT021413	MT025971	NA	Present study
<i>Parasesarma bengalense</i> (Davie, 2003)	Thailand: Phuket	KX400902*	KX423810*	KX394815*	MT022580	Shahdadi & Schubart (2017); present study
<i>Parasesarma bidens</i> (De Haan, 1835)	Japan: Nagasaki	KX761166*	KX761172*	KX761170*	NA	Shahdadi & Schubart (2017)
<i>Parasesarma brevicristatum</i> (Campbell, 1967)	Australia: Queensland: Cardwell	KX400906*	KX423800*	NA	NA	Shahdadi & Schubart (2017)
<i>Parasesarma calypso</i> (De Man, 1895)	Indonesia: Sumatra: Aceh	MT020733	NA	NA	NA	Present study
<i>Parasesarma capensis</i> Fratini, Innocenti & Cannicci, 2019	South Africa: Natal: Umlazi Lagoon	MT020728	MT021424	NA	NA	Present study
<i>Parasesarma catenatum</i> (Ortmann, 1897)	South Africa: Durban Bay: Salisbury Island; South Africa: Mgazana	MT020709	MT021399	MT025976	MF554647*	Present study; Cannicci <i>et al.</i> (2017)
<i>Parasesarma charis</i> Rahayu & Ng, 2005	Indonesia: Irian Jaya: Kamora	MT020715	MT021409	NA	NA	Present study
<i>Parasesarma corallicum</i> Ng, Davie & Li, 2016	Taiwan: Pingtung: Kenting	MT020722	MT021417	MT025972	MT022583	Present study
<i>Parasesarma cricotum</i> (Rahayu & Davie, 2002)	Indonesia: Irian Jaya: Kamora River	KX400897*	KX423796*	KX394811*	NA	Shahdadi & Schubart (2017)
<i>Parasesarma darwinense</i> (Campbell, 1967)	Australia: Northern Territory: Darwin Island	KX400904*	KX423798*	MT025983	NA	Shahdadi & Schubart (2017); present study
<i>Parasesarma dumacense</i> (Rathbun, 1914)	Philippines: Cebu: Kawasam waterfall	KX400929*	KX423837*	KX394831*	NA	Shahdadi & Schubart (2017)
<i>Parasesarma ellenae</i> (Pretzmann, 1968)	Vanuato Island	MT023410	NA	NA	NA	Present study
<i>Parasesarma eumolpe</i> (De Man, 1895)	China: Hainan: Wenchang	KX400891*	KX423811*	KX394816*	NA	Shahdadi & Schubart (2017)

Table 2. Continued

Species	Locality/localities	COXI	16S	NaK	28S	Reference(s)
<i>Parasarma foresti</i> (Rahayu & Davie, 2002)	Indonesia: Irian Jaya: Kamora	KX431204*	KX423794*	KX394810*	NA	Shahdadi & Schubart (2017)
<i>Parasarma gazi</i> Cannicci, Innocenti & Fratini, 2017	Tanzania: Mtoni	MF564006*	MF564029*	MT025981	MF554644*	Cannicci et al. (2017); present study
<i>Parasarma gecko</i> Li, Rahayu & Ng, 2018	Japan: Okinawa Island: Awase	MT020732	NA	NA	NA	Present study
<i>Parasarma gemmatum</i> Li, Shih & Ng, 2019	Taiwan: Pingtung Philippines: Cebu	LC510467* MT023415	MT021426	NA	NA	Li et al. (2019)
<i>Parasarma gracilipes</i> Li, Rahayu & Ng, 2018	Indonesia: Irian Jaya: Kamora	MT023411	MT021422	NA	NA	Present study
<i>Parasarma guttatam</i> (A. Milne-Edwards, 1869)	Kenya: Gazi	KX400903*	KX423816*	KX394819*	MF554650*	Cannicci et al. (2017); Shahdadi & Schubart (2017)
<i>Parasarma hartogi</i> Davie & Pabriks, 2010	Australia: Western Australia: Onslow	KX400928*	KX423836*	KX394830*	NA	Shahdadi & Schubart (2017)
<i>Parasarma holthuisi</i> (Davie, 2010)	Australia: Western Australia: Ashburton River	KX400907*	KX423806*	KX394813*	NA	Shahdadi & Schubart (2017)
<i>Parasarma indiarum</i> (Tweedie, 1940)	Indonesia: Ambon	KX761164*	KX761171*	NA	NA	Shahdadi & Schubart (2017)
<i>Parasarma kuekenthali</i> (De Man, 1902)	Philippines: Cebu: Kawasan	MT020713	MT021407	MT025968	NA	Present study
<i>Parasarma kui</i> Li, Rahayu & Ng, 2018	Philippines: Cebu	MT020730	MT021427	NA	NA	Present study
<i>Parasarma lanchesteri</i> (Tweedie, 1936)	Singapore	KX761168*	KX761174*	KX761169*	NA	Shahdadi & Schubart (2017)
<i>Parasarma lenzii</i> (De Man, 1895)	Cocos (Keeling) island	MK584922*	MT021404	NA	NA	Shahdadi et al. (2019c); present study
<i>Parasarma leptosoma</i> (Hilgendorf, 1869)	Mida Creek, Kenya	MT020711	MT021401	MT025980	MF554645*	Cannicci et al. (2017); present study
<i>Parasarma liho</i> Koller, Liu & Schubart, 2010	Taiwan: Hualien city	LC490880*	MT021402	MT025979	MT022584	Shih et al. (2019); present study
<i>Parasarma lividum</i> (A. Milne-Edwards, 1869)	New Caledonia	KX400893*	KX423802*	KX394812*	NA	Shahdadi & Schubart (2017)
<i>Parasarma longicristatum</i> (Campbell, 1967)	Australia: Queensland: Port Alma	KY198240*	KY198245*	KY198249*	NA	Shahdadi & Schubart (2017)
<i>Parasarma luomi</i> Serène, 1982	Vietnam	MT023416	MT021418	NA	NA	Present study
<i>Parasarma macaco</i> Li, Rahayu & Ng, 2018	Taiwan	LC490888*	NA	NA	NA	Shih et al. (2019)

Table 2. Continued

Species	Locality/localities	COXI	16S	N _α K	28S	Reference(s)
<i>Parasesarma maipoense</i> (Soh, 1978)	Vietnam: Red River	KX400931*	NA	NA	NA	Shahdadi & Schubart (2017)
<i>Parasesarma melissa</i> (De Man, 1887)	Singapore	MF564015*	MF564031*	MT025977	MF554648*	Cannicci <i>et al.</i> (2017); present study
<i>Parasesarma messa</i> (Campbell, 1967)	Australia: Queensland: Brisbane: Redland	KX431205*	KX423795*	KX394835*	NA	Shahdadi & Schubart (2017)
<i>Parasesarma moluccense</i> (De Man, 1892)	Indonesia: Moluccas	MT020710	MT021400	NA	NA	Present study
<i>Parasesarma obliquifrons</i> (Rathbun, 1924)	Samoa: Pago Pago	LC510480*	MT021405	NA	NA	Li <i>et al.</i> (2019); present study
<i>Parasesarma onychophorum</i> (De Man, 1895)	Singapore	KX400913*	KX423812*	KX394817*	NA	Shahdadi & Schubart (2017)
<i>Parasesarma parvulum</i> Li, Rahayu & Ng, 2018	Mindoro, Philippines	MT020727	MT021423	NA	NA	Present study
<i>Parasesarma paucitorum</i> Rahayu & Ng, 2009	Indonesia: Sulawesi: Manado	LC490886*	MT021403	MT025984	NA	Shih <i>et al.</i> (2019); present study
<i>Parasesarma peninsulare</i> Shahdadi, Ng & Schubart, 2018	Singapore: Besar mangroves	KX400890*	MT021421	MT025975	NA	Shahdadi <i>et al.</i> (2018b); present study
<i>Parasesarma persicum</i> Naderloo & Schubart, 2010	Persian Gulf: Iran: Nayband Bay	MT020721	MT021416	MT025974	NA	Present study
<i>Parasesarma pictum</i> (De Haan, 1835)	Japan: Hiroshima: Kamo River	MT020719	MT021414	MT025973	MT022582	Present study
<i>Parasesarma plicatum</i> (Latreille, 1803)	Thailand: Phuket	KX400912*	KX423823*	KX394821*	MT022581	Shahdadi & Schubart (2017); present study
<i>Parasesarma prashadi</i> (Chopra & Das, 1937)	Thailand: Phuket	MT020720	MT021415	NA	NA	Present study
<i>Parasesarma purpureum</i> Li, Rahayu & Ng, 2018	Malaysia: Tioman	MT020731	NA	NA	NA	Present study
<i>Parasesarma raoouli</i> Rahayu & Ng, 2009	Singapore: Lim Chu Kans	MT020714	MT021408	NA	NA	Present study
<i>Parasesarma samawati</i> (Gillikin & Schubart, 2004)	Kenya: Watamu; Kenya: Mida Creek	KX400895*	KX423821*	MH552924*	MF554649*	Cannicci <i>et al.</i> (2017); Shahdadi & Schubart (2017)
<i>Parasesarma sanguimanus</i> Li, Shih & Ng, 2019	Taiwan: Pingtung Philippines: Bohol	LC510481* KX400899	KX423820	NA	NA	Li <i>et al.</i> (2019); present study
<i>Parasesarma semperi</i> (Bürger, 1893)	Indonesia: Irian Jaya: Ajkwa	MF173024*	MF173039*	MT025982	NA	Shahdadi <i>et al.</i> (2018a); present study
<i>Parasesarma sigillatum</i> (Tweedie, 1950)	Cocos (Keeling) Islands	MT020729	MT021425	NA	NA	Present study

Table 2. Continued

Species	Locality/localities	COXI	16S	NaK	28S	Reference(s)
<i>Parasesarma tarantula</i> Li, Rahayu & Ng, 2018	Indonesia: Sulawesi: Bunaken Island	MT020726	MT021420	NA	NA	Present study
<i>Parasesarma tripectinis</i> (Shen, 1940)	Taiwan: Chunan	MT020716	MT021411	NA	NA	Present study
<i>Parasesarma tuerkayi</i> (Shahdadi, Davie & Schubart, 2017)	Vietnam: Tan Thoi Island: Cua Tieu River	KY198241*	KY198247*	KY198248*	NA	Shahdadi et al. (2017)
<i>Parasesarma unguilatum</i> (H. Milne Edwards, 1853)	Indonesia: Irian Jaya: Ajkwa River	KX400930*	KX423838*	KX394832*	NA	Shahdadi & Schubart (2017)
<i>Bresedium brevipes</i> (De Man, 1889)	Australia: Queensland: Flame Tree Creek	MT020723	AM180685*	NA	NA	Schubart et al. (2006); present study
<i>Chiromantes delatani</i> (H. Milne Edwards, 1853)	Japan: Satsuma Peninsula	MT020724	FN296221*	NA	NA	Schubart et al. (2006); present study
<i>Chiromantes eulimene</i> (De Man, 1895)	Mida Creek, Kenya	MF564019*	AJ784017*	NA	MF554652*	Cannicci et al. (2017); present study
<i>Chiromantes haematocheir</i> (De Haan, 1833)	Japan: Wakayama: Samusaura	MT017656	AJ308414*	NA	MT022578	Schubart et al. (2006); present study
<i>Chiromantes ortmanni</i> (Crosnier, 1965)	Gazi Bay, Kenya	MF564018*	AJ784016*	NA	MF554653*	Cannicci et al. (2017); present study
<i>Clitocaeloma villosum</i> (A. Milne-Edwards, 1869)	Kenya, Mida Creek	KX400922*	KX423827*	KX394823*	NA	Shahdadi & Schubart (2017)
<i>Eneosesarma azizi</i> Brösing, Spiridonov, Al-Aidaros & Türkay, 2014	Red Sea: Saudi Arabia: Jizan: Farasan Island	MT020725	MT021419	NA	NA	Present study
<i>Fasciaria fasciatum</i> (Lanchester, 1900)	Singapore, Lim Chu Kang	KX400921*	KX423824*	KX394822*	NA	Shahdadi & Schubart (2017)
<i>Guineasarma alberti</i> (Rathbun, 1921)	Ghana, Ada Foah	KX400917*	KX423817*	NA	NA	Shahdadi & Schubart (2017)
<i>Guineasarma huzardi</i> (Desmarest, 1825)	Ghana, Elmina	KX400919*	KX423832*	KX394828*	NA	Shahdadi & Schubart (2017)
<i>Guineasarma kamermani</i> (De Man, 1883)	Angola, Luanda	KX400937*	KX423839*	NA	NA	Shahdadi & Schubart (2017)
<i>Metagrapsus curvatus</i> (H. Milne Edwards, 1837)	Ghana, Ada Foah	KX400936*	KX423840*	KX394834*	NA	Shahdadi & Schubart (2017)
<i>Neosarmatium africanum</i> (Ragionieri, Fratini & Schubart, 2012)	South Africa	KX400925*	KX423831*	KX394827*	FN392199*	Cannicci et al. (2017); Shahdadi & Schubart (2017)
<i>Perisesarma dusumieri</i> (H. Milne Edwards, 1853)	Thailand: Phuket	KX400916*	KX423814*	KX394818*	MT022579	Shahdadi & Schubart (2017); present study
<i>Sarmatium crassum</i> (Dana, 1851)	Kenya: Dabaso	MF564021*	AJ784015*	MT025978	MF554653*	Cannicci et al. (2017); present study

Table 2. Continued

Species	Locality/localities	<i>COX1</i>	16S	<i>NrαK</i>	28S	Reference(s)
<i>Selatium brockii</i> (De Man, 1887)	Kenya, Mida Creek	KX400934*	KX423828*	KX394824*	MF554654*	Cannicci <i>et al.</i> (2017); Shahdadi & Schubart (2017)
<i>Selatium elongatum</i> (A. Milne-Edwards, 1869)	Kenya: Mida Creek	KX400924*	KX423830*	KX394826*	NA	Shahdadi & Schubart (2017)
<i>Sesarma reticulatum</i> (Say, 1817)	USA, Delaware	KX400927*	KX423826*	KX394829*	NA	Shahdadi & Schubart (2017)
<i>Sesarmoides longipes</i> (Krauss, 1843)	Kenya, Mida Creek	KX400923*	KX423829*	KX394825*	MF554654*	Cannicci <i>et al.</i> (2017); Shahdadi & Schubart (2017)

Abbreviation: NA, not applicable here for this study.
*Sequences were recovered from previous studies from GenBank.

segment (~577 bp). Different primer combinations had to be used to amplify fragments of varying lengths of the mitochondrial genes *COX1* and 16S, owing to the variation in quality of the extracted DNA. The primer combination COL6–COH6 (in a few cases, LCO1490–HCO2198) was used to amplify a segment of 709 bp of *COX1* (including primer regions). For old museum specimens with strong DNA degradation and fragmentation, sequencing of two overlapping shorter fragments (~350–400 bp) allowed amplification of the same segment using the taxon-specific primer combinations COL6–COH7P and COL7–COH6. The primer combination 16L2–16H11 was used to amplify a fragment of the 16S gene with a length of ~585–600 bp (for detailed primer information, see Table 3).

The PCR products were outsourced for sequencing to MacroGen Europe or 1st BASE Singapore. Sequences were proofread using Chromas Lite (v.2.1.1; Technelysium Pty Ltd, South Brisbane, Queensland, Australia). Primer regions were removed and the remaining sequences aligned with ClustalW (Thompson *et al.*, 1994) implemented in BioEdit v.7.0.5 (Hall, 1999). New sequences were submitted to the National Center for Biotechnology Information (NCBI) and are available from GenBank under the accession numbers shown in Table 2. Homologous sequences from previous studies were also recovered from GenBank and included in further statistical analyses (Table 2).

