Zoological Studies **58:** 40 (2019)
doi:10.6620/ZS.2019.58-40

Zoological Studies

Open Access

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

Jheng-Jhang Li[1,2], Hsi-Te Shih[3,*], and Peter K. L. Ng[4]

[1]*Department of Marine Biotechnology and Resources, National Sun Yat-sen University, 70 Lienhai Road, Kaohsiung 80424, Taiwan*
[2]*East Peak Ecological Consultants, Inc., 22 Wanggong Road, Kaohsiung 83249, Taiwan*
[3]*Department of Life Science and Research Center for Global Change Biology, National Chung Hsing University, 250, Kuo Kuang Road, Taichung 402, Taiwan. *Correspondence: E-mail: htshih@dragon.nchu.edu.tw*
[4]*Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117546, Republic of Singapore*

Received 16 September 2019 / Accepted 28 November 2019 / Published 16 December 2019
Communicated by Benny K.K. Chan

Three new coastal crabs, *Parasesarma aurifrons* n. sp., *P. sanguimanus* n. sp. and *P. gemmatum* n. sp. (Sesarmidae), are described from Taiwan and the Philippines. *Parasesarma aurifrons* is morphologically similar to *P. ungulatum* (H. Milne Edwards, 1853), *P. liho* Koller, Liu & Schubart, 2010, and *P. obliquefrons* (Rathbun, 1924); *P. sanguimanus* most closely resembles *P. cricotus* (Rahayu & Davie, 2002); and *P. gemmatum* is related to *P. lenzii* (De Man, 1895), but they can be distinguished by a suite of characters, including the structures of the chelipeds, gonopods and vulvae. The three new species are also supported by genetic data from the mitochondrial cytochrome oxidase subunit I (*COI*). Two species, *P. lenzii* and *P. dumacense* (Rathbun, 1914), are also recorded from Taiwan for the first time. The poorly known *P. obliquefrons* (Rathbun, 1924) from Samoa is figured for the first time as part of the comparisons and its taxonomically important gonopod structures are illustrated.

Key words: *COI*, Taxonomy, New species, *Parasesarma aurifrons*, *P. sanguimanus*, *P. gemmatum*, *P. obliquefrons*, Morphology, Mitochondrial cytochrome oxidase subunit I.

BACKGROUND

Parasesarma De Man, 1895 is the most species-rich genus in the Sesarmidae Dana, 1851, with 68 recognised species. Most of the species of *Perisesarma* De Man, 1895 were transferred to the genus by Shahdadi and Schubart (2017) (see also Shih et al. 2019). In Taiwan, nine species of this genus have been reported, with one, *P. cognatum* Rahayu & Li, 2013, recently synonymised with *P. liho* Koller, Liu & Schubart, 2010 (Ng et al. 2001 2017; Hsu and Shih 2018; Li et al. 2018 2019; Shih et al. 2019).

Recent intensive surveys in the Hengchun Peninsula in southern Taiwan found three species that could not be identified with known congeners. In this study, we describe them as new, with one species also occurring in the Philippines. Molecular evidence from mitochondrial cytochrome oxidase subunit I (*COI*) was also used to support the taxonomy.

MATERIALS AND METHODS

Specimens examined are deposited in Muzium

Citation: Li JJ, 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. Zool Stud **58:**40. doi:10.6620/ZS.2019.58-40.

Zoologicum Bogoriense in the Indonesian Institute of Sciences, Jakarta, Indonesia (MZB); Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (NMMBA); National Museum of Natural Science, Taichung, Taiwan (NMNS); The Naturalis Biodiversity Center, Leiden, The Netherlands (NNM) (which now includes the collections of the Zoological Museum of the University of Amsterdam); Ryukyus University Museum, Fujukan, University of the Ryukyus, Okinawa, Japan (RUMF); U.S. National Museum for Natural History, Smithsonian Institution, Washington D.C., USA (USNM); and Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC). Measurements, in millimetres, are of the maximum carapace width and length. The following abbreviations are used: CW = carapace width, CL = carapace length; G1 = male first gonopod; G2 = second male gonopod, P2–P5 = first to fourth ambulatory legs, respectively.

Sequences of *COI* from related or morphological similar species of *Parasesarma* were included in this study (Table 1). The sequences were obtained following the method described by Shih et al. (2016) after verification with the complimentary strand. Sequences of the different haplotypes have been deposited in the DNA Data Bank of Japan (DDBJ) (accession numbers in Table 1).

The best-fitting model for sequence evolution was determined by PartitionFinder (vers. 2.1.1; Lanfear et al. 2017), selected by the Bayesian information criterion (BIC). The obtained best model (GTR + G) was subsequently used for a Bayesian inference (BI) analysis. The BI analysis was performed with MrBayes (vers. 3.2.3; Ronquist et al. 2012). The analyses were run with four chains for 10 million generations and four independent runs, with trees sampled every 1000 generations. The convergence of chains was determined by the average standard deviation of split frequency values below the recommended 0.01 (Ronquist et al. 2019) and the first 800 trees were discarded as the burnin accordingly. The maximum likelihood (ML) analysis was conducted in RAxML (vers. 7.2.6; Stamatakis 2006). Because RAxML does not accept the GTR + I model, the second best model, GTR + G (*i.e.*, GTRGAMMA), was used with 100 runs, and the best ML tree wad found by comparing the likelihood scores. The robustness of the ML tree was evaluated

Table 1. The haplotypes of *COI* gene of specimens in the genus *Parasesarma* used in this study. See MATERIALS AND METHODS for abbreviations of museums or universities

Species	Locality	Sample size	Catalogue no. of NCHUZOOL (unless indicated)	Haplotype of *COI*	Access. no. of *COI*
P. affine	China: Xiamen, Fujian	1	ZRC 2002.0561	affine (SE China; W Taiwan)	LC490891
	Taiwan: Danshuei, New Taipei City	1	15426	affine (SE China; W Taiwan)	LC490891
	Taiwan: Keya R. estuary, Hsinchu City	1	15505	affine (SE China; W Taiwan)	LC490891
P. anambas	Indonesia: Teluk Baruk, Anambas	1	ZRC 2003.0726 (paratype)	anambas 1 (Anambas, Indonesia)	LC510452
	China: Sanya, Hainan	1	15514	anambas 2 (Hainan, China)	LC510453
P. aurifrons n. sp.	Taiwan: Baoli R. estuary, Hengchun, Pingtung	1	15533	aurifrons 1 (Pingtung, Taiwan)	LC510454
	Taiwan: Baoli R. estuary, Hengchun, Pingtung	1	15534	aurifrons 2 (Pingtung, Taiwan)	LC510455
P. bengalense	India: Kerala	1	ZRC 2017.0521	bengalense (Kerala, India)	LC510456
	Thailand: Phuket	1	-	bengalense (Phuket, Thailand)	KX400901
P. bidens	Japan: Iriomote, Ryukyus	1	15509	bidens (Japan)	LC510457
	Japan: Miyako, Ryukyus	1	15510	bidens (Japan)	LC510458
	Japan: Nagasaki	1	15511	bidens (Japan)	LC510459
	Japan: Okinawa, Ryukyus	1	15506	bidens (Japan)	LC510460
	Japan: Iriomote, Ryukyus	1	15709	bidens (Japan)	LC510461
	Taiwan: Caiyuan, Penghu	1	15507	bidens (SW Taiwan)	LC510462
	Taiwan: Gueishandao, Yilan	1	15508	bidens (NE Taiwan)	LC510463
P. cricotus	Indonesia: Kamora R., Irian Jaya	1	-	cricotus 1 (Papua, Indonesia)	KX400897
	Indonesia: Kamora R., Irian Jaya	1	-	cricotus 2 (Papua, Indonesia)	KX400898
P. dumacense	Philippines: Cebu	1	ZRC 2008.0833	dumacense 1 (Cebu, Philippines)	LC510464
	Philippines: Cebu	1	-	dumacense 2 (Cebu, Philippines)	KX400929
	Taiwan: Dongsha, Kaohsiung	1	15704	dumacense 1 (Dongsha, Taiwan)	LC510465
P. foresti	Indonesia: Ajkwa R., Irian Jaya	1	-	foresti 1 (Papua, Indonesia)	KX400885
	Indonesia: Portsite, Irian Jaya	1	ZRC 2002.0608	foresti 2 (Papua, Indonesia)	LC510466
P. gemmatum n. sp.	Taiwan: Dingtanzih, Hengchun, Pingtung	1	15532	gemmatum 1 (Pingtung, Taiwan)	LC510467

Table 1. (Continued)

Species	Locality	Sample size	Catalogue no. of NCHUZOOL (unless indicated)	Haplotype of *COI*	Access. no. of *COI*
	Taiwan: Siatanzih, Hengchun, Pingtung	1	15531	gemmatum 2 (Pingtung, Taiwan)	LC510468
P. guttatum	Kenya: Gazi	1	-	guttatum (Kenya)	KX400903
P. kuekenthali	Taiwan: Gangkou R. estuary, Hengchun, Pingtung	1	15711	kuekenthali 1 (S Taiwan)	LC510469
	Taiwan: Dongsha I., Kaohsiung	1	15702	kuekenthali 2 (Dongsha, Taiwan)	LC510470
	Taiwan: Dongsha I., Kaohsiung	1	15703	kuekenthali 3 (Dongsha, Taiwan)	LC510471
P. kui	Taiwan: Gangkou R., Hengchun, Pingtung	1	NMNS-7779-015	kui (Pingtung, Taiwan)	LC490887
P. lenzii	Indonesia: Sumatra	1	NNM Crus. D. 102653	lenzii (Sumatra, Indonesia)	MF564014
	Cocos (Keeling) Islands	1	ZRC 2018.1373	lenzii (Cocos-Keeling)	MK584922
	Taiwan: Dingtanzih, Hengchun, Pingtung	1	15643	lenzii (Pingtung, Taiwan)	LC510472
	Taiwan: Dingtanzih, Hengchun, Pingtung	1	15642	lenzii (Pingtung, Taiwan)	LC510473
	Taiwan: Dingtanzih, Hengchun, Pingtung	2	15645	lenzii (Pingtung, Taiwan)	LC510474, LC510475
	Taiwan: Siangjiaowan, Hengchun, Pingtung	1	15644	lenzii (Pingtung, Taiwan)	LC510476
P. liho	Taiwan: Meilun, Hualien	1	15027	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Dulanwan, Taitung	2	15025	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Niousi, Hengchun, Pingtung	1	15031	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Gangkou R. estuary, Hengchun, Pingtung	1	NMMBCD 3976	liho 2 (S Taiwan; C Philippines)	LC490882
	Taiwan: Gangkou R. estuary, Hengchun, Pingtung	1	15028	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Gangkou R. estuary, Hengchun, Pingtung	2	NMMBCD 3976	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Gangkou R. estuary, Hengchun, Pingtung	1	NMMBCD 3975	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Baoli R. estuary, Hengchun, Pingtung	1	15024	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Houwan, Hengchun, Pingtung	1	15022	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Houwan, Hengchun, Pingtung	2	15022	liho 1 (S Taiwan; C Philippines)	LC490881
	Taiwan: Houwan, Hengchun, Pingtung	1	15425	liho 1 (S Taiwan; C Philippines)	LC490881
	Philippines: Kawasan, Cebu	1	15034	liho 2 (S Taiwan; C Philippines)	LC490882
	Philippines: Kawasan, Cebu	1	ASIZCR	liho 1 (S Taiwan; C Philippines)	LC490881
	Philippines: Kawasan, Cebu	1	ASIZCR	liho 1 (S Taiwan; C Philippines)	LC490881
P. nr. *lividum*	Japan: Ishigaki, Ryukyus	1	RUMF-ZC-3779	nr_lividum (Ishigaki, Japan)	LC510477
P. macaco	Baoli R., Hengchun, Pingtung, Taiwan	1	NMNS-7779-005	macaco (Pingtung, Taiwan)	LC490888
P. maipoense	Vietnam: Dong Rui, Quang Ninh	1	15512	maipoense (N Vietnam)	LC510478
	Vietnam: Red River Delta	1	ZRC 2009.0800	maipoense (S Vietnam)	LC510479
P. obliquifrons	Samoa: Pago Pago	1	USNM 45913 (holotype)	obliquifrons (Samoa)	LC510480
P. paucitorum		1	-	paucitorum (Sulawesi, Indonesia)	LC490885
	Taiwan: Baoli R. estuary, Hengchun, Pingtung	1	15515	pictum (Taiwan)	LC490890
	Taiwan: Baoli R. estuary, Hengchun, Pingtung	1	15516	pictum (Taiwan)	LC490890
	Taiwan: Chihdong, Penghu	1	15517	pictum (Taiwan)	LC490890
	Taiwan: Hanbao, Changhua	1	15518	pictum (Taiwan)	LC490890
	Taiwan: Houlong, Miaoli	1	15519	pictum (Taiwan)	LC490890
	Taiwan: Houwan, Hengchun, Pingtung	1	15520	pictum (Taiwan)	LC490890
	Taiwan: Houwan, Hengchun, Pingtung	1	15521	pictum (Taiwan)	LC490890
	Taiwan: Nangan, Matsu	1	15427	pictum (Taiwan)	LC490890
	Taiwan: Chaishan, Kaohsiung	2	15522	pictum (Taiwan)	LC490890
	Taiwan: Siangjiaowan, Hengchun, Pingtung	2	15523	pictum (Taiwan)	LC490890
	Taiwan: Yanshuei R. estuary, Tainan	1	15524	pictum (Taiwan)	LC490890
P. sanguimanus n. sp.	Taiwan: Gangkou R. estuary, Hengchun, Pingtung	1	15525	sanguimanus (Pingtung, Taiwan)	LC510481
	Taiwan: Gangkou R. estuary, Hengchun, Pingtung	1	15714	sanguimanus (Pingtung, Taiwan)	LC510482
P. semperi	Indonesia: Tipoeka, Irian Jaya	1	-	semperi 1 (Papua, Indonesia)	KX400910
	Indonesia: Tipoeka, Irian Jaya	1	-	semperi 2 (Papua, Indonesia)	KX400911
P. tripectinis	Taiwan: Dajia, Taichung	1	15703	tripectinis (W Taiwan)	LC490889
	Taiwan: Miaoli	1	15526	tripectinis (W Taiwan)	LC490889
P. ungulatum	Taiwan: Hengchun, Pingtung	1	15530	ungulatum (S Taiwan; Borneo)	LC510483
	Malaysia: Labuan	1	15527	ungulatum (S Taiwan; Borneo)	LC510484
	Malaysia: Mersing, Johor	1	15528	ungulatum (Johor, Malaysia)	LC510485
	Singapore	1	ZRC 2011.0500	ungulatum (Singapore)	LC510486
Total		85			

by 1000 bootstrap pseudoreplicates under the model GTRGAMMA.