The best evolutionary models describing our various datasets were determined with the aid of jModelTest (v.2.1.4; Durriba *et al.*, 2012) and selected with the Akaike information criterion (AIC; Posada & Buckley, 2004). Three alignments, one for the concatenated dataset of the two mitochondrial genes and two from the individual nuclear genes, were converted to Nexus files with FaBox (Villesen, 2007) as input files for subsequent phylogenetic analyses. The data of the concatenated alignment were partitioned by gene, because the markers have different mutation characteristics. Pairwise genetic distances for the *COX1* gene [Kimura two-parameter model (K2P)] were calculated with the software MEGA v.5.2.2 (Tamura *et al.*, 2011).

Two methods of phylogenetic inference were applied to our data: maximum likelihood (ML) using the software raxmlGUI (v.1.3; Silvestro & Michalak, 2012) and Bayesian inference (BI) as implemented in MrBayes (v.3.2; Huelsenbeck & Ronquist, 2001). Maximum likelihood trees were obtained for each alignment with 1000 bootstrap pseudoreplicates. For the BI analysis, we used two million generations with four chains (one heated) and a sample frequency of one tree per 1000 generations.

To clarify the phylogenetic positions of representatives of *Parasesarma* within the Sesarmidae, species of other sesarmid genera were

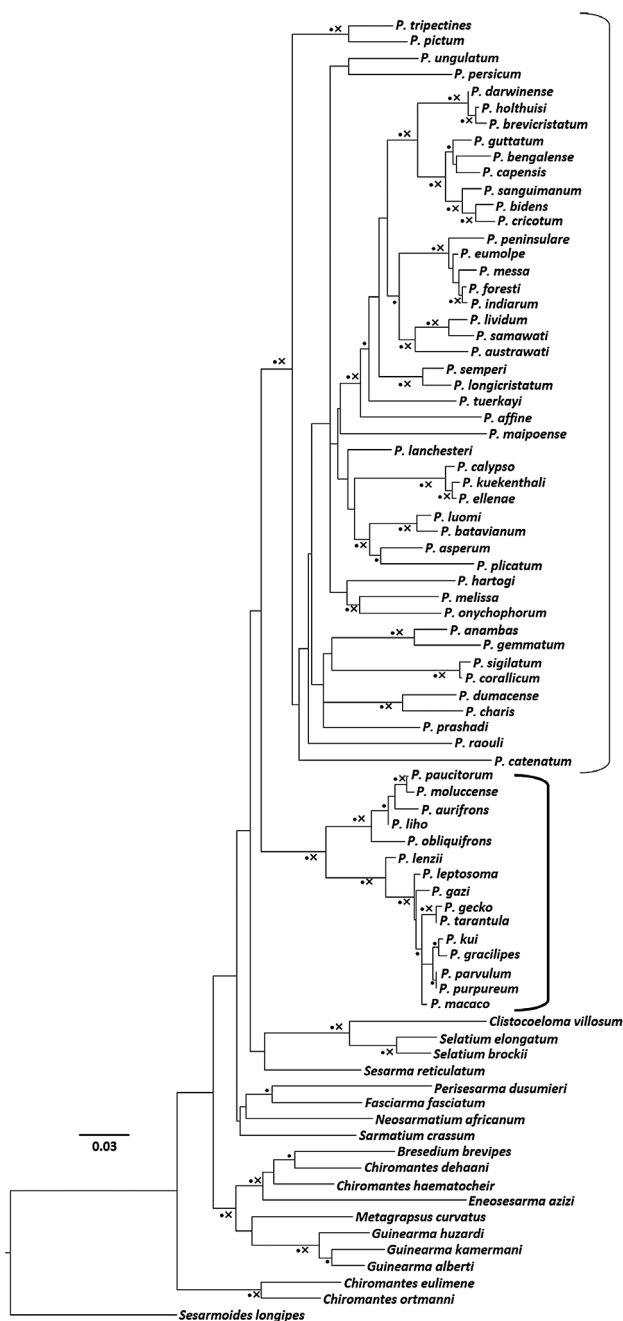


Figure 2. Maximum likelihood (ML) consensus tree topology inferred from the concatenated dataset (*COX1*, 16S) of selected sesarmid crabs (focusing on *Parasesarma*).
 • sign refers to bootstrap values > 50% in ML; × sign refers to posterior probabilities > 0.95 in Bayesian inference. *Sesarmoides longipes* was used as the outgroup. Thin bracket refers to the *Parasesarma plicatum* group; thick bracket refers to the clade of the *Parasesarma leptosoma* group.

included in the analyses (Table 1) as representatives of different phylogenetic clades (see Schubart *et al.*, 2006; Shahdadi & Schubart, 2017). *Sesarmoides*

longipes (Krauss, 1843) was used as the outgroup in tree constructions according to its basal phylogenetic position within the family, as recovered in previous studies (see Schubart *et al.*, 2006).

RESULTS

MOLECULAR ANALYSIS

After removal of the primer sequences and adjacent regions, the cropped alignments of *NaK*, 28S, 16S and *COX1* consisted of 540, 578, 553 and 645 bp, respectively, and the concatenated alignment of the two mitochondrial genes consisted of 1198 bp. The alignments of the protein-coding genes did not reveal any stop codons or indels, which would have indicated the presence of pseudogenes. The best evolutionary model for genetic analyses obtained with jModelTest (Guindon & Gascuel, 2003) for the 28S, *NaK* and *COX1* + 16S alignments was the general time reversible plus gamma (GTR+G; Rodríguez *et al.*, 1990). Six phylogenetic trees were obtained by applying ML and BI analyses to each of the three alignments. Given that the trees from ML and BI analyses had similar topologies, here we present only the ML trees, but including confidence values of both analyses (bootstrap values for ML and posterior probabilities for BI; Figs 2–4).

In all phylogenetic trees, species of *Parasesarma* are split into two distinct clades: a main clade of *Parasesarma* containing most species of the genus, including the type species [here referred to as *Parasesarma plicatum* (Latreille, 1803) group and shown in thin brackets in Figs 2–4], and a second clade of *Parasesarma*, including *P. leptosoma* and 14 related species (*P. leptosoma* group; thick brackets in Figs 2–4). The two reciprocally monophyletic groups are highly supported in most cases by both analyses, with bootstrap values > 50 and posterior probabilities > 0.95 (Figs 2–4). Members of the *P. leptosoma* group are also clearly separated from all other examined genera of Sesarmidae (Figs 2–4).

The tree constructed from the two mitochondrial genes includes more species than the other two trees. It provides evidence that the clade of the *P. leptosoma* group consists of two distinct and well-supported subclades (Fig. 2). In the subclade composed of *P. aurifrons*, *Parasesarma liho* Koller, Liu & Schubart, 2010, *Parasesarma moluccense* (De Man, 1892), *Parasesarma paucitorum* Rahayu & Ng, 2009 and *Parasesarma obliquifrons* (Rathbun, 1924), the last species is isolated from the others, of which *P. moluccense* and *P. paucitorum* show a tight association. The second subclade includes *Parasesarma lenzii* (De Man, 1895) (holding a basal position) and nine closely related species. These nine species (i.e. *P. leptosoma*,

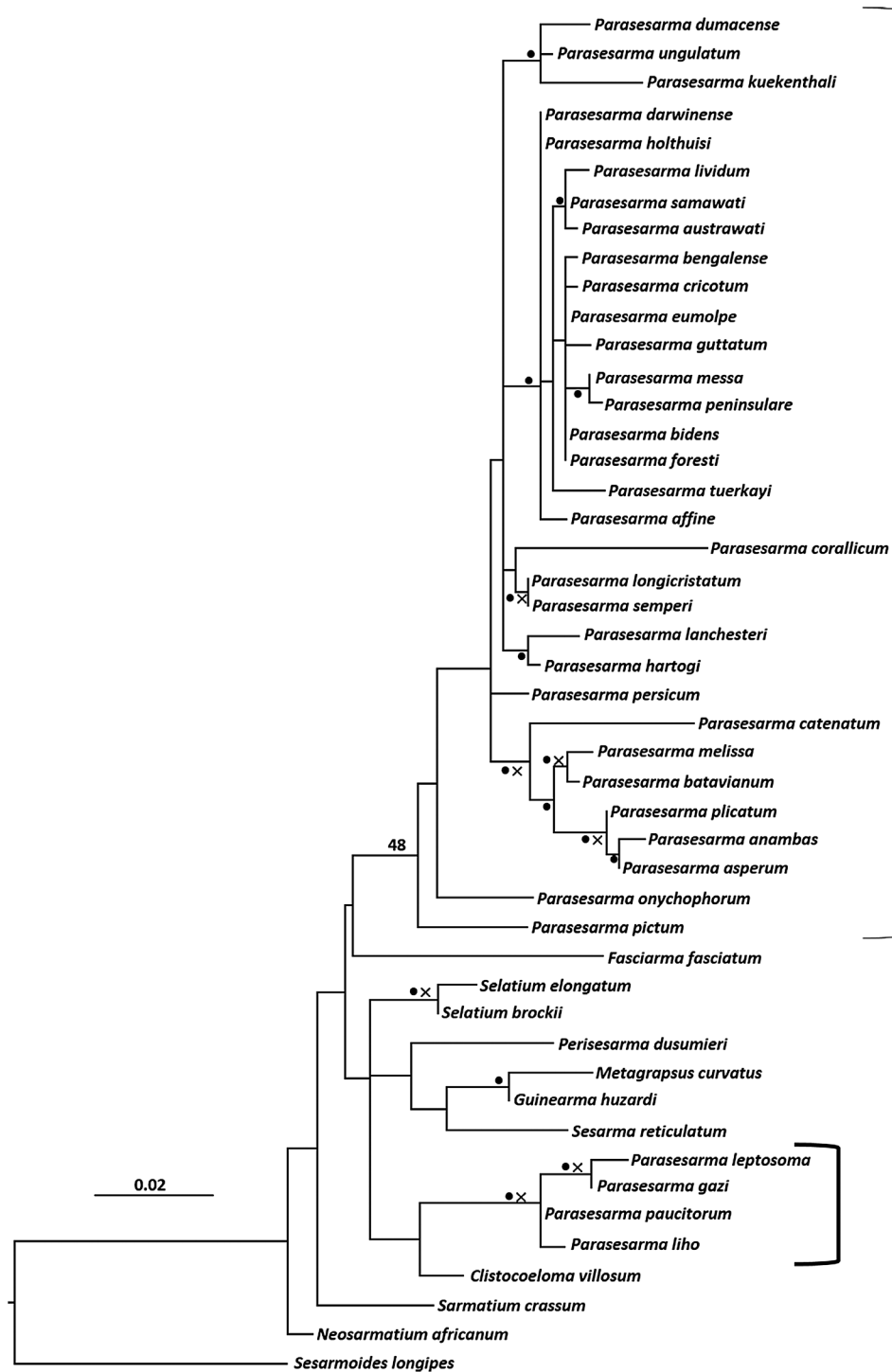


Figure 3. Maximum likelihood (ML) consensus tree topology inferred from the *NaK* gene of selected sesarmid crabs (focusing on *Parasesarma*). • sign refers to bootstrap values > 50% in ML; × sign refers to posterior probabilities > 0.95 in Bayesian inference. *Sesarmoides longipes* was used as the outgroup. Thin bracket refers to the *Parasesarma plicatum* group; thick bracket refers to the clade of the *Parasesarma leptosoma* group.

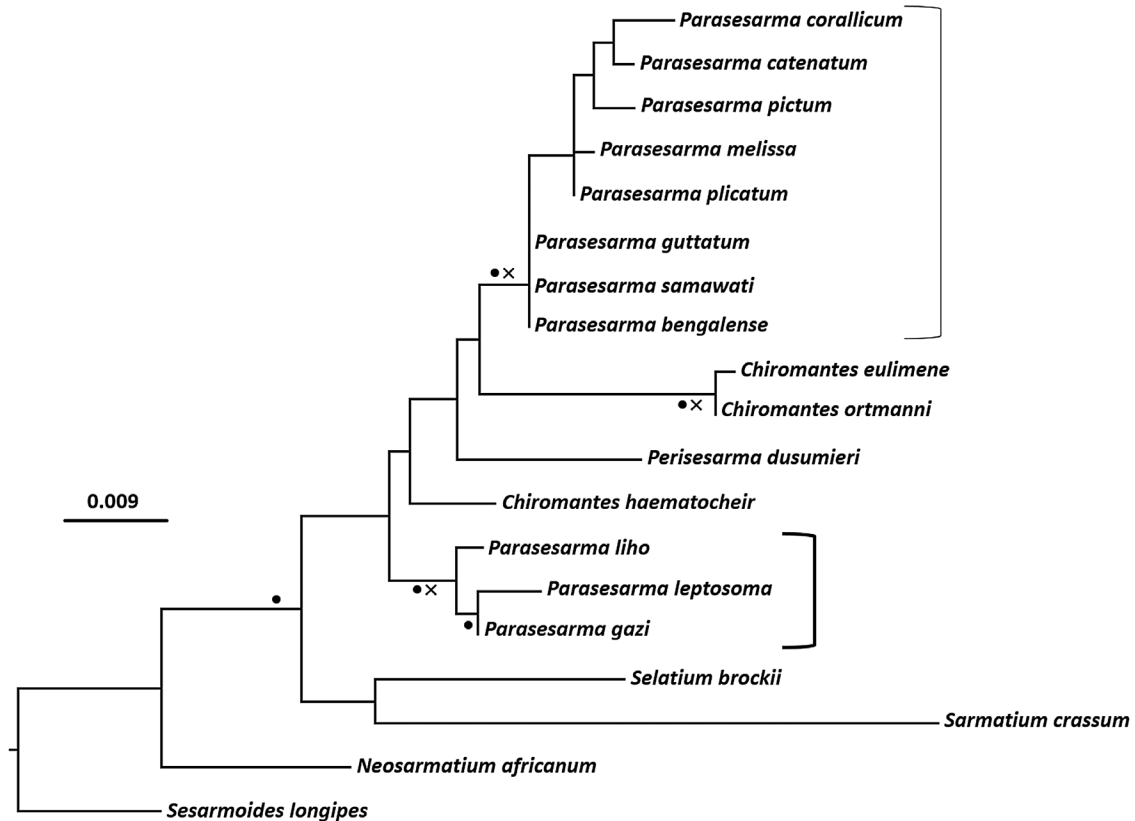


Figure 4. Maximum likelihood (ML) consensus tree topology inferred from 28S gene of selected sesarimid crabs (focusing on *Parasesarma*). • sign refers to bootstrap values > 50% in ML; × sign refers to posterior probabilities > 0.95 in Bayesian inference. *Sesarmoides longipes* was used as the outgroup. Thin bracket refers to the *Parasesarma plicatum* group; thick bracket refers to the clade of the *Parasesarma leptosoma* group.

P. gazi, *Parasesarma macaco* Li, Rahayu & Ng, 2018, *Parasesarma parvulum* Li, Rahayu & Ng, 2018, *Parasesarma purpureum* Li, Rahayu & Ng, 2018, *Parasesarma kui* Li, Rahayu & Ng, 2018, *Parasesarma gracilipes* Li, Rahayu & Ng, 2018, *Parasesarma gecko* Li, Rahayu & Ng, 2018 and *Parasesarma tarantula* Li, Rahayu & Ng, 2018) show low genetic divergences in the mitochondrial tree (Fig. 2). Among them, the pairs formed by *P. gecko* with *P. tarantula* and *P. kui* with *P. gracilipes* are closely associated. *Parasesarma purpureum* and *P. parvulum* share the same haplotype in the *COX1* gene.

In the clade of the *P. plicatum* group, there are also several supported and stable subclades. The subclade of *P. tripectinis*–*Parasesarma pictum* (De Haan, 1833) holds a basal position within this group. The three species *Parasesarma calypso* (De Haan, 1895), *Parasesarma kuekenthali* (De Man, 1902) and *Parasesarma ellenae* (Pretzmann, 1968) show a tight association. There are several other highly supported species pairs [e.g. *Parasesarma anambas* Yeo, Rahayu & P. K. L. Ng, 2004–*Parasesarma gemmatum* Li, Shih & Ng, 2019; *Parasesarma luomi* Serène, 1982–*Parasesarma*

bataavianum (De Man, 1890); *Parasesarma dumacense* (Rathbun, 1914)–*Parasesarma charis* Rahayu & Ng, 2005; and *Parasesarma corallicum* Ng, Davie & Li, 2016–*Parasesarma sigillatum* (Tweedie, 1950)]. The largest stable and supported cluster comprises 21 species, with *Parasesarma affine* (De Haan, 1837) and *Parasesarma tuerkayi* Shahdadi, Davie & Schubart, 2017 holding a basal position. In this group, there are several solid groups [i.e. *Parasesarma lividum* (A. Milne-Edwards, 1869) group, *Parasesarma indiarum* (Tweedie, 1940) group, *Parasesarma darwinense* (Campbell, 1967) group, *Parasesarma bidens* (De Haan, 1833) group and *Parasesarma semperi* (Bürger, 1893) group], but the phylogenetic relationships among several other species of *Parasesarma* are otherwise not fully resolved, as shown by the occurrence of several clades with low support values.

The subdivision of the genus *Parasesarma* into two monophyletic clades is also confirmed by the nuclear markers, although the phylogenies within each clade are less resolved (Figs 3, 4). *Parasesarma leptosoma* and *P. gazi* are stably associated in both trees (Figs 3, 4). However, in the NaK tree some supported clusters can be

Table 3. Primers used in the present study with the corresponding DNA sequences (5'–3') and references

Gene	Primer	Sequences	References
<i>COX1</i>	COL6	TYTCHACAAAYCATAAAGAYATYGG	Schubart (2009)
	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer <i>et al.</i> (1994)
	COL7P	GGTGTKGGMACMGGATGAACTGT	Shahdadi <i>et al.</i> (2018a)
	COH7P	GRAGAGAAAAATACCTA	Shahdadi & Schubart (2017)
	COH6	TADACTTCDGGRTGDCCAAARAAYCA	Schubart & Huber (2006)
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer <i>et al.</i> (1994)
16S	16L2	TGCCTGTTTATCAAAAACAT	Schubart <i>et al.</i> (2002)
	16H11	AGATAGAAACCRACCTGG	Schubart (2009)
<i>NaK</i>	NaK for-b2	ATGACAGTCGCYAYATGTGGTT	Modified from NaK for-b (from Tsang <i>et al.</i> , 2008)
	NaK rev3	GGAGGRTCAATCATRGACAT	Tsang <i>et al.</i> (2014)
28S	28L4	TATTTCCCTCGTGATGTAGGTC	Ragionieri <i>et al.</i> (2009)
	28H6	AGCARAGCCGCGAGGCCAACA	New
	28H4	ACTCCGGACAGAGCAGGAT	Ragionieri <i>et al.</i> (2009)

recognized in the *P. plicatum* clade (Fig. 3). For instance, a cluster of six species holds a basal position, and the association of *Parasesarma asperum* (Heller, 1865), *P. anambas*, *P. plicatum*, *P. batavianum* and *Parasesarma melissa* (De Man, 1888) together with *Parasesarma catenatum* (Ortmann, 1897) is highly supported. This cluster also includes two smaller groups with high support, i.e. *P. melissa* + *P. batavianum* and *P. plicatum* + *P. anambas* + *P. asperum* (Fig. 3). In the *P. plicatum* group, the same cluster of 15 species as found in the mitochondrial tree forms the largest supported cluster in the *NaK* tree, with *P. affine* holding a basal position (Fig. 3).

MORPHOLOGICAL ANALYSES

Morphological examinations of the chelae show that adult males in all described species of *Parasesarma* have two or three oblique pectinated crests on the upper surface of the palm and a series of tubercles on the dorsal face of the dactyli (Fig. 5). The patterns of the tuberculation, i.e. the numbers and shapes of these tubercles, are some of the most variable features among species of *Parasesarma* (Fig. 5). However, careful examinations of the pectinated crests of the palms show that members of the *P. leptosoma* group have a slightly different palm crest and dactylar tuberculation pattern in comparison to species of the *P. plicatum* group. In species of the *P. leptosoma* group, the pectinated crests on the upper palm surface are oblique, but more longitudinal, with each one extending into a line of coarse granules on the outer side (Fig. 5F–J). The innermost and proximal pectinated crest and its extended granule line create a ridge and divide the upper surface of the palm into two separate parts,

an outer and an inner part (Fig. 6D–F). In the case of the dactyli, the proximal tubercles are positioned towards the mid-dactylar dorsal face, and a virtual line of dactylar tubercles would extend proximally to the outer granules of the distal pectinated crest (Fig. 7B). In members of the *P. plicatum* group, the pectinated crests have a more transverse orientation on the upper palm surface, which is undivided despite the presence of some granules (Figs 5A–E, 6A–C). The proximal dactylar tubercles are found on the inner side of the dactylar dorsal face, and the virtual line of dactylar tubercles would extend proximally to the inner teeth of the distal pectinated crest (Fig. 7A).

The two groups of *Parasesarma* also differ in eye morphology (Fig. 8). The eyestalk in members of the *P. leptosoma* group is relatively shorter than wide (in dorsal view, the ratio of eyestalk length/width ranges from 0.74 to 0.98; Fig. 8H–N), whereas in members of the *P. plicatum* group the eyestalk is longer than wide (the ratio of eyestalk length/width ranges from 1.08 to 1.71; Figs 8A–G, 9A; Table 1). Consequently, species of the *P. leptosoma* group (Fig. 8H–N) have proportionally deeper orbits compared with members of the *P. plicatum* group (Fig. 8A–G).

Species of the *P. leptosoma* group have proportionally long ambulatory legs: P4 (ischium–dactylus)/cw values range from 1.81 (in *P. lenzii*) to 2.20 (in *P. gecko*). In contrast, there is a wider range concerning P4 (ischium–dactylus)/cw values among species of the *P. plicatum* group, i.e. from 1.49 (in *P. carolinense*) to 1.96 (in *P. pictum*) (Fig. 9B; Table 1).

Morphological analyses of G1 indicate a high variability within both groups, each one containing species with moderately different G1 (Fig. 10), but generally sharing a similar shape overall.

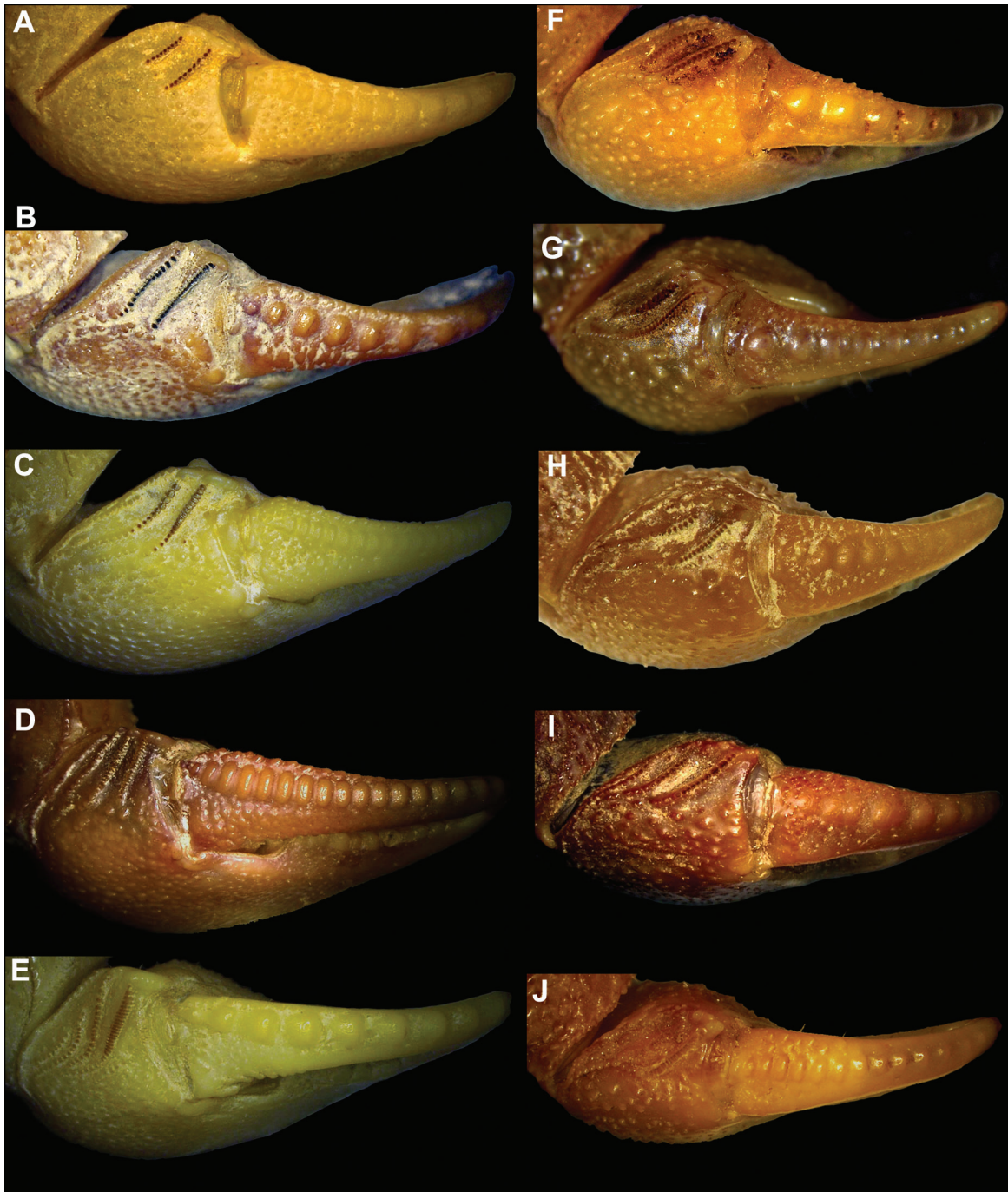


Figure 5. Dorsal view of male right chelae (palm pectinated crests and dactylar tubercles) in selected species of *Parasesarma*; A–E, members of the *Parasesarma plicatum* group; F–J, members of *Parasesarma leptosoma* group. A, *P. plicatum* (17.6 mm × 14.1 mm; NHMW 1637), Sri Lanka. B, *Parasesarma affine* (24.0 mm × 19.4 mm; ZSM-A20171197), Hong Kong: Mai Po mangrove. C, *Parasesarma asperum* (18.7 mm × 15.5 mm; NHMW 10408), Nicobar Islands: Novara. D, *Parasesarma bengalense* (19.4 mm × 16.4 mm; SMF 49919), Thailand: Phuket. E, *Parasesarma longicristatum* (18.5 mm × 14.9 mm; QM-W2464), Australia: Queensland: Port Alma. F, *P. leptosoma* (17.7 mm × 16.0 mm; MZUF 4977), Kenya, Mida Creek. G, *Parasesarma purpureum* (13.0 mm × 11.5 mm; ZRC 1017.1240), Malaysia: Tioman. H, *Parasesarma liho* (13.0 mm × 11.6 mm; ZRC 2013 1757), Taiwan: Pingtung Manchow. I, *Parasesarma paucitorum* (19.9 mm × 18.8 mm; MZB.cru.2243), Indonesia: Sulawesi: Manado. J, *Parasesarma gazi* (15.5 mm × 13.1 mm; MZUF 3671), Kenya: Gazi Bay.

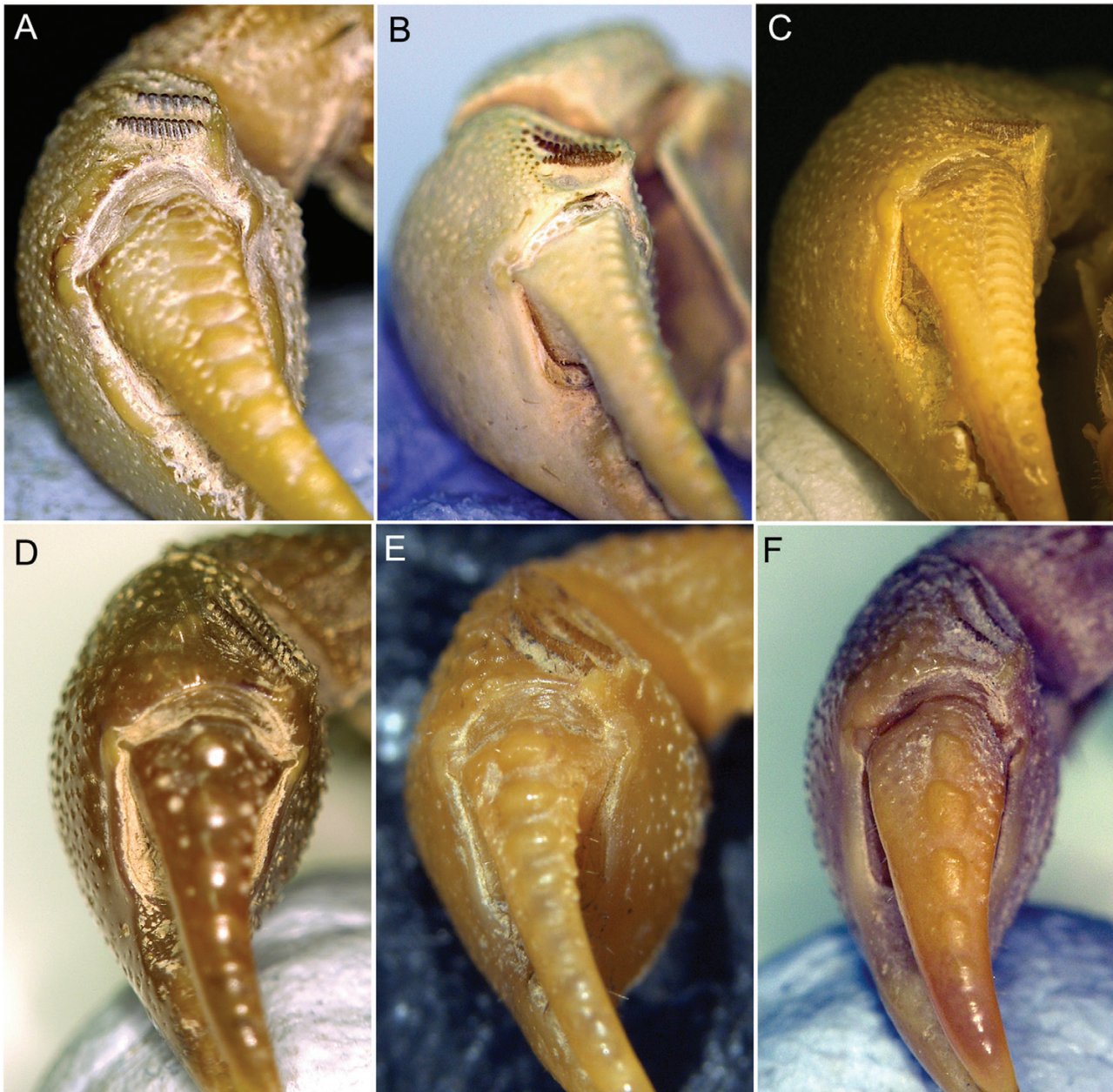


Figure 6. Dorsal view of male right chelae (palm pectinated crests and dactylar tubercles) in selected species of *Parasesarma*; A–C, members of *Parasesarma plicatum* group; D–F, members of *Parasesarma leptosoma* group. A, *P. plicatum* (21.7 mm × 17.4 mm; SMF 49926), Sri Lanka. B, *Parasesarma lepidum* (10.4 mm × 7.8 mm; ZRC1964.9.3.466), Malaysia: Labuan. C, *Parasesarma batavianum* (15.7 mm × 13.9 mm; RMNH.CRUS.D1201), Indonesia: Java: Batavia. D, *P. leptosoma* (19.0 mm × 17.5 mm; MZUF 4978), Kenya: Mida Creek. E, *Parasesarma kui* (13.1 mm × 12.1 mm; ZRC 2018.0792), Taiwan: Pingtung. F, *Parasesarma moluccense* (14.6 mm × 13.6 mm; RMNH.CRUS.D102590), Indonesia: Flores.