RESULTS

TAXONOMY

Family Sesarmidae Dana, 1851
Genus *Parasesarma* De Man, 1895

Parasesarma aurifrons n. sp.

(Figs. 1A, B, 2A–D, 3, 4, 11A)
urn:lsid:zoobank.org:act:DA0C9021-6010-41B8-9CAB-4EA210F38FC0

Parasesarma aff. *ungulatum* – Li and Chiu 2013: 81.

Material examined: Holotype: ♂ (10.4 × 8.5 mm) (NCHUZOOL 15602), Gangkou River (= R.) estuary (21°59'16.1"N 120°50'29.7"E), Hengchun, Pingtung, Taiwan, coll. J.-J. Li, 25 Mar. 2016. Paratypes: Taiwan: Gangkou R. estuary, Hengchun, Pingtung: 2 ♀♀ (10.4 × 8.2 mm, 13.6 × 11.0 mm) (NCHUZOOL 15611), coll. J.-J. Li, 7 Jun. 2012; 1 ♂ (12.7 × 10.2 mm), 1 ♀ (12.3 × 10.4 mm) (NCHUZOOL 15605), coll. J.-J. Li, 11 Apr. 2015; 1 ♂ (14.2 × 10.9 mm) (ZRC 2019.1075), coll. J.-J. Li, 17 May 2015; 1 ♂ (12.4 × 10.2 mm) (NCHUZOOL 15610), coll. J.-J. Li, 15 Jul. 2015; 1 ♂ (10.1 × 8.2 mm) (ZRC 2019.0819), coll. J.-J. Li, 18 Aug. 2015; 2 ♂♂ (11.2 × 8.8 mm, 12.1 × 10.3 mm) (NCHUZOOL 15603), coll. J.-J. Li, 1 May 2016; 1 ♀ (12.4 × 10.0 mm) (NCHUZOOL 15606), coll. J.-J. Li, 24 May 2016; 2 ♀♀ (13.6 × 11.1 mm, 13.8 × 11.2 mm), 2 ovig. ♀♀ (11.1 × 9.3 mm, 14.0 × 11.6 mm) (NCHUZOOL 15609), coll. J.-J. Li, 15 Jun. 2016; 3 ♂♂ (11.0–12.4 × 9.6–10.4 mm) (NCHUZOOL 15607), coll. J.-J. Li, 20 Jun. 2016; 1 ♂ (12.0 × 10.0 mm) (NCHUZOOL 15608), coll. J.-J. Li, 24 Jul. 2016; 9 ♂♂ (9.8–11.1 × 8.2–9.5 mm), 4 ♀♀ (10.7–11.5 × 8.4–9.1 mm), 1 ovig. ♀ (11.8 × 10.2) (ZRC 2019.0822), coll. J.-J. Li, 11 Jul. 2017; 4 ♂♂ (8.4–13.2 × 7.0–10.6 mm) (NCHUZOOL 15604), coll. J.-J. Li, 15 Jun. 2019. Baoli R. estuary (22°03'27.1"N 120°42'28.4"E), Hengchun, Pingtung: 1 ♂ (12.4 × 11.0 mm) (ZRC 2019.0823), coll. J.-J. Li, 6 Aug. 2015; 1 ♂ (12.6 × 10.6 mm) (NCHUZOOL 15533), coll. P.-Y. Hsu et al., 4 Sep. 2017; 1 ovig. ♀ (11.0 × 9.2 mm) (NCHUZOOL 15534), coll. P.-Y. Hsu et al., 18 Mar. 2018.

Other material: Taiwan: Gangkou R. estuary, Hengchun, Pingtung: 1 ♀ (10.6 × 8.5 mm) (NCHUZOOL 15616), coll. J.-J. Li, 27 Jun. 2012; 2 ♂♂ (10.1 × 8.9 mm, 10.9 × 9.2 mm) (NCHUZOOL 15615), coll. J.-J. Li, 18 May 2015; 1 ♀ (11.4 × 9.6 mm) (NCHUZOOL 15618), coll. J.-J. Li, 1 Jun. 2015; 1 ♂ (11.3 × 9.2 mm), 1 ♀ (9.9 × 8.1 mm) (NCHUZOOL 15621), coll. J.-J. Li, 5 Aug. 2015; 1 ♂ (11.7 × 9.7 mm) (NCHUZOOL 15619), coll. J.-J. Li, 15 Aug. 2015; 1 ♂ (11.0 × 9.0 mm) (NCHUZOOL 15620), coll. J.-J. Li, 24 Sep. 2015; 2 ♂♂ (10.7 × 8.9 mm, 11.4 × 9.5 mm) (NCHUZOOL 15617), coll. J.-J. Li, 7 Jul. 2016; 2 ♂♂ (10.1 × 6.2 mm, 10.8 × 6.2 mm) (NCHUZOOL 15612), coll. J.-J. Li, 2 Dec. 2016; 1 ♀ (11.5 × 9.4 mm) (NCHUZOOL 15613), coll. J.-J. Li, 17 Jul. 2017; 1 ♂ (11.0 × 9.1 mm) (NCHUZOOL 15614), coll. J.-J. Li, 11 Aug. 2017. Philippines: 1 ovig. ♀ (11.6 × 9.7 mm) (NCHUZOOL 15622), Kawasan, Cebu, coll. J.-J. Li, 6 Sep. 2018.

Comparative material: *Parasesarma ungulatum* (H. Milne Edwards, 1853): 2 ♂♂ (14.3 × 11.0 mm, 19.6 × 15.6 mm) (ZRC 1999.0566), Chonburi, eastern Thailand, coll. P. K. L. Ng, 29 Sep. 1998. *Parasesarma obliquefrons* (Rathbun, 1924): holotype ♂ (12.8 × 11.3 mm) (USNM 45913a), in fresh water, Pago Pago, Samoa, coll. 28 Jul. 1902; 4 ♂♂, 9 ♀♀ (5 ovig.) (USNM 45913b), same data as holotype.

Diagnosis: Carapace (Figs. 1A, 2A, 3A, 4A) almost squarish in dorsal view, 1.2 times broader than long; front (Fig. 3B) with margin straight in dorsal view; external orbital tooth triangular, directed obliquely outwards, representing point of greatest width of carapace; lateral margins straight, slightly converging posteriorly, without trace of tooth or indentation behind external orbital tooth. Male chela (Figs. 3C, D, 4B–D) with 2 transverse pectinate crests on upper surface; distal crest composed of 14–19 high corneous teeth; second crest well developed, shorter than proximal crest, with 8 or 9 corneous teeth; dactylus with 12–15 asymmetrical tubercles on upper surface, proximal 4 to 5 tubercles large, remaining tubercles smaller, distal tubercle almost indiscernible. Ambulatory legs (Figs. 1A, 2A, 3A) slender; P3 and P4 about 1.5 times carapace width; merus of P3 2.1 times as long as broad; upper margin with acute subdistal spine; propodus of P3 2.4 times as long as broad; dactylus of P3 0.8 times length of propodus. Male pleon (Figs. 1B, 11A) relatively broad, telson semicircular, somite 6 almost twice as long as wide, lateral margins slightly convex. G1 (Figs. 3E, F, 4E) straight, relatively stout; apical process very short, corneous part short, ending in truncated tip; setae long, simple, originating at base of apical process. Vulva (Figs. 3G, 4F) near anterior edge of sternite 5, with central operculum, oval shaped.

Description of holotype male: Carapace (Fig. 3A) almost squarish in dorsal view, 1.2 times broader than long; regions well defined, separated by shallow grooves; upper surface laterally with oblique striae,

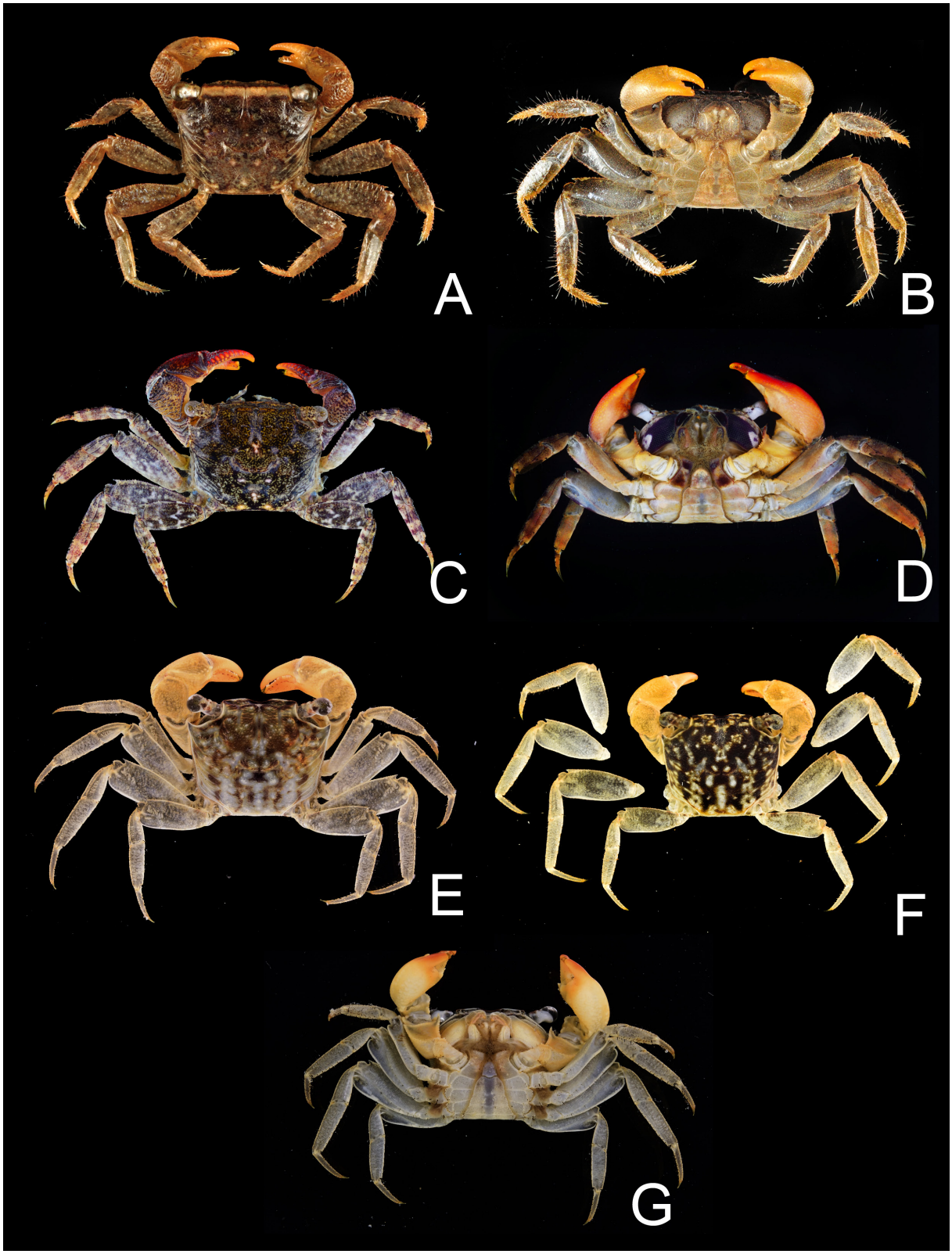

Fig. 1. Colour in life of three new species of *Parasesarma* from southern Taiwan. (A, B) *P. aurifrons* n. sp., paratype male (12.4 × 10.2 mm, NCHUZOOL 15610); (C, D) *P. sanguimanus* n. sp., paratype male (17.6 × 15.1 mm, NCHUZOOL 15626); (E, G) *P. gemmatum* n. sp., holotype male (15.7 × 13.1 mm, NCHUZOOL 15639); (F) *P. gemmatum* n. sp., paratype female (14.8 × 12.4 mm, NCHUZOOL 15532). A, C, E, F, dorsal views; B, D, G, ventral views.

otherwise smooth; postfrontal region well delimited, separated into 4 lobes by shallow but distinct grooves; median lobes almost as wide as lateral lobes; front (Figs. 3B, 4A) deflexed downwards, margin straight in dorsal view; supraorbital margin gently convex; external orbital tooth triangular, directed obliquely outwards, representing point of greatest width of carapace; lateral margins straight, slightly converging posteriorly, without trace of tooth or indentation behind external orbital tooth. Cornea (Fig. 3A) reaching tip of external orbital tooth. Basal articles of antennae and antennules adjacent, not separated by septum; basal antennular article swollen; antennal flagellum relatively long, entering orbit. Third maxilliped with ischium bearing shallow median sulcus; merus with distinct submedian ridge; exopod slender, tip reaching half-length of outer margin of merus, flagellum long.