DISCUSSION

The establishment of a phylogeny-based classification of all living organisms is a fundamental aim of systematics. Convergent evolution, phenotypic plasticity, cryptic taxa and morphological changes during the ontogeny of a single species are common

factors that render this aim difficult through the history of systematics. Genetic approaches have been thus become an important tool in resolving phylogeny in different groups, including decapod Crustacea (Schubart, 2009). Thereby, mitochondrial and, increasingly, nuclear markers prove to be a helpful

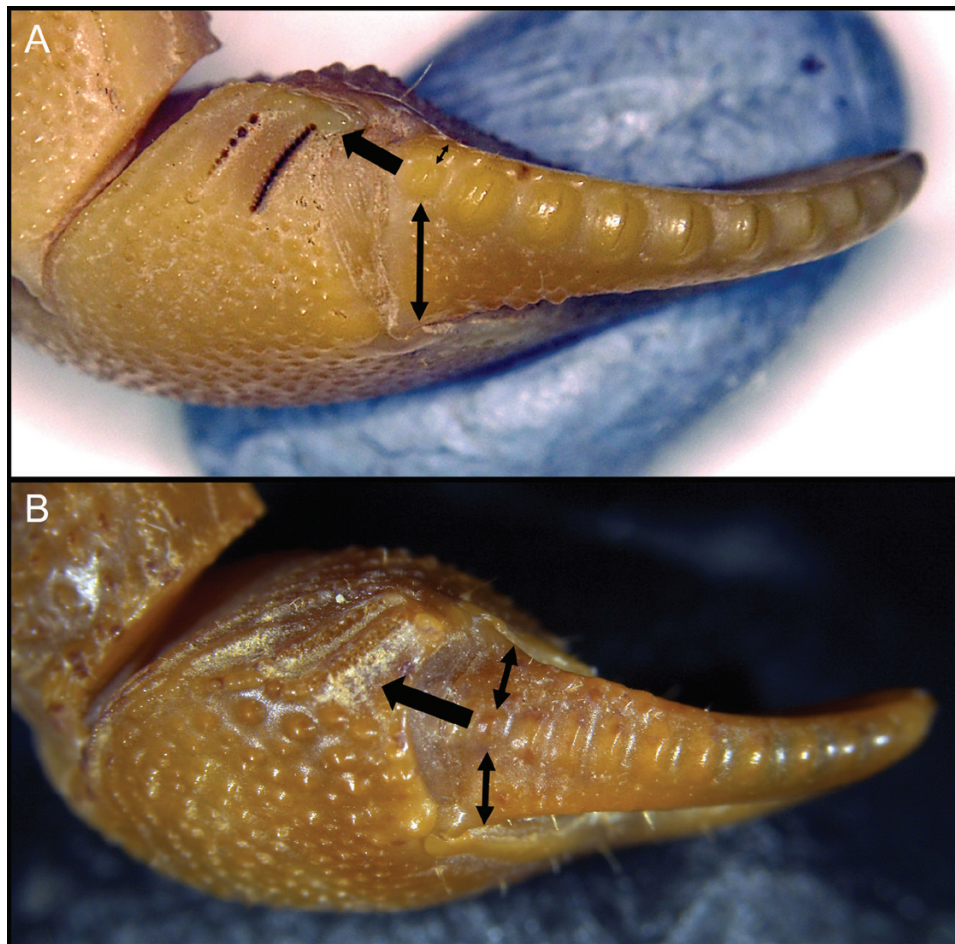


Figure 7. Morphological comparison of male palm pectinated crests and chelar dactylar tubercle of: A, *Parasesarma brevicristatum* (19.8 mm × 16.6 mm; QM-W2459), Australia: Queensland: Flying Fish Port (representative of *Parasesarma plicatum* group); B, *Parasesarma gecko* (15.8 mm × 14.3 mm; RUMF-ZC-4710), Japan: Okinawa Island (representative of *Parasesarma leptosoma* clade). Thick and thin arrows indicate virtual line of dactylar tubercles and distance from inner and outer margins of dactylar margins, respectively.

source to evaluate the phylogenetic value of specific morphological characters (e.g. [Shahdadi & Schubart, 2017](#)), especially in taxa, such as *Parasesarma*, that have a relatively small number of reliable morphological distinctions ([Shahdadi & Schubart, 2015](#)).

The present molecular phylogenetic results ([Figs 2–4](#)) indicate heterogeneity and, according to nuclear markers, possible polyphyly in *Parasesarma* (as defined before the present study). They strongly support the separation and transfer of some of the constituent species to a new genus. After this rearrangement, according to the examined species, both resulting genera appear as monophyletic taxa. This agrees with previous evidence of the para- or polyphyly of *Parasesarma*, as already noted by [Schubart *et al.* \(2006\)](#) and [Cannicci *et al.* \(2017\)](#). Both clades of *Parasesarma*

show a comb-like topology, with many closely related species pairs and complexes, suggesting recent and rapid radiations.

Species of *Parasesarma s.l.* share many morphological characters, the most conspicuous of which are the two transverse pectinated crests on the upper surface of the male chelar palms ([Naderloo & Schubart, 2010](#)). Nevertheless, the present comparisons show that there are at least two different crest patterns among species of *Parasesarma*. Species of the *P. leptosoma* group show minor but consistent differences in these features compared with members of the *P. plicatum* group (see Results and [Figs 5–7](#)). Several sesarmid genera are known to have chitinous pectinated crest(s) on the upper surface of the chelar palm, combined with dactylar tuberculation ([Serène & Soh, 1970](#); [Schubart *et al.*, 2009](#); [Davie, 2012](#)). These

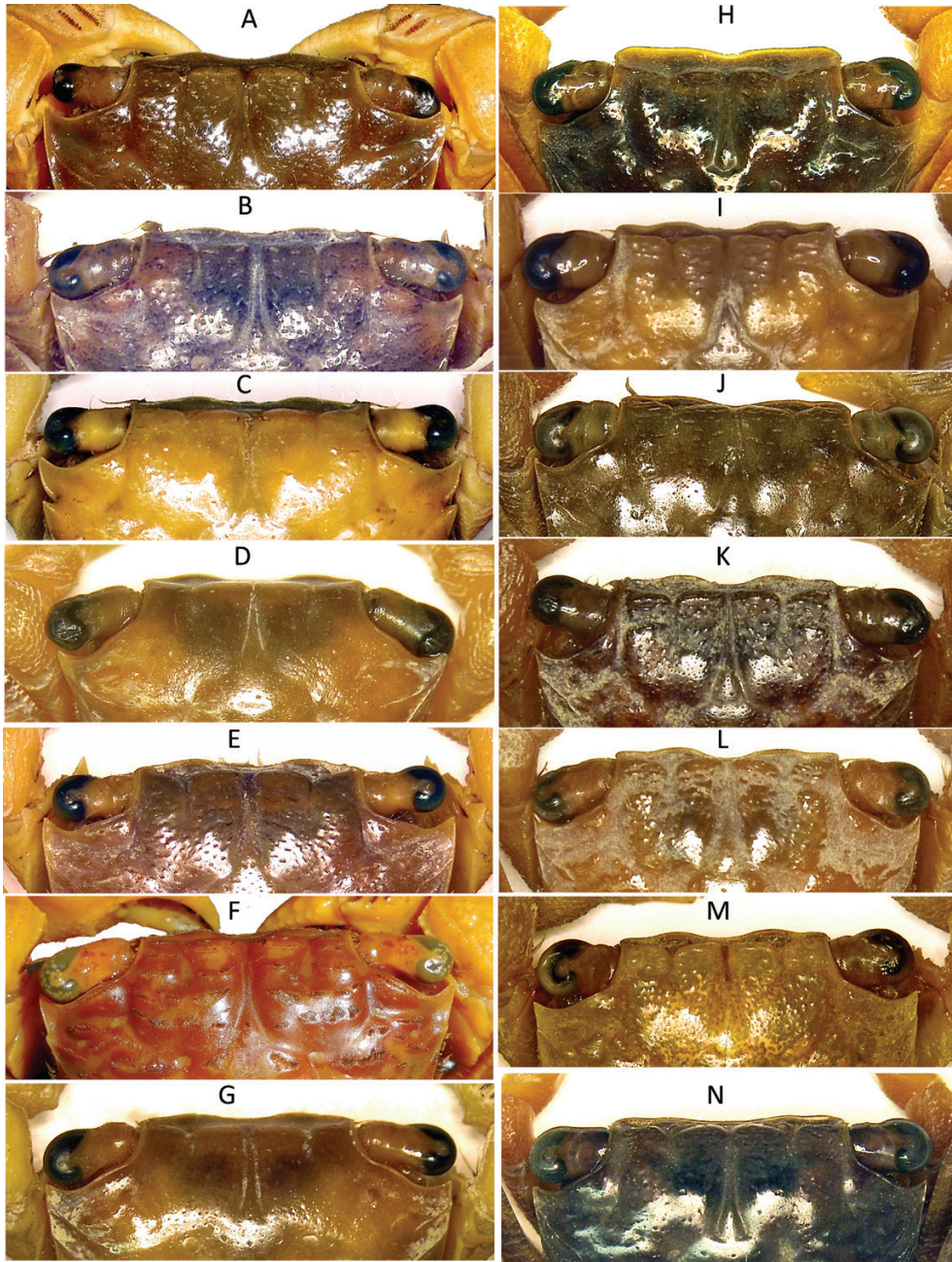


Figure 8. Dorsal view of carapace front, postorbital lobes, eyes and orbits in selected species of *Parasesarma*. A–G, members of *Parasesarma plicatum* group; H–N, members of *Parasesarma leptosoma* clade. A, *P. plicatum*, male (22.4 mm × 17.8 mm; SMF 49918), Thailand: Phuket. B, *Parasesarma asperum*, male (16.0 mm × 13.0 mm; ZRC 2001.0851), India: Tamil Nadu. C, *Parasesarma brevicristatum*, male (19.8 mm × 16.6 mm; QM-W2459), Australia: Queensland: Flying Fish Port. D, *Parasesarma charis*, male (8.9 mm × 6.7 mm; ZRC 2002.0594), Indonesia: Irian Jaya: Kamora. E, *Parasesarma dumacense*, male (18.7 mm × 15.7 mm; ZRC 2008.0833), Philippines: Cebu. F, *Parasesarma lanchesteri*, male (20.8 mm × 16.2 mm; NHM1947.11.18.24), Singapore: Jurong. G, *Parasesarma tripectinis*, male (9.9 mm × 8.0 mm; ZSM-A20171189), Taiwan: Chunan Hsintong. H, *P. leptosoma*, male (17.7 mm × 16.1 mm; MZUF 4977), Kenya: Mida Creek. I, *Parasesarma jamelense*, male (11.5 mm × 10.0 mm; USNM 45917), Philippines: Luzon. J, *Parasesarma lenzii*, male (11.8 mm × 9.9 mm; ZRC 2018.1373), Cocos (Keeling) Islands. K, *Parasesarma liho*, male (13.0 mm × 11.6 mm; ZRC 2013 1757), Taiwan: Pingtung Manchow. L, *Parasesarma moluccense*, male (14.6 mm × 13.6 mm; RMNH.CRUS.D102590), Indonesia: Flores. M, *Parasesarma obliquifrons*, male (12.7 mm × 11.1 mm; USNM 45913), Samoa Island: Pago Pago. N, *Parasesarma gazi*, female (12.6 mm × 10.3 mm; MZUF 3673), Kenya: Gazi Bay.

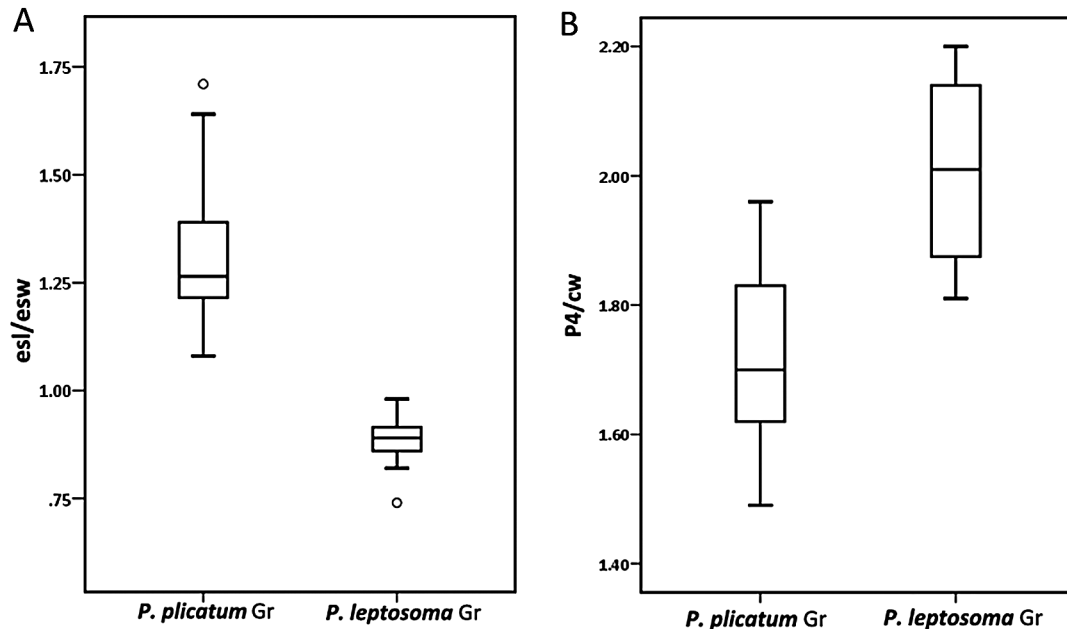


Figure 9. A, boxplots of morphometric comparisons between species of *Parasesarma plicatum* group ($N = 52$) and *Parasesarma leptosoma* clade ($N = 16$): the ratio between eye stalk length (esl) and eye stalk width (esw). B, boxplots of morphometric comparisons between species of main *Parasesarma* clade ($N = 37$) and *P. leptosoma* ($N = 16$): the ratio between length of pereopod 4 (P4) and carapace width (cw).

structures are recognized as key features in inter- and intraspecific communication (Chen *et al.*, 2014, 2017). Boon *et al.* (2009) described the mechanisms of the resulting stridulation (i.e. rubbing dactylar tubercles against pectinated crests of opposite chela) and showed that different types of tubercles result in different signals (Boon *et al.*, 2009: figs 1–4). Species within a sesarimid genus generally differ in the number, pattern and type of the tuberculation, whereas the pectinated crests appear to be similar (e.g. Fig. 5). However, among sesarimid genera these crests may differ in orientation, pattern and type of chitinous teeth (e.g. Shahdadi & Schubart, 2017: figs 3, 4). These authors also considered the similarity of these features as important phylogenetic indicators for close kinship. However, they also discussed how differences in these characters could also be a key reason for isolation in behaviour and communication (see also Shahdadi *et al.*, 2018b), with consequent reproductive isolation leading to different evolutionary lineages, as shown in the two cases of *Perisesarma dusumieri* (H. Milne Edwards, 1853) and *Fasciarma fasciatum* (Lanchester, 1900) by Shahdadi & Schubart (2017).

Separation between sister species of *Parasesarma* has also been associated with allopatric speciation events, without evolution of strong morphological differences. Shahdadi *et al.* (2018a, 2019a) discussed how the genetic divergence between two northern Australian species of *Parasesarma* (i.e. *P. semperi*

and *Parasesarma austrawati* Shahdadi, Davie & Schubart, 2019) is a result of gene flow disjunction between Australia and other areas. Otherwise, these species are morphologically similar to their relatives [i.e. *Parasesarma longicristatum* (Campbell, 1967) and *Parasesarma samawati* (Gillikin & Schubart, 2004), respectively]. In contrast, *Parasesarma eumolpe* (De Man, 1895) is genetically close to other related species of its group (e.g. *Parasesarma peninsulare* Shahdadi, Ng & Schubart, 2018), but distinctly different from all other relatives in the morphology of chelar dactylar tubercles (Shahdadi *et al.*, 2018b).

Within *Parasesarma*, a probable case of speciation attributable to an interspecific hybridization event was also reported for *P. leptosoma* and *P. gazi* (Cannicci *et al.*, 2017), two species that live in sympatry in mangrove forests in Kenya and Tanzania. This was the first report of a hybridization event for sesarimid crabs in general.

Another possibly important feature for the taxonomy of these crabs is the morphology of G1 (Shahdadi & Schubart, 2017; Li *et al.*, 2018). Li *et al.* (2018) described seven new species of the long-legged *Parasesarma* with distinct morphological identities, especially regarding the morphology of G1 and chelar dactylar tubercles. However, in the present study these species show close genetic affinity in their mitochondrial DNA sequences. Our comparisons show that G1 morphology is a useful and diagnostic



Figure 10. Morphology of right G1 in selected species of *Parasesarma*: A–D, members of *Parasesarma plicatum* group; E–H, members of *Parasesarma leptosoma* clade. A, *Parasesarma pictum* (19.8 mm × 17.6 mm; ZSM-A20171191), Japan: Hiroshima. B, *Parasesarma tripectinis* (9.9 mm × 8.0 mm; ZSM-A20171189), Taiwan: Chunan Hsintong. C, *P. plicatum* (17.6 mm × 14.1 mm; NHMW 1637), Ceylon. D, *Parasesarma tuerkayi* (28.2 mm × 24.0 mm; QM-W28348), Vietnam: Tan Thoi Island. E, *P. leptosoma* (19.0 mm × 17.5 mm; MZUF 4978), Kenya: Mida Creek. F, *Parasesarma gazi* (15.5 mm × 13.1 mm; MZUF 3671), Kenya: Gazi Bay. G, *Parasesarma moluccense* (14.6 mm × 13.6 mm; RMNH.CRUS.D102590), Indonesia: Flores. H, *Parasesarma jamelense* (11.5 mm × 10.0 mm; USNM 45917), Philippines: Luzon.

character for many species identifications (Fig. 10), but does not necessarily exhibit a consistent difference between major phylogenetic groups. This irregular pattern of G1 diversity has been documented previously, for example in the case of the *Chiromantes obtusifrons* (Dana, 1851) species complex (Davie & Ng, 2013). It appears that the G1 shape is often one of the first steps of morphological differentiation during reproductive isolation in speciation processes. For example, both *P. pictum* (Fig. 10A) and *P. tripectinis* (Fig. 10B), in addition to *P. leptosoma* (Fig. 10E) and *P. gazi* (Fig. 10F), are phylogenetically close species with conspicuously different G1. It thus appears that morphological divergence of the G1 can be a rapid mechanism evolving to prevent hybridization.

Following the above reasoning, it thus seems that different evolutionary mechanisms (allopatric speciation, hybridization and evolution of reproductive barriers) might have contributed to triggering a rapid speciation within both clades of *Parasesarma*. Proportionally fast changes in the morphology of dactylar tubercles and G1 were followed by the divergence of pectinated crest patterns, resulting in the formation of different evolutionary lineages with

many newly evolved species, as in the case of these two groups of *Parasesarma*.

The remarkably low *COX1* genetic distances among the newly described long-legged species by Li *et al.* (2018) (e.g. between *P. gecko* and *P. tarantula*; see Results) might also be a result of a historical mitochondrial introgression event, as shown in the case of *P. gazi* and *P. leptosoma* (see Cannicci *et al.*, 2017). Alternatively, it could be the result of rapid evolution causing fast morphological deviation that cannot be detected in genetic markers such as the mitochondrial DNA *COX1*. However, using highly variable nuclear markers (e.g. microsatellites) might help to address their phylogeny with more certainty.

In the more recent literature, *Parasesarma* has been divided into two morphogroups, based on their ambulatory legs, i.e. the long-legged vs. the short-legged ones (Rahayu & Ng, 2009, 2010; Li *et al.*, 2018). Congruently, in the present phylogeny the clade of *P. leptosoma* contains species with proportionally long ambulatory legs (P4). Members of the *P. plicatum* group include some long-legged species (e.g. *P. pictum*), but most of them have proportionally shorter ambulatory legs. However, the phylogenetic value of this character has been questioned before, because it

can be an ecological response to the respective lifestyle and habitat. This has been reported for mangrove tree-climbing crabs as a case of convergent evolution (Fratini *et al.*, 2005) and intraspecifically in freshwater crabs of the genus *Sesarma* that show longer and more slender legs in subterranean habitats (Schubart *et al.*, 2010).

Another character distinguishing the two groups of *Parasesarma* is their eye morphology. Both groups show a certain variability in the proportional length of the eyestalk, which may also be an ontogenic modification through individual development. However, our morphological comparisons show that in adult males, species of the *P. leptosoma* group have short and stout eyestalks compared with the longer eyestalks of the *P. plicatum* group. As a resulting morphological diagnosis related to eye shape, it can be claimed that species of the *P. leptosoma* group have proportionally deeper orbits in comparison to other members of *Parasesarma* (Fig. 8).

As a distinct monophyletic group, separated from other phylogenetic units and from the main cluster of *Parasesarma*, the sesarmid species forming the *P. leptosoma* group are here classified as a new genus, diagnosed by several morphological features (e.g. palm pectinated crests, chelar dactylar tubercles, ambulatory legs and eye morphology). Below, we establish the name ***Leptarma* gen. nov.** for this new genus.

SYSTEMATIC ACCOUNT

SESARMIDAE DANA, 1851

PARASESARMA De Man, 1895

Type species: The Indian *Cancer quadratus* Fabricius, 1798, which is a preoccupied name and a synonym of *Ocypode plicatum* Latreille, 1803 (subsequent designation by Rathbun, 1918; see Ng *et al.*, 2008; Rahayu & Ng, 2010).

Diagnosis: Small- to medium-sized crabs (usually < 25 mm cw; largest specimen studied here, cw = 29.4 mm; see Table 1). Carapace rectangular (broader than long; cw/cl ranging from 1.13 to 1.38 in examined material), with carapace regions well defined: front moderately deflexed, with median concavity; four postfrontal lobes with median groove extending to gastric region (Figs 8A–G, 11A); gastric region well defined; lateral margins of carapace either without tooth, with shallow indentation or with epibranchial tooth of varying size. Eyestalk longer than wide, longer than corneal part in dorsal view; cornea almost as wide as eyestalk (Figs 8A–G, 9A). Male chelipeds robust; palm with one to three (usually two) oblique (more transverse) pectinated crests on upper surface (Fig. 5A–E), which consist of tall chitinous teeth, flanked by a large tubercle

on inner side (Fig. 6A–C; except for *P. gemmatum*, which has a row of fine granules instead of the pectinated crest; see Remarks on this species); chelar dactylus dorsally with a row of tubercles; proximal tubercles at inner side of dorsal face, with virtual line of proximal dactylar tubercles directed towards inner tubercle of pectinated crests (Fig. 7A). Ambulatory legs dorsoventrally flattened, proportionally short (P4/cw ranges from 1.49 to 1.96; Figs 9B, 11A). Pleon of male relatively short, triangular; somite 3 widest; somite 6 slightly longer than somite 5; telson small, slightly wider than long in most species. Female pleon broad, touching coxae of walking legs; vulvae on anterior part of sternite 6.

Remarks: Members of this genus have experienced several rearrangements and taxonomic changes (e.g. Tesch, 1917; Serène & Soh, 1970; Ng *et al.*, 2008; Shahdadi & Schubart, 2017), and many were originally described under different names (see Table 4). The genus is distributed exclusively in the Indo-West Pacific (for the type localities, see Table 4) and in our revised system now contains 54 nominal species that are listed in Table 4. For a list of synonyms, see Ng *et al.* (2008) and Shahdadi & Schubart (2017).

The type species of *Parasesarma*, *P. plicatum*, has experienced a complicated and unstable taxonomic history until Rahayu & Ng (2010) revised the taxonomy of this species and presumed allied taxa. These authors also recognized *P. affine* and *Parasesarma unguatum* (H. Milne Edwards, 1853) as valid species, which were previously synonymized under *P. plicatum* by Tesch (1917). Our genetic results also confirmed the separate identities of these species, but did not recognize them as allies.

Shahdadi *et al.* (2019a) described *P. austrawati* from northern Australian mangroves and highlighted its phylogenetic position among other related species, focusing on *P. lividum* from the South Pacific and *P. samawati* from East Africa. However, *P. lividum* *s.l.* has been recorded from different places in Southeast Asia (Tesch, 1917; Shahdadi *et al.*, 2018a; Li *et al.*, 2019), and the phylogenetic and taxonomic positions of these populations are still unresolved.

Parasesarma bengalense (Davie, 2003) and *Parasesarma haswelli* (De Man, 1887) were described from the Bay of Bengal, i.e. *P. bengalense* from Sri Lanka (Davie, 2003) and *P. haswelli* from the Mergui Archipelago (De Man, 1887; Table 4), and both have ~16–19 chelar dactylar tubercles. While describing *P. bengalense*, Davie (2003) did not include *P. haswelli* for comparison, but Davie (2010) diagnosed *P. haswelli* in his identification key as having asymmetrical chelar dactylar tubercles (vertical distal slope) vs. symmetrical tubercles in *P. bengalense*. We examined the morphology of a series of *P. bengalense* specimens

Table 4. List of species of *Parasesarma* and *Leptarma* with their type locality, original name and composition

Species	Original name and composition	Type locality
<i>Parasesarma affine</i> (De Haan, 1837)	<i>Grapsus (Pachysoma) affinis</i>	Japan
<i>Parasesarma anambas</i> Yeo, Rahayu & Ng, 2004	<i>Parasesarma anambas</i>	Anambas: Pulau Jemaja; Pulau Siantan
<i>Parasesarma asperum</i> (Heller, 1865)	<i>Sesarma aspera</i>	Sri Lanka
<i>Parasesarma austrawati</i> Shahdadi, Davie & Schubart, 2019	<i>Parasesarma austrawati</i>	Australia: Northern Territory
<i>Parasesarma batavianum</i> (De Man, 1890)	<i>Sesarma batavianum</i>	Indonesia: Java: Jakarta (Batavia)
<i>Parasesarma bengalense</i> (Davie, 2003)	<i>Perisesarma bengalense</i>	Sri Lanka: Colombo
<i>Parasesarma bidens</i> (De Haan, 1835)	<i>Grapsus (Pachysoma) bidens</i>	Japan
<i>Parasesarma brevicristatum</i> (Campbell, 1967)	<i>Sesarma (Chiromantes) brevicristatum</i>	Australia: Queensland: Lucinda
<i>Parasesarma calypso</i> (De Man, 1895)	<i>Sesarma (Parasesarma) calypso</i>	Indonesia: Sumatra: Aceh
<i>Parasesarma capensis</i> Fratini, Cannicci & Innocenti, 2019	<i>Parasesarma capensis</i>	South Africa: Mngazana
<i>Parasesarma carolinense</i> (Rathbun, 1907)	<i>Sesarma (Parasesarma) carolinensis</i>	Caroline Islands: Kusaie Island
<i>Parasesarma catenatum</i> (Ortmann, 1897)	<i>Sesarma catenata</i>	See the Remarks section
<i>Parasesarma charis</i> Rahayu & Ng, 2005	<i>Parasesarma charis</i>	Indonesia: Papua: Timika
<i>Parasesarma corallicum</i> (Rahayu & Li, 2016)	<i>Parasesarma corallicum</i>	Taiwan: Pingtung: Kenting
<i>Parasesarma cricotum</i> (Rahayu & Davie, 2002)	<i>Perisesarma cricotum</i>	Indonesia: Irian Jaya: Ajkwa
<i>Parasesarma darwinense</i> (Campbell, 1967)	<i>Sesarma (Chiromantes) darwinensis</i>	Australia: Northern Territory: Darwin Island
<i>Parasesarma dumacense</i> (Rathbun, 1914)	<i>Sesarma (Parasesarma) dumacense</i>	Philippines: Luzon: Dumaca River
<i>Parasesarma ellenae</i> (Pretzmann, 1968)	<i>Sesarma (Parasesarma) calypso ellenae</i>	New Caledonia: Tioua
<i>Parasesarma erythodactyla</i> (Hess, 1865)	<i>Sesarma erythodactyla</i>	Australia: New South Wales: Sydney (see the Remarks section on this species)
<i>Parasesarma eumolpe</i> (De Man, 1895)	<i>Sesarma (Perisesarma) eumolpe</i>	Malaysia: Penang
<i>Parasesarma exquisitum</i> (Dai & Song, 1986)	<i>Sesarma (Parasesarma) exquisitum</i>	China: Guangxi: Qinzhou
<i>Parasesarma foresti</i> (Rahayu & Davie, 2002)	<i>Perisesarma foresti</i>	Indonesia: Irian Jaya: Kamora
<i>Parasesarma gemmatum</i> Li, Shih & Ng, 2019	<i>Parasesarma gemmatum</i>	Taiwan: Pingtung
<i>Parasesarma guttatum</i> (A. Milne-Edwards, 1869)	<i>Sesarma guttatum</i>	Zanzibar
<i>Parasesarma hartogi</i> Davie & Pabriks, 2010	<i>Parasesarma hartogi</i>	Australia: Shark Bay
<i>Parasesarma hasswelli</i> (De Man, 1887)	<i>Sesarma hasswelli</i>	Myanmar: Mergui Archipelago
<i>Parasesarma holthuisi</i> (Davie, 2010)	<i>Perisesarma holthuisi</i>	Australia: Western Australia: Ashburton River
<i>Parasesarma indiarum</i> (Tweedie, 1940)	<i>Sesarma bidens</i> var. <i>indica</i> (see Shahdadi et al., 2018b)	Indonesia: Ambon
<i>Parasesarma kuekenithali</i> (De Man, 1902)	<i>Sesarma (Parasesarma) calypso</i> var. <i>kuekenithali</i>	Indonesia: Halmahera: Soah
<i>Parasesarma lanchesteri</i> (Tweedie, 1936)	<i>Sesarma (Parasesarma) calypso lanchesteri</i>	Singapore: Jurong
<i>Parasesarma lepidum</i> (Tweedie, 1950)	<i>Sesarma lepidum</i>	Malaysia: Labuan
<i>Parasesarma lividum</i> (A. Milne-Edwards, 1869)	<i>Sesarma lividum</i>	New Caledonia
<i>Parasesarma longicristatum</i> (Campbell, 1967)	<i>Sesarma (Chiromantes) semperi longicristatum</i>	Australia: Queensland: Townsville
<i>Parasesarma luomi</i> Serène, 1982	<i>Parasesarma luomi</i>	Vietnam: Nha Trang
<i>Parasesarma maipoense</i> (Soh, 1978)	<i>Chiromantes maipoensis</i>	Hong Kong: Mai Po