Male chelipeds (Figs. 3C, D, 4B–D) relatively

Fig. 2. Colour in life of three new species of *Parasesarma* from southern Taiwan in the field. (A–D) *P. aurifrons* n. sp. (specimens not collected); (E) *P. sanguimanus* n. sp. (specimen not collected); (F) *P. gemmatum* n. sp. (paratype male, 14.8 × 12.4 mm, NCHUZOOL 15532). A, B, E, on riverbed from Gangkou R. estuary; C, D, climbing on vegetations (Gangkou R. estuary, Pingtung, Taiwan); F, climbing on an eroded coral reef under a coastal forest (east coast to Tanzih Fishing Port, Pingtung, Taiwan).

large, robust. Merus with carinate outer margin, without subdistal spine; inner margin with small granules ending in large subdistal protuberance; outer surface with dorsal striation, ventrally tuberculate. Carpus with inner angle not produced. Palm with 2 transverse pectinate crests on upper surface; distal crest composed of 15 (right chela) and 14 (left chela) high corneous teeth; distal crest well developed, shorter than proximal crest, with 10 (right chela) and 8 (left chela) corneous teeth; crests followed by several tubercles; rows of small tubercles below second crest; outer and inner surfaces of palm with numerous granules. Fingers each with chitinous tip, with distinct proximal hiatus; cutting edges each with row of rounded teeth; fixed finger smooth on outer surface; dactylus with 12 asymmetrical tubercles (both chelae) on upper surface, tubercles short, gradually sloping distally; proximal 4 tubercles large, distal 8 tubercles smaller, last tubercle almost indiscernible.

Ambulatory legs (Fig. 3A) slender, laterally flattened; P3 and P4 subequal, longer than others, about 1.5 times carapace width. Merus of P3 2.1 times as long as broad; upper margin with acute subdistal spine.

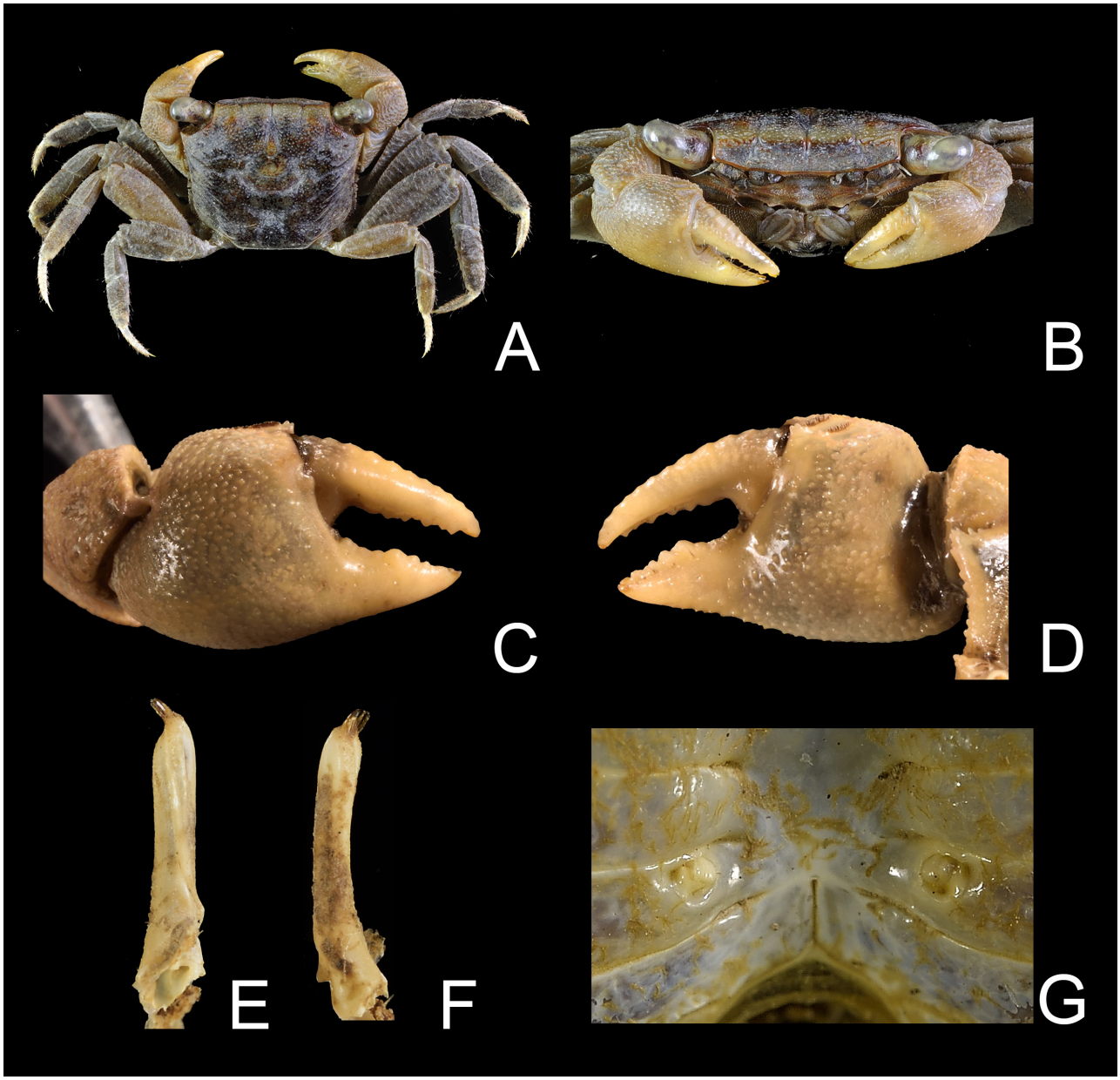

Fig. 3. *Parasesarma aurifrons* n. sp., southern Taiwan. (A–D) holotype male (10.4 × 8.5 mm, NCHUZOOL 15602); (E–F) paratype male (14.2 × 10.9 mm, ZRC 2019.1075); (G) paratype female (13.8 × 11.2 mm, NCHUZOOL 15609). A, dorsal view; B, frontal view; C, D, right chela; E, F, left G1; G, vulvae. C, outer view; D, inner view; E, ventral (pleonal) view; F, dorsal (sternal) view.

Meri of P2–P5 each with transverse striae on upper surface. Carpi of P2–P5 each with 2 accessory carinae on outer surface. Propodus of P3 2.4 times as long as broad, with striae on inferior proximal portion of outer surface, dorsal and ventral margins with short stiff setae. Dactylus of P3 0.8 times length of propodus, slightly curved distally, terminating in acute calcareous tip; dorsal and ventral margins with short stiff setae.

Thoracic sternites 1–3 completely fused. Male pleon (Fig. 11A) relatively broad, all somites free. Telson semicircular, evenly rounded, as long as preceding somite. Somite 6 almost twice as long as wide, lateral margins slightly convex. Somites 3–5 more trapezoidal, lateral margins of somites 4 and 5 straight, lateral margins of somite 3 strongly convex. Somites 1 and 2 very narrow longitudinally. G1 (Fig. 4E) straight, relatively stout; apical process short, corneous part short, ending in truncate tip; setae long, simple, originating at base of apical process. G2 shorter than quarter length of G1.

Female characters: Chelipeds relatively small, pectinate crest on palms indistinct, dactylar tubercles low; pleon wide, rounded, telson semicircular, base half embedded in distal margin of somite 6; vulva (Figs.

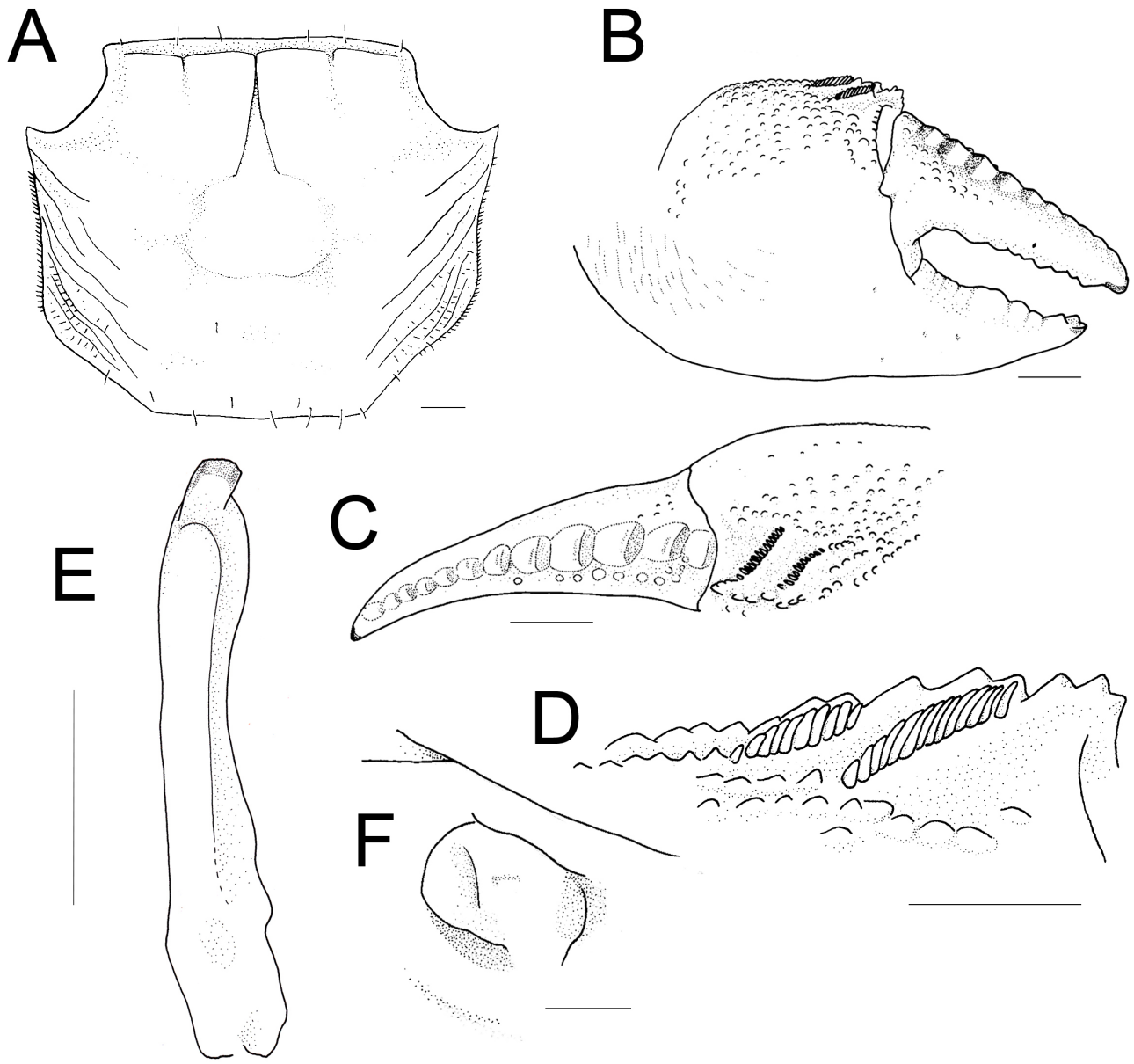

Fig. 4. *Parasesarma aurifrons* n. sp., southern Taiwan. (A–E) holotype male (10.4 × 8.5 mm, NCHUZOOL 15602); (F) paratype female (13.8 × 11.2 mm, NCHUZOOL 15609). A, carapace dorsal view; B–D, right chela; E, left G1 dorsal (sternal) view; F, left vulva. B, outer view; C, dorsal view of palm and dactylar finger; D, lateral view of pectinated cristae on palm. Scale bars: A–C, E, F = 1.0 mm; D = 0.5 mm.