Table 4. Continued

Species	Original name and composition	Type locality
<i>Parasarma melissa</i> (De Man, 1887)	<i>Sesarma melissa</i>	Myanmar: Mergui Archipelago
<i>Parasarma messa</i> (Campbell, 1967)	<i>Sesarma (Chironantes) messa</i>	Australia: Queensland: Townsville
<i>Parasarma onychophorum</i> (De Man, 1895)	<i>Sesarma (Perisesarma) onychophora</i>	Malaysia: Penang
<i>Parasarma palauense</i> (Takeda, 1971)	<i>Sesarma (Parasarma) palauense</i>	Palau Islands
<i>Parasarma pangauranense</i> (Rathbun, 1914)	<i>Sesarma (Parasarma) pangauranense</i>	Philippines: Busuanga Island; Pangauran River
<i>Parasarma peninsulare</i> (Shahdadi, Ng & Schubart, 2018)	<i>Parasarma peninsulare</i>	Singapore
<i>Parasarma persicum</i> (Naderloo & Schubart, 2010)	<i>Parasarma persicum</i>	Iran: Persian Gulf: Nayband
<i>Parasarma pictum</i> (De Haan, 1835)	<i>Grapsus (Pachysoma) pictus</i>	Japan
<i>Parasarma plicatum</i> (Latreille, 1803)	<i>Cancer quadratus</i> (see Rahayu & Ng, 2010)	East India
<i>Parasarma prashadi</i> (Chopra & Das, 1937)	<i>Sesarma (Parasarma) prashadi</i>	Myanmar: Mergui Archipelago
<i>Parasarma raouli</i> (Rahayu & Ng, 2009)	<i>Parasarma raouli</i>	Peninsular Malaysia: Johor Strait
<i>Parasarma rutilimanum</i> (Tweedie, 1936)	<i>Sesarma (Parasarma) rutilimana</i>	Singapore
<i>Parasarma samawati</i> (Gillikin & Schubart, 2004)	<i>Perisesarma samawati</i>	Kenya: Watamu
<i>Parasarma sanguimanus</i> Li, Shih & Ng, 2019	<i>Parasarma sanguimanus</i>	Taiwan: Pingtung
<i>Parasarma semperi</i> (Bürger, 1893)	<i>Sesarma semperi</i>	Philippines: Bohol
<i>Parasarma sigillatum</i> (Tweedie, 1950)	<i>Sesarma sigillata</i>	Cocos (Keeling) Islands
<i>Parasarma tuerkayi</i> (Shahdadi, Davie & Schubart, 2017)	<i>Perisesarma tuerkayi</i>	Vietnam: Tan Thoi Island
<i>Parasarma tripectinisi</i> (Shen, 1940)	<i>Sesarma (Parasarma) tripectinisi</i>	China: Fukien: Tsimei
<i>Parasarma unguatum</i> (H. Milne Edwards, 1853)	<i>Sesarma unguata</i>	Sulawesi
<i>Leptarma aurifrons</i> (Li, Shih & Ng, 2019) comb. nov.	<i>Parasarma aurifrons</i>	Taiwan: Pingtung
<i>Leptarma gazi</i> (Cannicci, Innocenti & Fratini, 2017) comb. nov.	<i>Parasarma gazi</i>	Kenya: Gazi Bay
<i>Leptarma gecko</i> (Li, Rahayu & Ng, 2018) comb. nov.	<i>Parasarma gecko</i>	Japan: Okinawa Island
<i>Leptarma gracilipes</i> (Li, Rahayu & Ng, 2018) comb. nov.	<i>Parasarma gracilipes</i>	Indonesia: Papua: Ajkwa River
<i>Parasarma jamelense</i> (Rathbun, 1914) comb. nov.	<i>Sesarma (Parasarma) jamelense</i>	Philippines: Luzon: Batangas
<i>Leptarma kui</i> (Li, Rahayu & Ng, 2018) comb. nov.	<i>Parasarma kui</i>	Taiwan: Pingtung
<i>Leptarma lenzii</i> (De Man, 1895) comb. nov.	<i>Sesarma (Parasarma) lenzii</i>	Indonesia: Sumatra: Aceh
<i>Leptarma leptosoma</i> (Hilgendorf, 1869) comb. nov.	<i>Sesarma leptosoma</i>	Zanzibar
<i>Leptarma liho</i> (Koller, Liu & Schubart, 2010) comb. nov.	<i>Parasarma liho</i>	Taiwan: Hualien County: Hualien City
<i>Leptarma limbense</i> (Rathbun, 1914) comb. nov.	<i>Sesarma (Holometopus) limbense</i>	Indonesia: North Sulawesi: Lembeh Island
<i>Leptarma macaco</i> (Li, Rahayu & Ng, 2018) comb. nov.	<i>Parasarma macaco</i>	Taiwan: Pingtung: mouth of Paoli River
<i>Leptarma moluccense</i> (De Man, 1892) comb. nov.	<i>Sesarma (Parasarma) moluccensis</i>	Indonesia: Flores Island: Mbawa
<i>Leptarma obliquifrons</i> (Rathbun, 1924) comb. nov.	<i>Sesarma (Parasarma) obliquifrons</i>	Samoa: Pago Pago

Table 4. Continued

Species	Original name and composition	Type locality
<i>Leptarma parvulum</i> (Li, Rahayu & Ng, 2018) comb. nov.	<i>Parasesarma parvulum</i>	Philippines: Mindoro Island: Naujan
<i>Leptarma paucitorum</i> (Rahayu & Ng, 2009) comb. nov.	<i>Parasesarma paucitorum</i>	Indonesia: Sulawesi: Manado
<i>Leptarma purpureum</i> (Li, Rahayu & Ng, 2018) comb. nov.	<i>Parasesarma purpureum</i>	Peninsular Malaysia: Tioman Island
<i>Leptarma tarantula</i> (Li, Rahayu & Ng, 2018) comb. nov.	<i>Parasesarma tarantula</i>	Indonesia: Sulawesi: Bitung

of different size (age) from different areas and also a small syntype of *P. hasswelli* (NHM London; see Table 1). It appears that smaller specimens have asymmetric tubercles, whereas in larger males these tubercles are symmetrically ovate. A possible hypothesis is that this difference is caused by a developmental change through ageing. However, morphological examination of more material of *P. hasswelli* and genetic comparison can help to address the doubt of conspecificity.

Parasesarma bidens was originally described from Japan by De Haan (1833) and was known to be distributed widely in Korea, Taiwan, the Philippines and along the Chinese coast to the Andaman Sea (Dai & Yang, 1991). However, Li *et al.* (2019) described the new species *Parasesarma sanguimanus* Li, Shih & Ng, 2019, based on some Taiwanese specimens that were shown to be morphologically and genetically distinct from the Japanese *P. bidens* and other members of *Parasesarma*. We here examined a male sample of *P. sanguimanus* from Bohol Island (Philippines), indicating an enlarged distribution of this new species beyond its type locality (for the material examined, see Table 1). The specimen from Bohol shares the same haplotype with the Taiwanese paratype in the barcode region of the *COX1* gene (for the GenBank accession numbers, see Table 2).

In his description of *P. catenatum*, Ortmann (1897) mentioned New Zealand as its collection site, but he was not sure about the exact locality of the material. This species is common in East Africa (Fratini *et al.*, 2005; Cannicci *et al.*, 2017; Fratini *et al.*, 2019), but there are no records from any other part of the world. We examined some specimens from East Africa and compared them with photographs of the type material (see section: Material examined) and they are identical in general morphology. Therefore, we assume that New Zealand as the collection site for the type must have been a labelling error. This species seems aberrant in chelar morphology in comparison to other *Parasesarma* species, because it has setae on the palm and dactylus and a wide gap between the fingers when closed (Emmerson, 2016). However, according to the phylogenetic position in this study and having two rows of transverse pectinated crests on the upper face of the palm and a long eyestalk, *P. catenatum* is assigned here within the genus *Parasesarma*.

While describing *Parasesarma acis* Davie, 1993 (which was later synonymized under *P. tripectinis* by Rahayu & Ng, 2005), Davie (1993) also redescribed *P. erythodactyla* based on material collected from eastern Australia (deposited in the Queensland Museum and Museum of Victoria). He considered that the types of Hess' species (*P. erythodactyla*) are missing (for details about type history and material examined in the study, see Davie, 1993). He also separated the Australian *P. erythodactyla* from *P. acis* (now *P. tripectinis*) via

several morphological characters (e.g. the morphology of G1 and chelar dactylar tubercles; Davie 1993: fig. 1). Our present generic assignment for this species is based on the description and illustration given by Davie (1993) and on the examination of three male specimens collected near Sydney (Table 1).

Given that no material of *P. exquisitum* is examined here, its generic assignment is based on the original description and illustrations (Dai & Song, 1986) and new photographs (see section: Material examined).

In his identification key, Davie (2010) did not distinguish *P. indiarum* from *Parasesarma foresti* (Rahayu & Davie, 2002), and their type localities are close (Ambon and Irian Jaya, respectively; De Man, 1902; Rahayu & Davie, 2002; see Table 4). Genetic pairwise comparisons (K2P based on *COX1*) also revealed a close affinity between these two species (Shahdadi *et al.*, 2017: table 3; Shahdadi *et al.*, 2018b: table 2). Based on this evidence, they may be considered conspecifics, and their taxonomy needs to be evaluated by examining material from their entire area of distribution, including the type material.

The phylogeographic study by Silva *et al.* (2010) showed that *Parasesarma guttatum* (A. Milne-Edwards, 1869) forms two separate clades in the south and north of Mozambique. Confirming this separation, Fratini *et al.* (2019) recently split *P. guttatum* into two pseudocryptic species, of which the newly described *P. capensis* Fratini, Innocenti & Cannicci, 2019 is endemic to mangrove forests south of the Mozambique Channel. Thus, *P. guttatum* (whose type specimen, described by Alphonse Milne-Edwards in 1869, was from Zanzibar) is now restricted to populations distributed from the Gulf of Oman (Naderloo, 2011) and the Red Sea to northern Mozambique (Fratini *et al.*, 2019).

Four species [*P. calypso*, *P. ellenae*, *P. kuekenthali* and *P. lanchesteri* (Tweedie, 1936)] were originally described as subspecies of *P. calypso* (see Table 4), sharing longitudinal lines on the proximal slopes of the chelar dactylar tubercles (De Man, 1895, 1902; Tweedie, 1936; Pretzmann, 1968). Accordingly, three of them cluster tightly together in our phylogenetic analyses, whereas *P. lanchesteri* is more distantly related (Fig. 2). *Parasesarma ellenae* was the latest described species of this group. Pretzmann (1968) briefly described this species based on a single small male from New Caledonia (Table 1) and highlighted differences from other members of the *P. calypso* group. For the present study, we examined the holotype, which turned out to be a juvenile male with undeveloped G1. Here, we also examined an adult male from New Caledonia and two larger males from Vanuatu Island (Table 1). A separate study will provide a detailed redescription of *P. ellenae* along with morphological comparisons with other related species.

Parasesarma panguaranense was originally described based on a single female (Rathbun, 1914), with no further record. In our study, we examined the holotype of this species, but we were not able to study any male specimen or to obtain any sequences from the type locality. Therefore, our generic assignment is based merely on structures such as orbit and eye morphology (Fig. 11B), which are assumed to be less affected by sexual dimorphism. More specimens from both sexes are necessary to confirm the taxonomy and phylogeny of the species.

Parasesarma rutilimanum was described from Singapore (Tweedie, 1936), and 1 year later *Parasesarma prashadi* (Chopra & Das, 1937) was described from the nearby Mergui Archipelago without a comparison to *P. rutilimanum*. According to their original descriptions and illustrations, these two species show high morphological similarity in their general appearance (e.g. carapace morphology, ambulatory legs, number of chelar dactylar tubercles and long primary pectinated crest) and might be conspecific. In the present study, we examined a series of material from Phuket (Thailand), Singapore, Labuan (Malaysia) and a syntype of *P. rutilimanum* (from Pulau Senang). It is hard to distinguish the two species morphologically, and therefore in this study species assignments were based on their geography (i.e. specimen from Phuket as *P. prashadi*; specimens from Singapore and Labuan as *P. rutilimanum*). In this study, we were not able to examine the type of *P. prashadi* and we did not obtain any DNA sequence from *P. rutilimanum*. Therefore, a targeted study examining the corresponding type material and additional specimens from their distribution area should address this taxonomic issue.

Parasesarma corallicum and *P. sigillatum* show close genetic affinity in our mitochondrial analyses (Fig. 2). *Parasesarma sigillatum* was synonymized under *P. carolinense* by Serène (1968) and being treated as such until Ng *et al.* (2016) clarified the identities of *P. carolinense* and *P. sigillatum* and showed that they are separate species. Ng *et al.* (2016) also presented several morphological diagnoses to separate *P. corallicum*, *P. carolinense* and *P. sigillatum*.

Shahdadi *et al.* (2017) described *P. tuerkayi* as a member of the genus *Perisesarma* in the special volume dedicated to Michael Türkay, because the generic rearrangement by Shahdadi & Schubart (2017) had not yet been published. However, at the end of their paper, Shahdadi *et al.* (2017: p. 1175) clarified in an addendum that this species would become a member of *Parasesarma*.

Parasesarma gemmatum was recently described by Li *et al.* (2019) from Taiwan. A male specimen of this species, collected from Cebu Island (Philippines), was also examined in the present study, matching

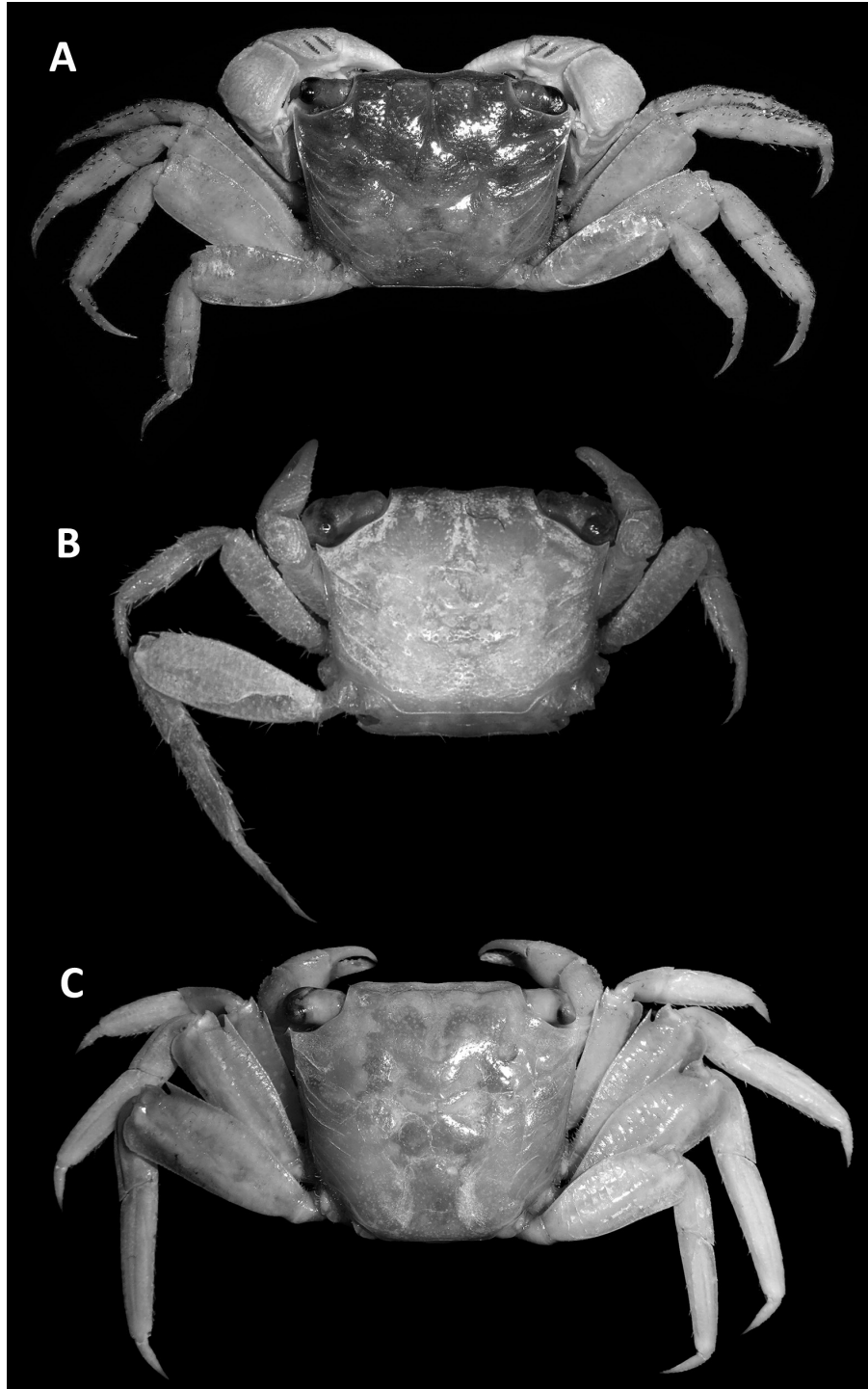


Figure 11. Dorsal habitus. A, *Parasesarma plicatum* male (22.4 mm × 17.8 mm; SMF 49918), Thailand: Phuket. B, *Parasesarma pangauranense* female (6.0 mm × 4.9 mm; USNM 45909 holotype), Philippines: Busuanga Island. C, *Leptarma leptosoma* female (17.0 mm × 16.0 mm; ZMB 3181, holotype), Zanzibar.

all diagnostic characters of the Taiwanese types. Genetically, there is only 1 bp difference between the Cebu specimen and the Taiwanese paratype (i.e.

~0.2% of genetic distance; for the GenBank accession numbers, see [Table 2](#)). Although this species is similar to other species of *Parasesarma* in general carapace

and chelar morphology, it differs by having rows of fine granules and no chitinous pectinate crest on the palm (Li *et al.*, 2019; present study). According to its phylogenetic position in the mitochondrial tree (Fig. 2; see also Li *et al.*, 2019: fig. 13), this species is well nested within the *P. plicatum* clade. Therefore, it appears that *P. gemmatum* could have lost the pectinated crest secondarily. This might also be the case for *Guinearma kamerani* (De Man, 1883), a West African sesarmid crab that, in comparison to its congeners [i.e. *Guinearma alberti* (Rathbun, 1921) and *Guinearma huzardi* (Desmarest, 1825)], has lost the oblique pectinated crest (Shahdadi *et al.*, 2019b).

LEPTARMA GEN. NOV.

lsid: zoobank.org:act:E4B034FF-1F44-434D-AC67-70CDE0D2E078

Type species: *Leptarma leptosoma* (Hilgendorf, 1869) comb. nov. = *Sesarma leptosoma* Hilgendorf, 1869, present designation.

Diagnosis: Small crabs (usually cw < 20 mm; largest specimen examined here with cw = 20.8 mm; Table 1). Carapace almost squarish (slightly broader than long; the ratio cw/cl ranges from 1.06 to 1.21 in examined material). Carapace regions well defined: front moderately deflexed, with median concavity; four postfrontal lobes; median groove extending to gastric region (Figs 8H–N, 11C); gastric region well defined (Fig. 11C). Eyestalk shorter than wide in dorsal view; cornea wider than eyestalk (Figs 8H–N, 9A). Male chelipeds robust, palm with one or two (usually two) oblique (more longitudinal) pectinated crests on the upper surface (Fig. 5F, G), which consist of tall chitinous teeth, each flanked by large tubercle on the inner side and a line of coarse granules on the outer side, which creates a ridge, dividing the upper surface of the palm into two separate parts (outer and inner; Fig. 6D–F); chelar dactylus dorsally with a row of tubercles; proximal tubercles at middle of dactylar dorsal face; a virtual line of dactylar tubercles proximally would be directed towards the outer tubercle of the distal pectinated crest (Fig. 7B). Ambulatory legs dorsoventrally flattened, proportionally long (P4/cw ranges from 1.81 to 2.2; Figs 9B, 11C). Pleon of male triangular; somite 3 widest and somite 6 longest. Female vulvae on the anterior part of sternite 6.

Etymology: The name *Leptarma* is composed of the Greek λεπτός, *leptos*, thin, referring to the name of the type species epithet *leptosoma*, derived from λεπτόσωμα, thin body, which in turn refers to the slim walking legs of the comprised representatives, and the suffix *-arma*, derived from the last part of the genus

Sesarma (in turn derived from the Greek σαιρω, the act of gaping; Say, 1817). The genus is gender neuter.

Remarks: This new genus includes 17 species as listed in Table 4, which were previously assigned to the genus *Parasesarma* (see Ng *et al.*, 2008; Shahdadi & Schubart, 2017; Li *et al.*, 2018, 2019).

Our morphological comparisons and genetic results revealed that two species with neighbouring distribution ranges, viz. *Leptarma moluccense* (De Man, 1892) comb. nov. and *Leptarma paucitorum* (Rahayu & Ng, 2009) comb. nov. (Indonesia: Flores Island and Sulawesi, respectively; for type localities, see Table 4), have a close relationship (see Fig. 1, ML tree). The description and comparison of *L. paucitorum* by Rahayu & Ng (2009) did not include *L. moluccense*. Here, we suggest targeted morphological and genetic comparisons in order to evaluate the validity of *L. paucitorum*.

Leptarma lenzii (De Man, 1895) comb. nov. was originally described from Aceh (Indonesia: Sumatra; De Man, 1895) and was later recorded from the Cocos (Keeling) Islands (Tweedie, 1950). In the redescription of *P. sigillatum* from the Cocos (Keeling) Islands, Ng *et al.* (2016) noted that specimens of a taxon allied to *L. lenzii* were also obtained. Shahdadi *et al.* (2019c) confirmed the identity of material from the Cocos (Keeling) Islands after morphological and genetic comparisons. Recently, Li *et al.* (2019) recorded this species from Taiwan and confirmed the identity using morphology and *COX1* as the genetic marker. However, Shahdadi *et al.* (2019c) doubted the identities of what has been reported as '*Parasesarma lenzii*' from Fiji (De Man, 1889: 434), the Moluccas (De Man, 1902: 536) and the Flores Sea (Tesch, 1918: 114). The material of Crosnier (1965; one male and one female) from Madagascar and the specimen of Poupin *et al.* (2012; one male) from Europa Island, which were reported as '*Parasesarma lenzii*', were also examined for the present study (see Table 1: material examined of *P. gazi*). As a result of DNA degradation, PCR amplifications failed for the specimens of Crosnier (1965). Both G1 of the male specimen from Madagascar were also missing. However, the specimens resemble *L. gazi* (Cannicci, Innocenti, & Fratini, 2017) comb. nov. in other features, as previously assigned by Cannicci *et al.* (2017) according to the drawings given by Crosnier (1965). The specimen from Europa Island differs from both *L. gazi* and *L. lenzii* and from other species of *Leptarma* and will therefore be described as a new species. The ZRC specimens from Singapore that were identified as '*P. lenzii*' were also examined. According to their horseshoe-like chelar dactylar tubercles, they are identified as *P. melissa* (e.g. ZRC 2000.1955; see Table 1).

Leptarma kui (Li, Rahayu & Ng, 2018) comb. nov. was described from Taiwan and is here reported from Cebu (Philippines). We have examined two male specimens, one from Cebu and one from Taiwan (Table 1), and both match the diagnostic characters described by Li *et al.* (2018). There is only one mutation in the barcode region of *COX1* between the sequences from Cebu and the holotype of *L. kui* (for the GenBank accession numbers, see Table 2).

After morphological re-examinations and genetic comparisons of the types and extra material of *P. cognatum* and *Leptarma liho* (Koller, Liu & Schubart, 2010) comb. nov., Shih *et al.* (2019) identified *P. cognatum* as a junior synonym of *L. liho*, which is now known from Japan (Okinawa, Miyako and Ishigaki), Taiwan (Hualien, Taitung and Pingtung), the Philippines (Cebu) and Indonesia (Sulawesi). *Leptarma liho* also resembles *Leptarma jamelense* (Rathbun, 1914) comb. nov. from Luzon (Philippines) in its general and G1 morphology. Koller *et al.* (2010) did not include *L. jamelense* for comparison in their description of *L. liho* as a new species. In the present study, the DNA amplification from *L. jamelense* was unsuccessful owing to DNA degradation. A targeted sampling from the type locality of *L. jamelense* (Philippines: Luzon: Batangas) and genetic comparisons should clarify this uncertainty.

The present generic assignment of *Leptarma aurifrons* (Li, Shih & Ng, 2019) comb. nov. is based on its position in the mitochondrial phylogenetic tree (Fig. 2; see also Li *et al.*, 2019: fig. 13). In our mitochondrial tree (Fig. 2), *L. aurifrons* is nested in the *Leptarma* clade, clustering with *L. moluccense*, *L. paucitorum* and *L. liho*. This is confirmed by the presence of proximal tubercles positioned on the mid-dorsal face of the chelar dactylus (see Li *et al.*, 2019: fig. 4C), which is one of the diagnostic characters of *Leptarma*.

ACKNOWLEDGEMENTS

We are indebted to many institutions and colleagues that/who facilitated specimens, allowed access to samples or assisted in the field. Among those, our special thanks go to Peter K. L. Ng, Jose Christopher E. Mendoza, Muhammad Dzaki Bin Safaruan, Ngan Kee Ng, Lee Be Yan, Ting Hui Ng and Wendy Wang Yanling from the National University of Singapore (Singapore); to Peter J. F. Davie and Marissa McNamara from the Queensland Museum in Brisbane (Queensland, Australia); to Angelika Brandt, Kristin Arnold, Moritz Sonnewald and Bianca Trautwein from the Senckenberg Museum in Frankfurt (Germany); to Charles Franssen and Karen van Dorp from Naturalis Biodiversity Center in Leiden (The Netherlands); to Paul Clark and Miranda Lowe from the Natural History Museum

in London (UK); to Gianna Innocenti and Stefano Cannicci from the University of Florence (Italy); to Laure Corbari, Paula Martin-Lefèvre and Danièle Guinot from the Muséum National d'Histoire Naturelle, Paris (France); to Andrew Hosie and Ana Hara from the Western Australian Museum in Perth (WA, Australia); to Dwi Listyo Rahayu from the Indonesian Institute of Sciences, Jakarta (Indonesia); to Tomoyuki Komai from the Natural History Museum and Institute Chiba (Japan); to Tohru Naruse from the University of the Ryukyus (Japan); to Stephen Keable, Shane T. Ahyong, Helen Stoddart and Alex Hegedus from the Australian Museum in Sydney (NSW, Australia); to Peter C. Dworschak from the Naturhistorisches Museum Wien, Vienna (Austria); to Roland Melzer and Stefan Friedrich from the Zoologische Staatssammlung München, Munich (Germany); to Charles Oliver Coleman from the Museum für Naturkunde Berlin (Germany); to Rafael Lemaitre, Lisa Comer and Karen Reed from the Smithsonian Institution, Washington (DC, USA); to Paul Callomon from the Academy of Natural Sciences of Drexel University, Philadelphia (PA, USA); to Hsi-Te Shih from National Chung Hsing University, Taichung (Taiwan); and to Gustav Paulay from the Florida Museum of Natural History, Gainesville (FL, USA). The first author's visits to Naturalis in Leiden (the Netherlands) (NL-TAF), the Natural History Museum in London (UK) (GB-TAF) and to the Muséum National d'Histoire Naturelle, Paris (France) (FR-TAF) received support from the SYNTHESYS Project (<http://www.synthesys.info/>), financed by the European Community, Research Infrastructure Action under the FP7 'Capacities', which is greatly appreciated. We also thank Peter K. L. Ng and Tohru Naruse for their useful comments during the review process.

REFERENCES

- Boon PY, Yeo DCJ, Todd PA. 2009. Sound production and reception in mangrove crabs *Perisesarma* spp. (Brachyura: Sesarmidae). *Aquatic Biology* 5: 107–116.
- Brösing A, Spiridonov VA, Al-Aidaros AM, Türkay M. 2014. Description of a new genus and new species of Sesarmidae (Decapoda: Brachyura) from the Farasan Islands, Saudi Arabia, Red Sea. *Journal of Crustacean Biology* 34: 273–282.
- Cannicci S, Burrows D, Fratini S, Smith TJ III, Offenberg J, Dahdouh-Guebas F. 2008. Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. *Aquatic Botany* 89: 186–200.
- Cannicci S, Schubart CD, Innocenti G, Dahdouh-Guebas F, Shahdadi A, Fratini S. 2017. A new species of the genus *Parasesarma* De Man 1895 from East African mangroves and evidence for mitochondrial introgression in sesarmid crabs. *Zoologischer Anzeiger* 269: 89–99.

- Chen P, Carrasco L, Ng PKL. 2014.** Post-contest stridulation used exclusively as a victory display in mangrove crabs. *Ethology* **120**: 532–539.
- Chen P, Carrasco L, Ng PKL. 2017.** Mangrove crab uses victory display to “browbeat” losers from re-initiating a new fight. *Ethology* **123**: 981–988.
- Chopra B, Das KN. 1937.** Further notes on Crustacea Decapoda in the Indian Museum. IX. On three collections of crabs from Tavoy and Mergui archipelago. *Records of the Indian Museum* **39**: 377–434.
- Crosnier A. 1965.** Crustacés décapodes Grapsidae et Ocypodidae. *Faune de Madagascar* **18**: 1–143, pl. 1–11.
- Dai A, Song YZ. 1986.** Intertidal crabs from Beibu Gulf of Guangxi. *Transactions of the Chinese Crustacean Society* **1**: 54–62.
- Dai A, Yang S. 1991.** *Crabs of the China seas*. Beijing: China Ocean Press (Chinese edition); Berlin, Heidelberg, New York, Tokyo: Springer (English edition).
- Darriba D, Taboada GL, Doallo R, Posada D. 2012.** jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**: 772.
- Davie PJF. 1992.** Revision of *Sarmatium* Dana (Crustacea: Brachyura: Sesarminae) with descriptions of three new species. *Memoirs of the Queensland Museum* **32**: 79–97.
- Davie PJF. 1993.** A new species of sesarminae crab (Brachyura: Grapsidae) from Japan and Taiwan, previously known as *Sesarma erythroactyla* Hess, 1865. *Crustacean Research* **22**: 65–74.
- Davie PJF. 1994.** Revision of the genus *Neosarmatium* Serene and Soh (Crustacea: Brachyura: Sesarminae) with description of two new species. *Memoirs of the Queensland Museum* **35**: 35–74.
- Davie PJF. 2003.** A new species of *Perisesarma* (Crustacea: Brachyura: Sesarminae) from the Bay of Bengal. *The Raffles Bulletin of Zoology* **51**: 387–391.
- Davie PJF. 2010.** A new species of *Perisesarma* (Crustacea: Brachyura: Sesarminae) from Western Australia. In: Fransen CHJM, De Grave S, Ng PKL, eds. *Studies on Malacostraca: Lipke Bijdeley Holthuis memorial volume. Crustaceana monographs*, Leiden: Brill, **Vol. 14**, 195–207.
- Davie PJF. 2012.** A revision of *Neosarma* (Crustacea: Decapoda: Sesarminae) with the description of a new species. *Memoirs of the Queensland Museum* **56**: 221–233.
- Davie PJF, Ng PKL. 2013.** A review of *Chiromantes obtusifrons* (Dana, 1851) (Decapoda: Brachyura: Sesarminae), with descriptions of four new sibling-species from Christmas Island (Indian Ocean), Guam and Taiwan. *Zootaxa* **3609**: 1–25.
- De Grave S, Pentcheff ND, Ah Yong ST, Chan TY, Crandall KA, Dworschak PC, Felder DL, Feldmann RM, Fransen CHJM, Goulding LYD, Lemaitre R, Low MEY, Martin JW, Ng PKL, Schweitzer CE, Tan SH, Tshudy D, Wetzer R. 2009.** A classification of living and fossil genera of decapod crustaceans. *The Raffles Bulletin of Zoology, Supplement* **21**: 1–109.
- De Haan HM. 1833–1849.** Crustacea [vol. 1]. In: von Siebold PF, ed. *Fauna Japonica, sive descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batavia imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus a adumbrationibus illustravit*. Leiden: published by the author, 1–243.
- De Man JG. 1887.** Uebersicht der Indo-pacischen Arten der Gattung *Sesarma* Say nebst einer Kritik der von W. Hess und E. Nauck in den Jahren 1865 und 1880 beschriebenen Decapoden. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere* **2**: 639–689.
- De Man JG. 1889.** Über einige neue oder seltene indopacifische Brachyuren. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* **4**: 409–452.
- De Man JG. 1892.** Decapoden des Indischen Archipels. *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien* **2**: 265–527.
- De Man JG. 1895–1898.** Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Tiere* **9**: 75–218.
- De Man JG. 1902.** Die von Herr Professor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden. In: Kükenthal W, ed. *Ergebnisse einer Zoologischen Forschungsreise in den Molukken und Borneo. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **25**: 467–929.
- Emmerson WD. 2016.** *A guide to, and checklist for, the Decapoda of Namibia, South Africa and Mozambique*, Newcastle: Cambridge Scholars Publishing, **Vol. 3**: 1–720.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994.** DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**: 294–299.
- Fratini S, Cannicci S, Porri F, Innocenti G. 2019.** Revision of the *Parasesarma guttatum* species complex reveals a new pseudocryptic species in south-east African mangroves. *Invertebrate Systematics* **33**: 208–224.
- Fratini S, Vannini M, Cannicci S, Schubart CD. 2005.** Tree-climbing mangrove crabs: a case of convergent evolution. *Evolutionary Ecology Research* **7**: 219–233.
- Guerao G, Anger K, Nettelmann U, Schubart CD. 2004.** Complete larval and early juvenile development of the mangrove crab *Perisesarma fasciatum* (Crustacea: Brachyura: Sesarminae) from Singapore, with a larval comparison of *Parasesarma* and *Perisesarma*. *Journal of Plankton Research* **26**: 1389–1408.
- Guindon S, Gascuel O. 2003.** A simple, fast and accurate method to estimate large phylogenies by maximum likelihood. *Systematic Biology* **52**: 696–704.
- Guinot D. 1977.** Propositions pour une nouvelle classification des crustacés décapodes brachyours. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, série D* **285**: 1049–1052.
- Hall TA. 1999.** BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.
- Hess W. 1865.** Beiträge zur Kenntniss der Decapoden-Krebse Ost-Australiens der philosophischen Facultät