3G, 4F) near anterior edge of sternite 5, with central operculum, oval shaped.

Variation: The number of teeth on the two transverse pectinate crests of the palms are variable with 14–19 (distal part) and 8 or 9 (proximal part). Some male specimens with some teeth on the two transverse pectinate crests are weak, probably due to damage or abrasion, but they can be observed by the residual trace. The number of tubercles on the upper surface of chelipedal dactyli is 12–15. The vulvae are near or close to anterior edge of sternite 5, and the central operculum is relatively raised in larger specimens (CW > 11.0 mm).

Colour in life: Carapace dark brown with a transverse golden-yellow band on frontal region, cheliped and ambulatory legs light brown, palm yellow to orange (Figs. 1A, B, 2A–D). The carapace of some female specimens is yellow, which makes the transverse golden-yellow band on the frontal region less obvious.

Distribution: So far known from Taiwan (estuaries of Baoli R. and Gangkou R.) and the Philippines (Kawasan, Cebu).

Etymology: The name "*aurifrons*" refers to the frontal band which is golden yellow in life. The name is used as a noun in apposition.

Ecological notes: In the Gangkou R. estuary, southern Taiwan, *P. aurifrons* is partly sympatric with *P. kuekenthali* (De Man, 1902), *Sesarmops intermedius* (De Haan, 1835) and *Neosarmatium indicum* (A. Milne-Edwards, 1868). Ovigerous females were found from June to September, suggesting that summer is the main reproductive season. We found that individuals will climb to the adjacent vegetation during high tide (Fig. 2C, D) and stay on the mudflat or in burrows during low tide. This behaviour is similar to the niche shifting behaviour reported in the Indian *P. plicatum* (Latreille, 1806) to escape from potential aquatic predators (Shanij et al. 2016). Ng and Schubart (2017: 663) also noted that *Pseudosesarma crassimanum* (De Man, 1887) also sometimes climbs low shrubs, especially at night, although it usually forages on the ground.

Remarks: Li and Chiu (2013: 81) depicted several ovigerous females of "*Parasesarma* aff. *ungulatum*" from Hengchun Peninsula, Pingtung, southern Taiwan, with a yellow band on its front. While their material superficially resembles *P. ungulatum* (H. Milne Edwards, 1853) from Sulawesi and Papua, Indonesia and eastern Thailand (Rahayu and Ng 2010: fig. 8), Li and Chiu (2013) noted that the general carapace and ambulatory leg features appeared somewhat different. Direct comparisons of both now show that they are different species.

The most important characters to distinguish *P. aurifrons* and *P. ungulatum* are the mature adult size (max. CW 15.4 mm versus 21.4 mm), the ratio of CW/CL of carapace (1.2 versus 1.3), and the length of ambulatory legs (relative more elongated versus relative shorter) (cf. Rahayu and Ng 2010). In addition, the length of the G1 tip is also proportionately shorter in *P. aurifrons* (Figs. 3E, F, 4E) (longer in *P. ungulatum*; cf. Rahayu & Ng 2010: fig. 10A–D).

In the BI tree (Fig. 13; see below), *P. aurifrons* is close to *P. liho* Koller, Liu & Schubart, 2010, *P. paucitorum* Rahayu & Ng, 2009, and *P. obliquifrons* (Rathbun, 1924), despite its different appearance. *Parasesarma aurifrons* can easily be separated from *P. liho* by its life coloration, especially the golden frontal band (Figs. 1A, 2A, B) (versus absent in *P. liho*); relatively broader carapace (width to length ratio 1.2, Figs. 1A, 4A) (versus 1.1 in *P. liho*), the dorsal surface is glabrous without distinct setae (Figs. 1A, 4A) (versus surface rougher with distinct setae in *P. liho*), and the ambulatory propodi are proportionately shorter (Figs. 1A–B, 2A) (versus distinctly longer in *P. liho*) (cf. Koller et al. 2010; Shih et al. 2019). The latter species, however, has a different colour in life (it lacks the distinct golden frontal band) and the ambulatory propodus and merus are proportionately more elongate and slender (cf. Rahayu and Ng 2009: figs. 1A, 3A).

Parasesarma obliquifrons is a poorly known species described from Samoa, but it has never been figured and its affinities are uncertain. Rathbun (1924: 127) recorded one holotype male 12.8 × 11.3 mm (USNM 45913), but made no mention of any other material. The USNM contains one bottle labelled USNM 45913, but it contains a total of five male and nine female specimens. The largest male matches the measurements and description in Rathbun (1924: 127–128) and is clearly the holotype. The other specimens are not types, as they were not mentioned at the time of description. The holotype, including the important G1 structure, is figured here for the first time (Figs. 5, 6). *Parasesarma aurifrons* can be distinguished from *P. obliquefrons* in having the frontal margin straighter and the median cleft hallow to almost not visible in dorsal view (Figs. 3A, 4A) (versus frontal margin distinctly sinuous with the median cleft pronounced in *P. obliquefrons*; Fig. 5A); the dorsal surface of the cheliped dactylus has 12 smaller tubercles (Figs. 3C, D, 4C) (versus dactylus with only 5 or 6 low, broad, simple tubercles in *P. obliquefrons*; Fig. 5E, F); the male pleon is relatively wider (Figs. 1B, 11A) (versus relatively narrower in *P. obliquefrons*; Fig. 5C); and most significantly, the G1 is proportionately more slender and the corneous distal part is directed more obliquely laterally (Figs. 3E, F, 4E) (versus G1 proportionately stouter with the corneous distal part directed more vertically in *P. obliquefrons*; Fig. 6A–D).

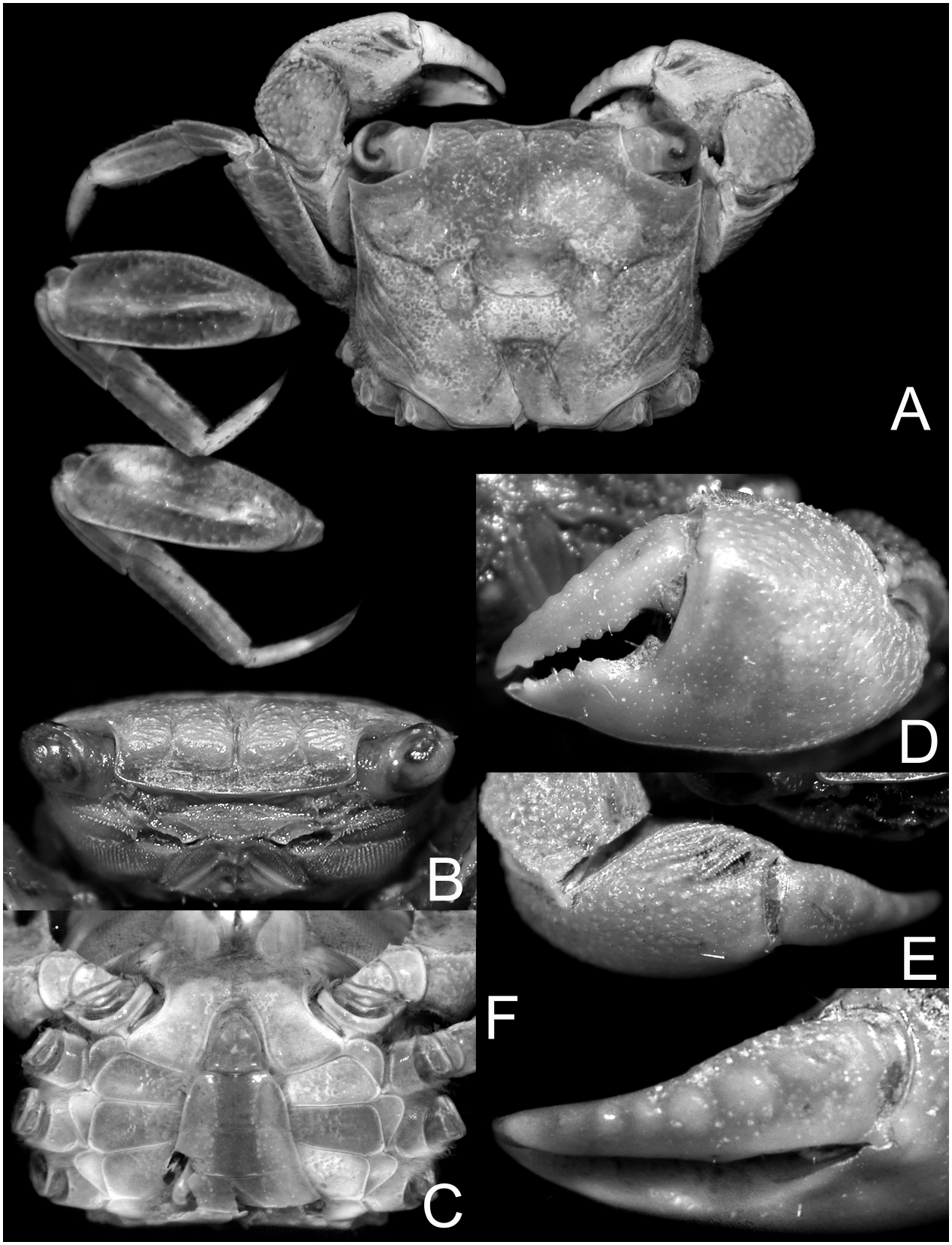

Fig. 5. *Parasesarma obliquefrons* (Rathbun, 1924), holotype male (12.8 × 11.3 mm) (USNM 45913a), Samoa. (A) dorsal view; (B) frontal view; (C) ventral view; (D) left chela; (E) dorsal view of right chela; (F) dorsal view of left dactylar finger.

***Parasesarma sanguimanus* n. sp.**

(Figs. 1C, D, 2E, 7A, B, E, F, I, J, K, 8A–D, 11B)

urn:lsid:zoobank.org:act:552ACCAF-91F2-4519-9E01-0DBA589F2F4D

Material examined: Holotype: 1 ♂ (15.2 × 13.0 mm) (NCHUZOOL 15623), Gangkou R. estuary (21°59'16.1"N 120°50'29.7"E), Hengchun, Pingtung, Taiwan, coll. J.-J. Li, 8 Jul. 2017. Paratypes: Taiwan: Gangkou R. estuary, Hengchun, Pingtung: 1 ♂ (12.3 × 10.0 mm) (NCHUZOOL 15632), coll. J.-J. Li, 10 Apr. 2014; 3 ♂♂ (14.1–14.6 × 12.0–12.1 mm) (NCHUZOOL 15625), coll. J.-J. Li, 10 Apr. 2015; 3 ♂♂ (12.1–14.6 × 9.9–11.7 mm) (NCHUZOOL 15629), coll. J.-J. Li, 11 Apr. 2015; 1 ♂ (15.5 × 13.0 mm) (NCHUZOOL 15630), coll. J.-J. Li, 18 May 2015; 1 ♂ (17.5 × 14.2 mm) (NCHUZOOL 15525), coll. J.-J. Li, 15 Jun. 2015; 1 ♂ (19.0 × 15.6 mm) (NCHUZOOL 15628), coll. J.-J. Li, 7 Jul. 2015; 1 ♂ (18.5 × 15.9 mm) (NCHUZOOL 15624), 1 ♂ (17.6 × 15.1 mm) (NCHUZOOL 15626), coll. J.-J. Li, 8 May 2016; 1 ♂ (18.4 × 15.0 mm) (ZRC 2019.1080), coll. J.-J. Li, 14 May 2016.1 ♀ (12.0 × 9.8 mm) (NCHUZOOL 15631), coll. J.-J. Li, 21 Mar. 2016; 3 ♂♂ (5.9–7.4 × 2.9–4.7 mm), 1 female (4.3 × 1.9 mm) (ZRC 2019.0821), coll. J.-J. Li, 18 Jun. 2016; 1 ♂ (13.8 × 11.6 mm) (NCHUZOOL 15627), coll. J.-J. Li, 17 Jul. 2017; 1 ♂ (16.7 × 13.9 mm) (ZRC 2019.0820), coll. J.-J. Li, 7 Jul. 2018; 1 ♂ (13.2 × 10.9 mm) (NCHUZOOL 15714), coll. J.-J. Li, 28 Aug. 2018. Baoli R. estuary (22°03'30.5"N 120°42'29.8"E), Hengchun, Pingtung: 1 ♂ (19.0 × 15.3 mm) (NCHUZOOL 15633), coll. J.-J. Li, 24 Jul. 2014.

Comparative material: *Parasesarma bidens* (De Haan, 1835): 2 ♂♂ (18.1 × 14.9 mm, 29.4 × 24.9 mm) (NCHUZOOL 15634), Okinawa, Japan, coll. J.-J. Li, 18 Jul. 2016; 5 ♂♂ (28.9–31.6 × 23.0–25.6 mm) (NCHUZOOL 15635), Kyushu, Japan, coll. T. Naruse et al., 3 Oct. 2017; 5 ♂♂ (15.7–25.5 × 12.6–21.7 mm) (NCHUZOOL 15636), Sicao, Tainan, Taiwan, coll. J.-J. Li, 4 Oct. 2015; 2 ♂♂ (16.5 × 13.6 mm, 18.5 × 15.8 mm) (NCHUZOOL 15637), Baoli R. estuary, Taiwan, coll. J.-J. Li, 19 Mar. 2016; 2 ♂♂ (16.7 ×

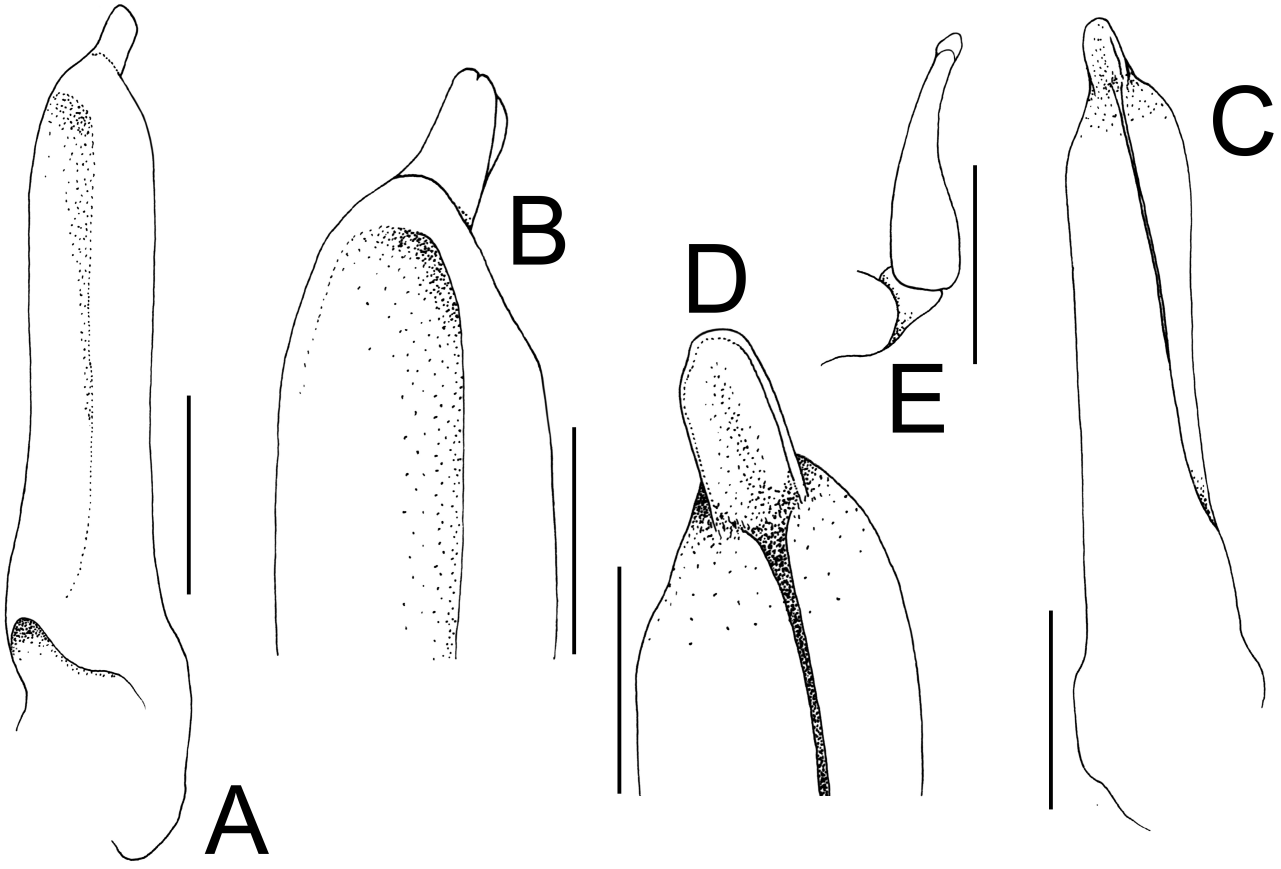

Fig. 6. *Parasesarma obliquefrons* (Rathbun, 1924), holotype male (12.8 × 11.3 mm) (USNM 45913a), Samoa. (A) left G1 (dorsal view); (B) distal part of left G1 (dorsal view); (C) left G1 (ventral view); (D) distal part of left G1 (ventral view); (E) left G2. Scale bars: A, C, E = 1.0 mm; B, D = 0.5 mm.

13.4, 18.8 × 15.3 mm) (ZRC 2002.0561), Xiamen, Fujian, China, coll. P. K. L. Ng, 22 Sep. 2002; 10 ♂♂ (13.6–17.3 × 14.2–11.6 mm), 1 ♀ (14.7 × 11.9 mm) (NCHUZOOL 15638), Kinmen, Taiwan, coll. J.-J. Li, 2 Jul. 2017. *Parasesarma cricotus* (Rahayu & Davie, 2002): 2 ♂♂ (18.7 × 4.9 mm, 19.2 × 15.0 mm), 2 ♀♀ (12.8 × 10.3, 16.9 × 3.5 mm) (MZB), Tipocka River, Papua, Indonesia, coll. D. L. Rahayu, 14 Mar. 2017. *Parasesarma foresti* (Rahayu & Davie, 2001): 1 ♂ (23.3 × 19.4 mm) (ZRC 2002.0608), Tipocka, Portsite, Papua, Indonesia, coll. Gesang, 13 Aug. 2002. *Parasesarma indiarum* (Tweedie, 1940): 1 ♂ (24.1 × 20.7 mm) (ZRC 2013.1613), Pasir Ris Park mangroves, Singapore, coll. B. Y. Lee, 28 Oct. 2011; 1 ♀ (24.9 × 19.8 mm) (ZRC 2000.1982), Mandai mangroves, Singapore, coll. C. D. Schubart and N. Sivasothi, 25 Jul. 2000. *Parasesarma semperi* (Bürger, 1893): 2 ♂♂ (20.8 × 17.8 mm, 23.5 × 19.5 mm) (ZRC 2015.0464), Sungcolan inlet, fringe mangroves, Panglao, Bohol, Philippines, coll. Panglao 2004 Expedition, 4 Jul. 2004. *Parasesarma* nr. *lividum* (A. Milne-Edwards, 1869): 1 ♂ (23.5 × 19.6 mm) (RUMF-ZC-3779), Miyara R., Ishigaki Island, Ryukyu Islands, Japan, coll. T. Maenosono, 26 Mar. 2016.

Diagnosis: Carapace (Figs. 1C, 7A) squarish in dorsal view, 1.2 times broader than long; front with margin straight in dorsal view; external orbital tooth triangular, directed obliquely outwards, representing point of greatest width of carapace; lateral margins straight, slightly converging posteriorly, without trace of tooth or indentation behind external orbital tooth. Male chela (Figs. 7E, F, 8A, B) with 2 transverse pectinate crests on upper surface; distal crest composed of 13–19 high corneous teeth; second crest well developed, shorter than proximal crest, with 9–16 corneous teeth; dactylus with 10–12 asymmetrical tubercles on upper surface, proximal tubercle smallest but distinct. Ambulatory legs (Figs. 1C, 7A) slender; P3 and P4 about 1.6 times carapace width; merus of P3 2.3 times as long as broad; upper margin with acute subdistal spine; propodus of P3 3.1 times as long as broad; dactylus of P3 1.3 times length of propodus. Male pleon (Figs. 1D, 11B) relatively broad, telson semicircular, somite 6 almost twice as long as wide, lateral margins slightly convex. G1 (Figs. 7I, J, 8C) straight, relatively stout; apical process very short, corneous part short, ending in truncate tip; setae long, simple, originating at base of apical process. Vulva (Figs. 7K, 8D) near anterior edge of sternite 5, with central operculum, oval shaped, protruded.

Description of holotype male: Carapace (Fig. 7A) almost squarish in dorsal view, 1.2 times broader than long; regions well defined, separated by shallow grooves; upper surface laterally with oblique striae, otherwise smooth; postfrontal region well delimited, separated into 4 lobes by shallow but distinct grooves; median lobes almost as wide as lateral lobes; front (Fig. 7B) deflexed downwards, margin straight in dorsal view; supraorbital margin gently convex; external orbital tooth triangular, directed obliquely outwards, representing point of greatest width of carapace; lateral margins straight, slightly converging posteriorly, without trace of tooth or indentation behind external orbital tooth. Cornea exceeding tip of external orbital tooth (Fig. 7A). Basal articles of antennae and antennules adjacent, not separated by septum; basal antennular article swollen; antennal flagellum relatively long, entering orbit. Third maxilliped with ischium bearing shallow median sulcus; merus with distinct submedian ridge; exopod slender, tip reaching half-length of outer margin of merus, flagellum long.

Male chelipeds (Figs. 7E, F, 8A, B) relatively large, robust. Merus with carinate outer margin, without subdistal spine; inner margin with small granules ending in large subdistal protuberance; outer surface with dorsal striation, ventrally granulate. Carpus with inner angle not produced. Palm with 2 transverse pectinate crests on upper surface; distal crest composed of 17 (right chela) and 14 (left chela) high corneous teeth; second crest well developed, shorter than proximal crest, with 13 (right chela) and 10 (left chela) corneous teeth; crests followed by several tubercles; rows of small tubercles below second crest; outer and inner surfaces of palm with numerous granules. Fingers each with chitinous tip, with distinct proximal hiatus; cutting edges each with row of rounded teeth; fixed finger smooth on outer surface; dactylus with 12 asymmetrical tubercles (both chelae) on upper surface, proximal tubercle smallest but distinct.

Ambulatory legs (Fig. 7A) slender, laterally flattened; P3 and P4 subequal, longer than others, about 1.6 times carapace width. Merus of P3 2.3 times as long as broad; upper margin with acute subdistal spine. Meri of P2–P5 with transverse striae on upper surface. Carpus of P2–P5 with 2 accessory carinae on outer surface. Propodus of P3 3.1 times as long as broad, with striae on inferior proximal portion of outer surface, dorsal and ventral margins with short stiff setae. Dactylus of P3 1.3 times length of propodus, slightly curved distally, terminating in acute calcareous tip; dorsal and ventral margins with short stiff setae.

Thoracic sternites 1–3 completely fused. Male pleon relatively broad, all somites free. Telson semicircular, evenly rounded, as long as preceding somite. Somite 6 almost twice as long as wide, lateral margins slightly convex. Somites 3–5 more trapezoidal, lateral margins of somites 4 and 5 straight, lateral margins of somite 3 strongly convex. Somites 1 and 2 very narrow longitudinally. G1 straight, relatively stout