- der Georg-August-Universität in Göttingen. *Archiv für Naturgeschichte* **31**: 127–173.
- Hilgendorf F. 1869.** Crustaceen. In: Von der Decken CC, ed. *Reisen in Ost-Afrika in dem Jahren 1859–1865*, Vol. 3. Leipzig, Heidelberg: C.F. Winter'sche Verlagshandlung, 69–116.
- Huelsenbeck JP, Ronquist F. 2001.** MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.
- Koller P, Liu H-C, Schubart CD. 2010.** A new semiterrestrial species of *Parasesarma* De Man, 1895, from Taiwan (Decapoda, Brachyura, Sesarmidae). In: Franssen CHJM, De Grave S, Ng PKL, eds. *Studies on Malacostraca: Lipke Bijdeley Holthuis memorial volume. Crustaceana Monographs*, Leiden: Brill, Vol. 14: 357–368.
- Lee SY. 1998.** Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research* **49**: 335–343.
- Lee SY. 2015.** Ecology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram F, von Vaupel Klein C, eds. *Treatise on zoology - anatomy, taxonomy, biology - The Crustacea, complementary to the volumes translated from the French of the Traité de Zoologie*, Leiden: Brill, Vol. 9(C) (I), 469–542.
- Li J-J, Rahayu DL, Ng PKL. 2018.** Identity of the tree-spider crab, *Parasesarma leptosoma* (Hilgendorf, 1869) (Decapoda: Brachyura: Sesarmidae), with descriptions of seven new species from the western Pacific. *Zootaxa* **4482**: 451–490.
- Li J-J, Shih HT, Ng PKL. 2019.** Three new species and two new records of *Parasesarma* De Man, 1895 (Crustacea: Brachyura: Sesarmidae) from Taiwan and the Philippines from morphological and molecular evidence. *Zoological Studies* **58**: e40.
- Naderloo R. 2011.** Grapsoid crabs (Decapoda: Brachyura: Thoracotremata) of the Persian Gulf and the Gulf of Oman. *Zootaxa* **3048**: 1–43.
- Naderloo R, Schubart CD. 2010.** Description of a new species of *Parasesarma* (Crustacea; Decapoda; Brachyura; Sesarmidae) from the Persian Gulf, based on morphological and genetic characteristics. *Zoologischer Anzeiger* **249**: 33–43.
- Naruse T, Ng NK. 2012.** Establishment of a new genus for *Cyclograpsus lophopus* Nobili, 1905, within Sesarmidae Dana, 1851 (Crustacea: Decapoda: Brachyura). *Zootaxa* **3572**: 63–68.
- Ng PKL, Davie PJF, Li J-J. 2016.** On the identities of *Parasesarma carolinense* (Rathbun, 1907) and *Parasesarma sigillatum* (Tweedie, 1950), with description of a new species from Taiwan (Crustacea: Brachyura: Sesarmidae). *The Raffles Bulletin of Zoology* **64**: 257–268.
- Ng PKL, Guinot D, Davie PJF. 2008.** Systema brachyurorum: part I. An annotated checklist of extant brachyuran crabs of the world. *The Raffles Bulletin of Zoology, Supplement* **17**: 1–286.
- Ng PKL, Shih HT, Cannicci S. 2019.** A new genus for *Sesarma (Holometopus) tangi* Rathbun, 1931 (Decapoda: Brachyura: Sesarmidae) from mangrove forests, with notes on its ecology and conservation. *Journal of Crustacean Biology* **40**: 89–96.
- Ortmann AE. 1897.** Carcinologische Studien. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere* **10**: 258–372.
- Posada D, Buckley TR. 2004.** Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* **53**: 793–808.
- Poupin J, Zubia M, Chabanet P, Malay M. 2012.** Illustrated checklist of the Decapoda at Europa Island. *WIO Journal of Marine Science* **11**: 1–25.
- Pretzmann G. 1968.** Neue südamerikanische Süßwasserkrabben der Gattung *Pseudothelphusa*. *Entomologisches Nachrichtenblatt* **15**: 1–15.
- Ragionieri L, Fratini S, Vannini M, Schubart CD. 2009.** Phylogenetic and morphometric differentiation reveal geographic radiation and pseudo-cryptic speciation in a mangrove crab from the Indo-West Pacific. *Molecular Phylogenetics and Evolution* **52**: 825–834.
- Rahayu DL, Davie PJF. 2002.** Two new species and a new record of *Perisesarma* (Decapoda, Brachyura, Grapsidae, Sesarminae) from Indonesia. *Crustaceana* **75**: 597–607.
- Rahayu DL, Li J-J. 2013.** A new species of the genus *Parasesarma* (Crustacea: Brachyura: Sesarmidae) from Taiwan and the Philippines, and redescription of *P. jamelese* (Rathbun, 1914). *The Raffles Bulletin of Zoology* **61**: 633–639.
- Rahayu DL, Ng PKL. 2005.** On two new species of the genera *Haberma* and *Parasesarma* (Crustacea: Decapoda: Brachyura: Sesarmidae) from Papua, Indonesia. *Zoologische Mededelingen* **79**: 167–178.
- Rahayu DL, Ng PKL. 2009.** Two new species of *Parasesarma* De Man, 1895, from Southeast Asia (Crustacea: Decapoda: Brachyura: Sesarmidae). *Zootaxa* **1980**: 29–40.
- Rahayu DL, Ng PKL. 2010.** Revision of *Parasesarma plicatum* (Latreille, 1803) species-group (Crustacea: Decapoda: Brachyura: Sesarmidae). *Zootaxa* **2327**: 1–22.
- Rathbun MJ. 1914.** New species of crabs of the families Grapsidae and Ocypodidae, in: scientific results of the Philippines Cruise of the fisheries steamer “Albatross” 1907–1910. *Proceedings of the United States National Museum* **47**: 69–85.
- Rathbun MJ. 1918.** Brachyura. Australasian Antarctic Expedition, 1911–1914, under the leadership of sir Douglas Mawson, D. Sc., B.E. *Scientific Reports, Series C, Zoology and Botany* **5**: 1–5.
- Rodríguez F, Oliver JL, Marín A, Medina JR. 1990.** The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* **142**: 485–501.
- Rohlf FJ. 2006.** *TpsDig, Version 2.10*. Sony Brook: Department of Ecology and Evolution, State University of New York at Stony Brook.
- Say T. 1817.** An account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* **1**: 57–81.
- Schubart CD. 2009.** Mitochondrial DNA and decapod phylogenies: the importance of pseudogenes and primer optimization. In: Martin JW, Crandall KA, Felder DL, eds. *Decapod Crustacean Phylogenetics. Crustacean Issues*, Boca Raton: CRC Press, Vol. 18: 47–65.
- Schubart CD, Cannicci S, Vannini M, Fratini S. 2006.** Molecular phylogeny of grapsoid crabs (Decapoda, Brachyura) and allies based on two mitochondrial genes and a proposal for refraining from current superfamily classification. *Journal of Zoological Systematics and Evolutionary Research* **44**: 193–199.

- Schubart CD, Cuesta JA, Felder DL. 2002.** Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoida. *Journal of Crustacean Biology* **22**: 28–44.
- Schubart CD, Huber MGJ. 2006.** Genetic comparison of German populations of the stone crayfish, *Austropotamobius torrentium* (Crustacea: Astacidae). *Bulletin Français de la Pêche et de la Pisciculture* **380–381**: 1019–1028.
- Schubart CD, Liu H-C, Ng PKL. 2009.** Revision of *Selatium* Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae), with description of a new genus and two new species. *Zootaxa* **2154**: 1–29.
- Schubart CD, Weil T, Stenderup JT, Crandall KA, Santl T. 2010.** Ongoing phenotypic and genotypic diversification in adaptively radiated freshwater crabs from Jamaica. In: Glaubrecht M, ed. *Evolution in action – adaptive radiations and the origins of biodiversity*. Berlin, Heidelberg: Springer, 323–349.
- Serène R. 1968.** The Brachyura of the Indo Pacific Region. In: Prodrum for a Check List of the Non-planctonic Marine Fauna of South East Asia. *Special Publication of the Singapore National Academy of Science* **1**: 33–120.
- Serène R, Soh CL. 1970.** New Indo-Pacific genera allied to *Sesarma* Say 1817 (Brachyura, Decapoda, Crustacea). *Treubia* **27**: 387–416.
- Shahdadi A, Davie PJF, Schubart CD. 2017.** *Perisesarma tuerkayi*, a new species of mangrove crab from Vietnam (Decapoda, Brachyura, Sesarmidae), with an assessment of its phylogenetic relationships. *Crustaceana* **90**: 1155–1175.
- Shahdadi A, Davie PJF, Schubart CD. 2018a.** Systematics and phylogeography of the Australasian mangrove crabs *Parasesarma semperi* and *P. longicristatum* (Decapoda: Brachyura: Sesarmidae) based on morphological and molecular data. *Invertebrate Systematics* **32**: 196–214.
- Shahdadi A, Davie PJF, Schubart CD. 2019a.** A new species of *Parasesarma* (Decapoda: Brachyura: Sesarmidae) from northern Australian mangroves and its distinction from morphologically similar species. *Zoologischer Anzeiger* **279**: 116–125.
- Shahdadi A, Mvogo Ndongo PA, Suess T, Schubart CD. 2019b.** Reappraisal and redescription of the three species of the recently defined genus *Guinearma* Shahdadi & Schubart, 2017, with a key to the West African Sesarmidae (Decapoda, Brachyura). *Crustaceana* **92**: 307–334.
- Shahdadi A, Ng PKL, Schubart CD. 2018b.** Morphological and phylogenetic evidence for a new species of *Parasesarma* De Man, 1895 (Decapoda, Brachyura, Sesarmidae) from the Malay Peninsula, previously referred to as *Parasesarma indiarum*. *The Raffles Bulletin of Zoology* **66**: 739–762.
- Shahdadi A, Schubart CD. 2015.** Evaluating the consistency and taxonomic importance of cheliped and other morphological characters that potentially allow identification of species of the genus *Perisesarma* De Man, 1895 (Brachyura, Sesarmidae). *Crustaceana* **88**: 1079–1095.
- Shahdadi A, Schubart CD. 2017.** Taxonomic review of *Perisesarma* (Decapoda: Brachyura: Sesarmidae) and closely related genera based on morphology and molecular phylogenetics: new classification, two new genera and the questionable phylogenetic value of the epibranchial tooth. *Zoological Journal of the Linnean Society* **182**: 517–548.
- Shahdadi A, Schubart CD, Ng PKL. 2019c.** Record of *Parasesarma lenzii* (De Man, 1895) (Decapoda, Brachyura, Sesarmidae) from the Cocos-Keeling Islands, with a redescription and designation of a lectotype. *Crustaceana* **92**: 739–747.
- Shedlock AM, Haygood MG, Pietsch TW, Bentzen P. 1997.** Enhanced DNA extraction and PCR amplification of mitochondrial genes from formalin-fixed museum specimens. *BioTechniques* **22**: 394–400.
- Shih HT, Hsu PY, Shahdadi A, Schubart CD, Li JJ. 2019.** The synonymy of the supratidal crabs species *Parasesarma cognatum* Rahayu & Li, 2013 with *P. liho* Koller, Liu & Schubart, 2010 (Decapoda: Brachyura: Sesarmidae) based on morphological and molecular evidence, with a note on *P. paucitorum* Rahayu & Ng, 2009. *Zoological Studies* **58**: 1–13.
- Silva IC, Mesquita M, Paula J. 2010.** Genetic and morphological differentiation of the mangrove crab *Perisesarma guttatum* (Brachyura: Sesarmidae) along an East African latitudinal gradient. *Biological Journal of the Linnean Society* **99**: 28–46.
- Silvestro D, Michalak I. 2012.** raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution* **12**: 335–337.
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011.** MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28**: 2731–2739.
- Tan CGS, Ng PKL. 1994.** An annotated checklist of mangrove brachyuran crabs from Malaysia and Singapore. *Hydrobiologia* **285**: 75–84.
- Tesch JJ. 1917.** Synopsis of the genera *Sesarma*, *Metasesarma*, *Sarmatium* and *Clistocoeloma* with a key to determination of the Indo-Pacific species. *Zoologische Mededelingen* **3**: 127–260.
- Tesch JJ. 1918.** The Decapoda Brachyura of the Siboga expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae, and Gecarcinidae. *Siboga-Expeditie Mon.* **39**: 1–148.
- Thompson JD, Higgins DG, Gibson TJ. 1994.** CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22**: 4673–4680.
- Tsang LM, Ma KY, Ah Yong ST, Chan TY, Chu KH. 2008.** Phylogeny of Decapoda using two nuclear protein-coding genes: origin and evolution of the Reptantia. *Molecular Phylogenetics and Evolution* **48**: 359–368.
- Tsang LM, Schubart CD, Ah Yong ST, Lai JC, Au EY, Chan TY, Ng PK, Chu KH. 2014.** Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution* **31**: 1173–1187.
- Tweedie MWF. 1936.** On the crabs of the family Grapsidae in the collection of the Raffles Museum. *Bulletin of the Raffles Museum* **12**: 44–70.
- Tweedie MWF. 1950.** Grapsoid crabs from Labuan and Sarawak. *Sarawak Museum Journal* **5**: 338–369.
- Villesen P. 2007.** FaBox: an online toolbox for FASTA sequences. *Molecular Ecology Notes* **7**: 965–968.