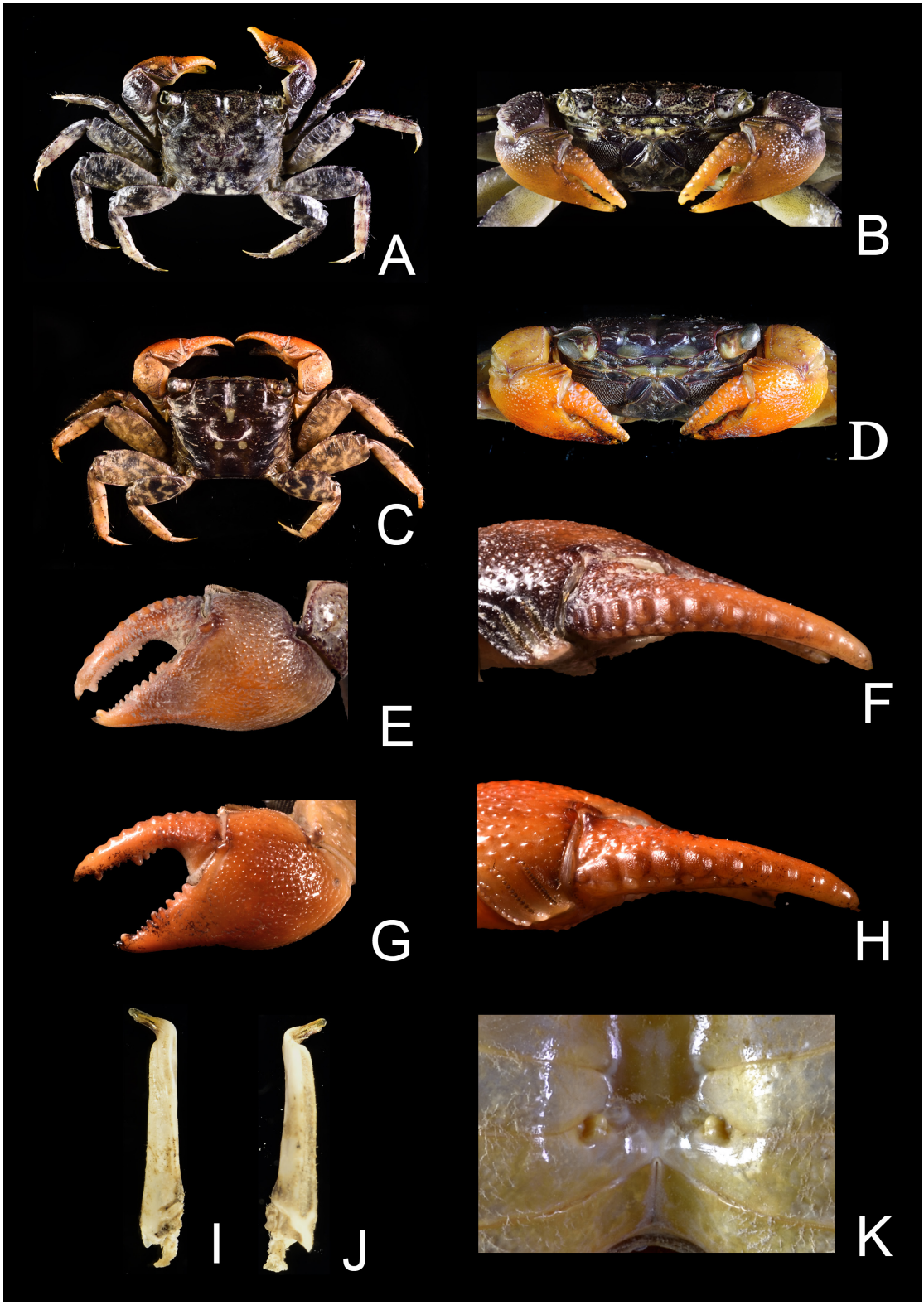

Fig. 7. (A, B, E, F) *Parasesarma sanguimanus* n. sp., holotype male (15.2 × 13.0 mm, NCHUZOOL 15623), southern Taiwan; (I, J) *P. sanguimanus* n. sp., paratype male (18.4 × 15.0 mm, ZRC 2019.1080), southern Taiwan; (K) *P. sanguimanus* n. sp., paratype female (13.8 × 11.6 mm, NCHUZOOL 15627), southern Taiwan; (C, D, G, H) *P. cricotus* (Rahayu and Davie, 2002) (male, 19.2 × 15.0 mm, MZB), Papua, Indonesia. A, C, dorsal views; B, D, frontal views; E, F, left chela; G, H, right chela; I, J, left G1; K, vulvae. E, G, outer views; E, F, dorsal (sternal) views; I, ventral (pleonal) view; J, dorsal (sternal) view.

(Fig. 8C); apical process very short, corneous part short, ending in truncated tip; setae long, simple, originating at base of apical process. G2 shorter than quarter length of G1.

Female characters: Chelipeds relatively small, pectinate crest on palms indistinct, dactylar tubercles low; pleon wide, rounded, telson semicircular, base half embedded in somite 6; vulva (Figs. 7K, 8D) near anterior edge of sternite 5, with central operculum, oval shaped, protruded.

Variation: The number of teeth on the two transverse pectinate crests of the palms are variable with 13–19 (distal part) and 9–16 (proximal part). Some male specimens with some teeth on the two transverse pectinate crests are weak, probably due to damage or abrasion, but they can be observed by the residual trace. The number of tubercles on the upper surface of chelipedal dactyli varies 10– 12.

Colour in life: Carapace and cheliped dark gray (palm exception). Cheliped palm outer surface deep red, inner surface yellowish orange (Figs. 1C, D, 2E).

Distribution: So far known from the estuaries of Baoli R. and Gangkou R. in Hengchun, Pingtung, southern Taiwan.

Etymology: The name is derived from the Latin "*sanguineus*" for blood-red, and "*manus*" (for hand); alluding to the deep-red palm of the species in life. The name is used as a noun.

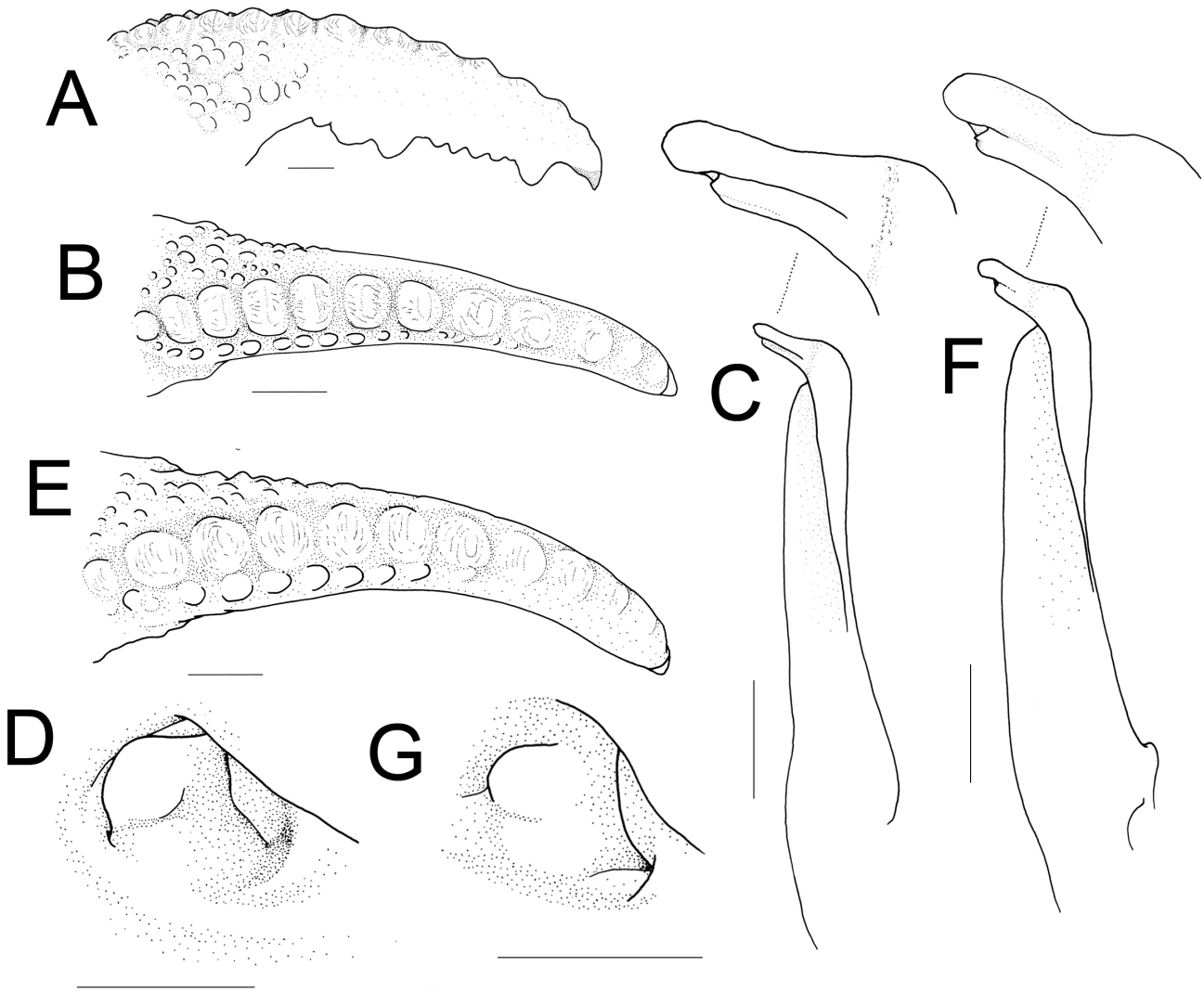

Fig. 8. (A–C) *Parasesarma sanguimanus* n. sp., holotype male (15.2 × 13.0 mm, NCHUZOOL 15623), southern Taiwan; (D) *P. sanguimanus* n. sp., paratype female (12.0 × 9.8 mm, NCHUZOOL 15631), southern Taiwan; (E, F) *P. cricotus* (Rahayu & Davie, 2002), male (19.2 × 15.0 mm, MZB), Papua, Indonesia; (G) *P. cricotus* (Rahayu & Davie, 2002), female (16.9 × 3.5 mm, MZB), Papua, Indonesia. A, B, E, left dactylar finger; C, F, left G1s ventral (pleonal) views; D, G, left vulvae. A, outer view; B, E, dorsal views. Scale bars = 1.0 mm.

Ecological notes: The habitat and behaviour of *P. sanguimanus* are generally similar to those of *P. aurifrons* n. sp. except that most specimens were collected closer to the water's edge.

Remarks: Among the Taiwanese *Parasesarma* species (Ng et al. 2001 2017), the only other species with two anterolateral teeth on the carapace is *P. bidens* (De Haan, 1835). *Parasesarma sanguimanus* n. sp. is found sympatrically with *P. bidens* and their morphology is superficially similar, but can be distinguished by the deep-red outer surface of the palm in life (Fig. 2E) (versus yellow to orange in *P. bidens*) and the ringed grooves on the upper surface of the dactylar tubercles (Figs. 7F, 8B) (versus without grooves in *P. bidens*) (cf. Li and Chiu 2013: 54).

Among the Indo-West Pacific *Parasesarma*, *P. foresti* (Rahayu & Davie, 2002), *P. indiarum* (Tweedie, 1940), *P. holthuisi* (Davie, 2010), *P. guttatum* (A. Milne-Edwards, 1869), *P. brevicristatum* (Campbell, 1967) and *P. dussumieri* (A. Milne-Edwards, 1853) have a similar number of male dactylar tubercles (11–13) to *P. sanguimanus*, but none of them have ringed grooves on the tubercles (cf. Davie 2010; Rahayu and Davie 2002). Species which have similar grooves on the dactylar tubercles however, have distinctly fewer tubercles: *P. semperi* (Bürger, 1893) has 7 or 8 dactylar tubercles (cf. Bürger 1893; Davie 2010; Shahdadi et al. 2018); and male *P. maipoense* (Soh, 1978) has 5–8 dactylar tubercles (cf. Soh 1978; Ng et al. 2010).

According to the BI tree (Fig. 13; see below), *P. sanguimanus* is sister to *P. cricotus* (Rahayu & Davie, 2002). Their morphologies are superficially similar, both possessing 11 or 12 dactylar ringed tubercles in males and with a similar colour in life (Rahayu and Davie 2002). *Parasesarma sanguimanus*, however, can be distinguished by its more rounded dactylar tubercles (especially the second to fifth tubercles) (Fig. 8B) (versus relatively ovate in *P. cricotus*; Fig. 8E); a proportionately wider G1 tip (Figs. 7I, J, 8C) (versus more narrow in *P. cricotus*; Fig. 8F); and the relatively smaller and lower female operculum of the vulva (Figs. 7K, 8D) (larger in *P. cricotus*; Fig. 8G). Both species can be separated in the field by the coloration of carapace; *P. cricotus* has clear light spots on the gastric region and frontal region (Rahayu and Setyadi 2009: 53; also see Fig. 7C), but these are absent in *P. sanguimanus* (Fig. 1C).

***Parasesarma gemmatum* n. sp.**

(Figs. 1E–G, 2F, 9, 10, 11C)
urn:lsid:zoobank.org:act:A8F0E575-86C0-41AB-A7BB-4B9F0002926A

Material examined: Holotype: ♂ (15.7 × 13.1 mm) (NCHUZOOL 15639), Dingtanzih, Hengchun, Pingtung, Taiwan, coll. J.-J. Li, 13 Jun. 2019. Paratypes: Taiwan: Hengchun, Pingtung: 1 ♂ (14.8 × 12.4 mm) (NCHUZOOL 15532), Dingtanzih, coll. J.-J. Li, 21 Aug. 2018; 1 ♂ (12.8 × 10.5 mm), 1 ovig. ♀ (11.7 × 9.8 mm) (ZRC 2019.1076), Tanzih Fishing Port, coll. J.-J. Li, 3 Jun. 2019; 1 ovig. ♀ (14.2 × 11.7 mm) (NCHUZOOL 15640), Tanzih Fishing Port, coll. J.-J. Li, 24 Sep. 2018; 1 ♀ (14.4 × 10.4 mm) (NCHUZOOL 15531), Siatanzih, coll. J.-H. Lee, 31 Aug. 2012; 2 ♀♀ (8.7 × 7.1 mm, 11.6 × 9.1 mm), 1 ovig. ♀ (12.8 × 10.4 mm) (NCHUZOOL 15641), Tanzih Fishing Port, coll. J.-J. Li, 27 May 2019; 1 ♂ (15.0 × 12.4 mm) (NCHUZOOL 15707), Tanzih Fishing Port, J.-J. Li, 28 Jun. 2019; 1 ♂ (14.7 × 11.9 mm) (NCHUZOOL 15708), east coast to Tanzih Fishing Port, J.-J. Li., 4 Jul. 2019.

Comparative material: *Parasesarma anambas* Yeo, Rahayu & Ng, 2004: paratype: 1 ♂ (8.1 × 7.1 mm), 1 ♀ (4.2 × 3.4 mm) (ZRC 2003.0726), Teluk Baruk, Anambas, eastern Pulau Siantan, 15 Mar. 2002; 1 ♂ (10.1 × 8.0 mm) (NCHUZOOL 15514), Sanya, Hainan, China, coll. H.-T. Shih, 28 Jun. 2004.

Diagnosis: Carapace (Figs. 1E, F, 9A, C, 10A) almost squarish in dorsal view, 1.2 times broader than long; front with margin gently concave in dorsal view; external orbital tooth sharp triangular, directed obliquely outwards, representing point of greatest width of carapace; lateral margins straight, slightly converging posteriorly, without trace of tooth or indentation behind external orbital tooth. Male chela (Figs. 1E, G, 9A, E, F, 10B, C) with 3–5 transverse granules row on upper surface, not pecinated, not corneous; outer and inner surfaces of palm with numerous granules; dactylus upper surface with 14–22 asymmetrical tubercles, starting at proximal or subproximal part of finger. Ambulatory legs (Figs. 1E–G, 9A–C) slender, P3 and P4 about 1.6 times carapace width; merus of P3 2.8 times as long as broad; upper margin with acute subdistal spine; meri of P2–P5 each with transverse striae on upper surface; propodus of P3 3.3 times as long as broad; dactylus of P3 1.2 times length of propodus. Male pleon (Figs. 1G, 10G, H, 11C) relatively broad; telson semicircular, base central edge embedded in distal margin of somite 6; somite 6 0.6 to 0.7 times as long as wide, lateral margins slightly convex. G1 (Figs. 9G, H, 10D, E) straight, relatively stout; apical process short, corneous part wide, ending in truncated tip; setae long, simple, originating at base of apical process. Vulva (Figs. 9I, 10F) near anterior edge of sternite 5, with central operculum, cone-shaped.

Description of holotype male: Carapace (Fig. 1E) almost squarish in dorsal view, 1.2 times broader than long; regions well defined, separated by shallow grooves; postfrontal region well delimited, separated

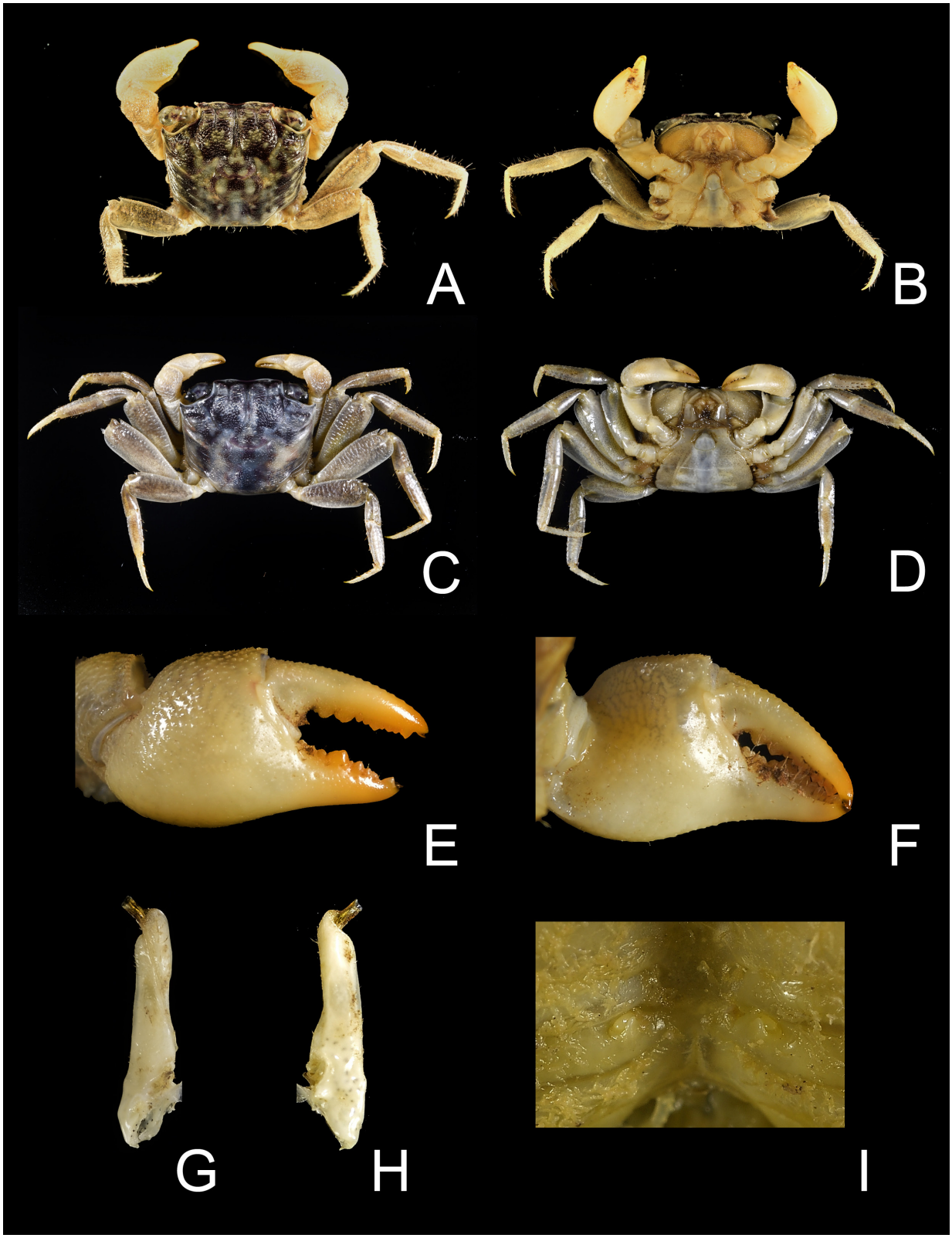

Fig. 9. *Parasesarma gemmatum* n. sp., southern Taiwan. (A, B, E, F) paratype male (14.8 × 12.4 mm, NCHUZOOL 15532); (C, D) paratype female (14.4 × 10.4 mm, NCHUZOOL 15531); (G, H,) paratype male (15.0 × 12.4 mm, NCHUZOOL 15707); (I) paratype female (12.8 × 10.4 mm, NCHUZOOL 15641). A, C, dorsal views; B, D, ventral views; E, F, right chelipeds; G, H, left G1; I, vulvae. E, outer view; F, inner view; G, ventral (pleonal) view; H, dorsal (sternal) view.

into 4 lobes by shallow but distinct grooves; median lobes slightly broader than lateral lobes; front deflexed downwards, margin gently concave in dorsal view; supraorbital margin slightly convex; external orbital tooth sharp triangular, directed obliquely outwards, representing point of greatest width; lateral margins straight, slightly converging posteriorly, without trace of tooth or indentation behind external orbital tooth. Cornea (Fig. 1E) exceeding tip of external orbital tooth. Basal articles of antennae and antennules adjacent, not separated by septum; basal antennular article swollen; antennal flagellum relatively long, entering orbit. Third maxilliped with ischium bearing shallow median sulcus; merus with distinct submedian ridge; exopod slender, tip reaching half-length of outer margin of merus, flagellum long.

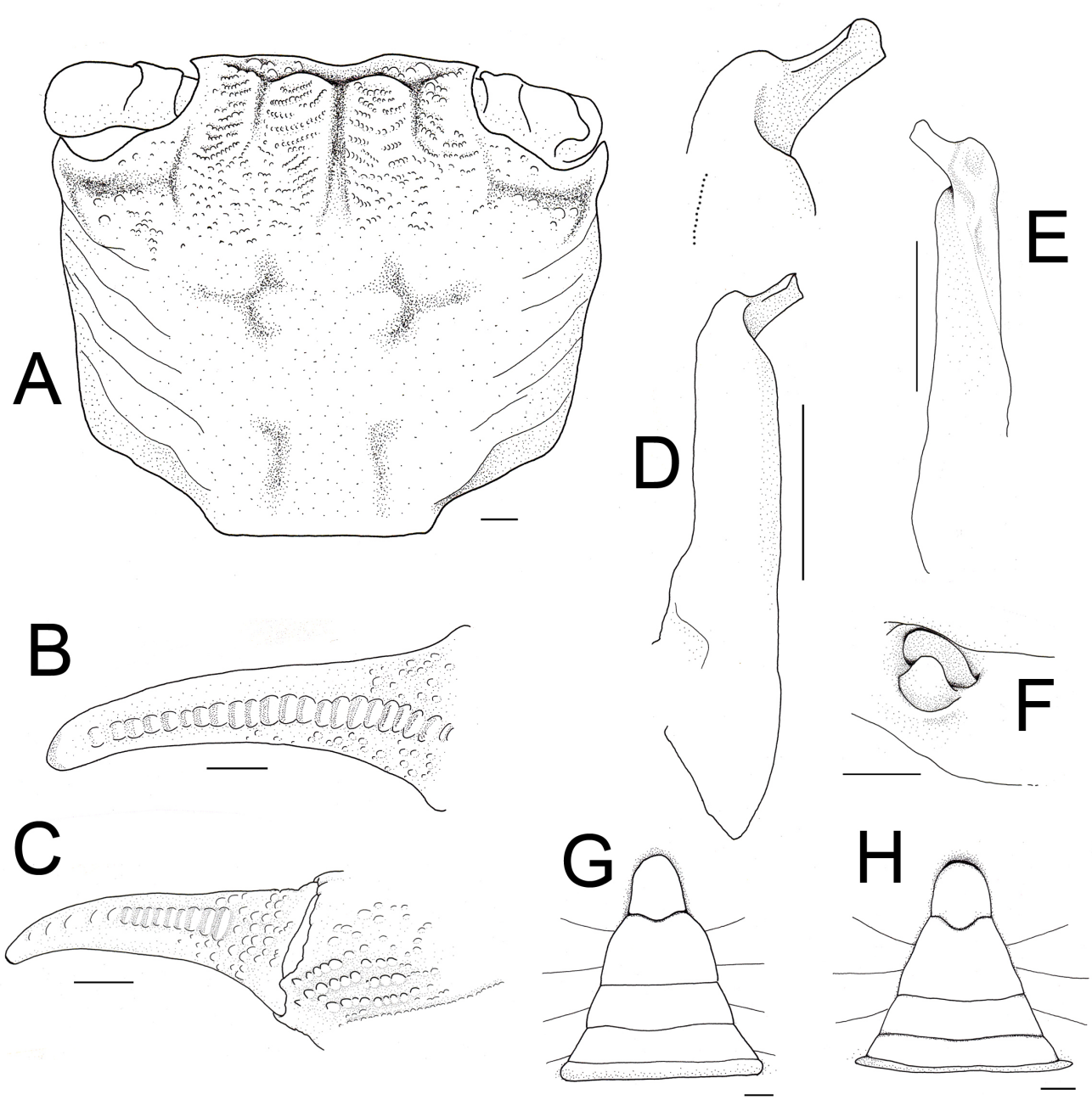

Fig. 10. *Parasesarma gemmatum* n. sp., southern Taiwan. (A, C–F, H) paratype male (14.8 × 12.4 mm) (NCHUZOOL 15532); (B, G) holotype male (15.7 × 13.1 mm) (NCHUZOOL 15639); (F) paratype female (14.2 × 11.7 mm, NCHUZOOL 15640). A, carapace; B, C, right dactylar finger; D, E, left G1; F, left vulvae; G, H, pleon. A–C, dorsal views; D, F, G, H, dorsal (sternal) view; E, ventral (pleonal) view. Scale bars: A–C, F–H = 1.0 mm; D, E = 0.5 mm.

Male chelipeds (Figs. 1E, 10B) relatively large, robust. Merus with carinate outer margin, without subdistal spine; inner margin with small granules ending in large subdistal protuberance; outer surface with dorsal striation, ventrally tuberculate. Carpus with inner angle not produced. Palm with 3 transverse non-pecinated granule rows on upper surface, not corneous; outer and inner surfaces of palm with numerous granules. Fingers each with chitinous tip, with distinct proximal hiatus; cutting edges each with row of rounded teeth; fixed finger smooth on outer surface; dactylus upper surface with 22 asymmetrical tubercles, proximal 9 tubercles oval shaped, each with dorsal keel; distal 5 tubercles rounded, smooth.

Ambulatory legs (Figs. 1E) slender, laterally flattened; P3 and P4 subequal, slightly longer than others, about 1.6 times carapace width. Merus of P3 2.8 times as long as broad; upper margin with acute subdistal spine. Meri of P2–P5 each with transverse striae on upper surface. Carpi of P2–P5 each with 2 accessory carinae on outer surface. Propodus of P3 3.3 times as long as broad, with striae on inferior proximal portion of outer surface, dorsal and ventral margins with short stiff setae. Dactylus of P3 1.2 times length of propodus, slightly curved distally, terminating in acute calcareous tip; dorsal and ventral margins with short stiff setae.

Thoracic sternites 1–3 (Fig. 1G) completely fused. Male pleon (Figs. 10G, 11C) relatively broad, all somites free. Telson semicircular, evenly rounded, as long as preceding somite, base central edge embedded in distal margin of somite 6. Somite 6 almost 0.6 times as long as wide, lateral margins slightly convex. Somites 3–5 more trapezoidal, lateral margins of somites 4 and 5 straight, lateral margins of somite 3 strongly convex. Somites 1 and 2 very narrow longitudinally. G1 straight, relatively stout; apical process short, corneous part wide, ending in truncated tip; setae long, simple, originating at base of apical process. G2 shorter than quarter length of G1.

Female characters: Chelipeds (Fig. 9C, D) relatively small, granules on palms indistinct, dactylar tubercles low; pleon (Fig. 9D) wide, rounded, telson semicircular, base half embedded in distal margin of somite 6; vulva (Figs. 9I, 10F) near anterior edge of sternite 5, with central operculum, cone-shaped.

Variation: Based on the male specimens examined, the length of the row of granules on dactylar upper surface is variable, being longer and reaching to the palm (Fig. 10B) in larger specimens, but is relatively shorter and not reaching the palm (Fig. 10C) in smaller crabs. The length of male somite 6 is relatively shorter (0.6 times as long as wide; Fig. 10G) in largest specimens (the holotype), but is proportionately longer (0.7 times as long as wide; Fig. 10H) in smaller ones.

Colour in life: Carapace and ambulatory legs dark greenish-brown, with yellowish-green patches; cheliped yellow, fingers with orange tips (Figs. 1E–G, 2F).

Distribution: Only known from southern Taiwan.

Etymology: The species name is derived from the Latin "*gemmatus*" which means covered in small gems, alluding to the light-coloured jewel-like spots on the

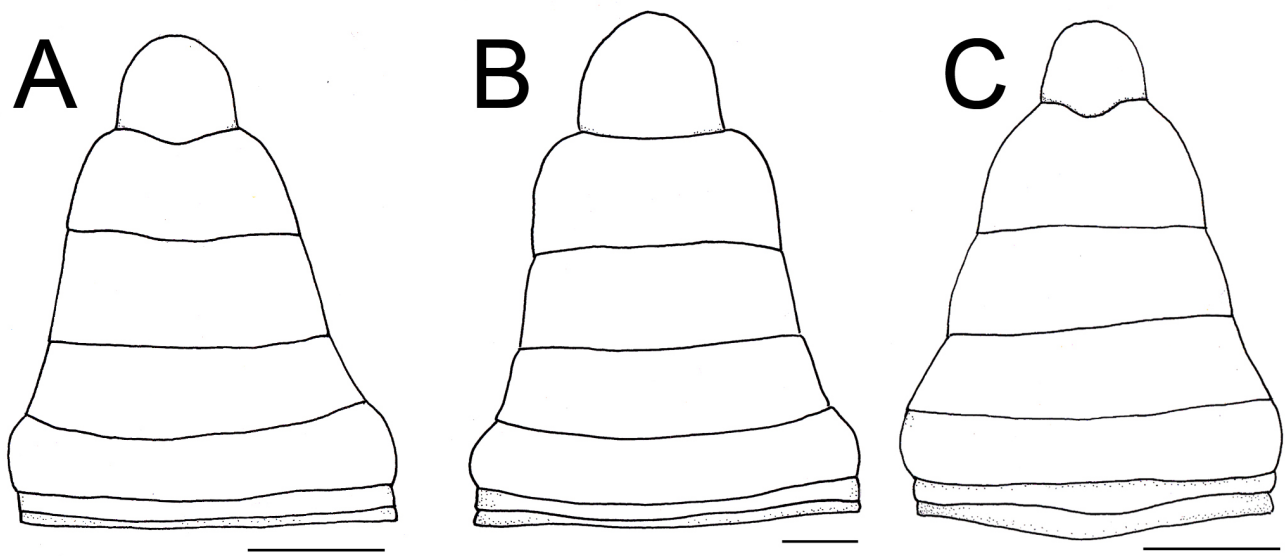

Fig. 11. Male pleon of three new species of *Parasesarma* from southern Taiwan. (A) *P. aurifrons* n. sp., holotype male (10.4 × 8.5 mm) (NCHUZOOL 15602); (B) *P. sanguimanus* n. sp., paratype male (14.1 × 12.1 mm, NCHUZOOL 15625); (C) *P. gemmatum* n. sp., holotype male (15.7 × 13.1 mm, NCHUZOOL 15639). Scale bars = 1.0 mm.

carapace.

Ecological notes: *Parasesarma gemmatum* was only found in eroded limestone with many crevices in supratidal zone, located on the outer edge of coastal forest. The species is sometimes sympatric with *P. lenzii* (De Man, 1895) (see DISCUSSION) and *Chiromantes leptomerus* Davie & Ng, 2013 from Taiwan.

Remarks: *Parasesarma gemmatum* is superficially most similar to *P. lenzii* (De Man, 1895) (see Comparative material) in having a similar coloration, especially the yellowish-green patches, but the margins of the patches are indistinct in the former (Fig. 1F) and distinct in the latter (Shahdadi et al. 2019b: fig. 3). In the external morphology, *P. gemmatum* can most easily be separated from *P. lenzii* by the dorsal surface of the male chela possessing rows of non-pectinated granules that do not have corneous tips (Fig. 10C) (versus with pectinated crests of corneous granules in *P. lenzii* and all other *Parasesarma* species; Shahdadi et al. 2019b: fig. 1C); the base of the male telson is partially embedded in the distal margin of somite 6 (Fig. 10F–G) (versus base not embedded in somite 6 in *P. lenzii*; Shahdadi et al. 2019b: fig. 1E); the male G1 is relatively stouter (Figs. 9G, H, 10D, E) (versus G1 more slender in *P. lenzii*; Shahdadi et al. 2019b: fig. 1F–G); and the female vulva has a cone-shaped operculum protruding upwards (Figs. 9I, 10F) (versus with triangular operculum which protrudes downwards in *P. lenzii*; Shahdadi et al. 2019b: fig. 2D). The latter species is also shown to be present in Taiwan, as a new record (see later).

The absence of a pectinated crest of granules on the dorsal surface of the male chela (Fig. 10C) is a unique character of *P. gemmatum*; all other congeners have this feature distinct, even if not all the granules are pectinated. There is precedence; in the West African *Guinearma* Shahdadi & Schubart, 2017, two of the species have distinct pectinated crests, with the crest of one taxon, *G. kamermani* (De Man, 1883) composed only of simple granules (Shahdadi et al. 2019a).

According to the BI tree (Fig. 13), *P. anambas* Yeo, Rahayu & Ng, 2004, from Anambas, Indonesia and Hainan, China, is sister to *P. gemmatum* n. sp. Both species are similar in carapace shape and G1 morphology, but *P. gemmatum* without transverse pectinate crests on upper surface of palm (Fig. 10C) (versus three transverse pectinate in *P. anambas*; Yeo et al. 2004: fig. 2b); the upper surface of the cheliped dactylus lined with closely spaced 22 tubercles (Fig. 10B) (versus more distantly spaced 17 tubercles in *P. anambas*; Yeo et al. 2004: fig. 2b); and the G1 is stout with the corneous distal process short and wide (Figs. 9G, H, 10D, E) (versus G1 slender, corneous distal process strongly produced and long in *P. anambas*; Yeo et al. 2004: fig. 2f).

Parasesarma lenzii (De Man, 1895)

(Fig. 12A, B)

Sesarma (*Parasesarma*) *lenzii* De Man, 1895: 199, pl. 30 (35).
Sesarma (*Parasesarma*) *lenzii* – Tesch 1917: 168 (list).
Sesarma lenzii – Tweedie 1950: 131.
Parasesarma lenzii – Serène 1968: 108 (list); Ng et al. 2008: 222 (list); Shahdadi & Schubart 2017: 536 (list); Cannicci et al. 2007: 91–97 (list), fig. 3; Ng et al. 2008: 222 (list); Shahdadi et al. 2019b: 740, figs. 1–3.
Parasesarma sp. 2 – Li and Chiu 2013: 83.
Parasesarma aff. *lenzii* – Ng et al. 2016: 261.

Material examined: Taiwan: Hengchun, Pingtung: 1 ♂ (18.6 × 16.5 mm) (NCHUZOOL 15642), Dingtanzih, Hengchun, coll. P.-Y. Hsu et al., 3 Mar. 2018; 1 ♀ (13.6 × 11.3 mm) (NCHUZOOL 15643), Dingtanzih, coll. P.-Y. Hsu et al., 3 Sep. 2017; 1 ♀ (16.5 × 14.2 mm) (NCHUZOOL 15644), Siangjiaowan, coll. J.-J. Li, 5 Sep. 2012; 2 ♀ ♀ (13.0 × 11.2 mm, 20.3 × 17.5 mm) (NCHUZOOL 15645), Dingtanzih, coll. P.-Y. Hsu et al., 27 Aug. 2018; 2 ♂ ♂ (18.6 × 16.6 mm, 14.6 × 12.0 mm), 1 ♀ (12.0 × 9.7 mm) (NMNS), Tanzih Fishing Port, coll. J.-J. Li, 10 Apr. 2019; 1 ♂ (19.5 × 17.4 mm, 15.4 × 13.5 mm) (NMNS), Tanzih Fishing Port, coll. J.-J. Li, 4 Jul. 2019; 1 ♀ (16.5 × 13.7 mm) (ZRC 2019.1077), Dingtanzih, coll. J.-J. Li, 28 Aug. 2018; 1 ♂ (14.1 × 11.8 mm) (ZRC 2019.1078), Tanzih Fishing Port, coll. J.-J. Li, 20 Aug. 2018; 8 ♂ ♂ (11.2–18.3 × 10.0–16.3 mm) (ZRC 2019.1079), Tanzih Fishing Port, coll. J.-J. Li, 29 Sep. 2018. See Shahdadi et al. (2019b: 740) for other material examined.

Remarks: The species was originally listed as "*Parasesarma* sp. 2" in Li & Chiu (2013: 83) but comparions with material of *P. lenzii* from the Indian Ocean (see Shahdadi et al. 2019) show that all the specimens are morphologically identical. Genetically it also clusters with specimens from Sumatra and Cocos (Keeling) Islands (Fig. 13), differing in only 1 or 2 bp. Previously, *P. lenzii* s. str. was only from the known from the eastern Indian Ocean, including Penang (Malaysia), northern Sumatra (Indonesia) and Cocos (Keeling) Islands (Shahdadi et al. 2019b). Our study extends the distribution of this species 4600 km to Taiwan in the East Asian Arc.

Parasesarma dumacense (Rathbun, 1914)

(Fig. 12C, D)

Sesarma (*Parasesarma*) *dumacensis* Rathbun, 1914: 80; Tesch 1917: 146.
Parasesarma dumacense — Ng et al. 2008: 222; Rahayu & Ng 2010: 15, figs. 11–14; Maenosono & Naruse 2015: 3, figs. 2A–C, 3, 11A, B.

Material examined: 1 ♂ (13.9 × 11.1 mm)

(NCHUZOOL 15704), coll. C.-Y. Chi et al., 12 Jun. 2019; 1 ♂ (23.9 × 19.1 mm) (NCHUZOOL 16088), coll. C.-Y. Chi et al., 19 Aug. 2019. See Rahayu & Ng (2010: 15) for additional material.

Remarks: This species was previously only reported in Luzon and Cebu, Philippines (Rathbun 1914; Rahayu and Ng 2010), as well as the Ryukyus, Japan (Maenosono and Naruse 2015). *Parasesarma dumacense* is sister to *P. ungulatum*, but the phylogenetic relationship of the two species is not clear (Fig. 13). The species has been treated at length by Rahayu and Ng (2010) and there is no need to elaborate on its taxonomy here.

DNA ANALYSIS

The molecular analysis of the *COI* marker, with 658 base pairs, comprised 23 species of *Parasesarma* from 85 specimens (Table 1). The BI tree, with ML support values on the nodes (Fig. 13), shows that the three new species in this study are well supported genetically. *Parasesarma sanguimanus* is distinct, but closely related to *P. bidens* and *P. cricotus*. The three species form a main clade with *P. bengalense* and *P. guttatum*. *Parasesarma aurifrons* is sister to *P. liho*, although the node is only moderately supported. The two species and *P. paucitorum* form a main clade, sister to another main clade, composed of *P. lenzii*, *P. kui* Li, Rahayu & Ng, 2018, and *P. macaco* Li, Rahayu & Ng, 2018. *Parasesarma gemmatum* is sister to *P. anambas*, but their phylogenetic positions cannot be confirmed from the tree at the moment.

DISCUSSION

The reconstructed *COI* tree (Fig. 13) is basically similar to that in Shahdadi and Schubart (2017: fig. 12A). *Parasesarma sanguimanus* is closely related to *P. bidens* from the East Asian Arc (*i.e.*, the main islands of Japan, the Ryukyus and Taiwan) and *P. cricotus* from Papua, Indonesia. It is worth noting that the molecular

Fig. 12. Coloration in life. (A, B) *Parasesarma lenzii* (De Man, 1895), male (CW about 15 mm, not collected) from Tanzih Fishing Port, Hengchun, Pingtung, Taiwan; (C, D) *P. dumacense* (Rathbun, 1914), male (23.9 × 19.1 mm, NCHUZOOL 16088) from Dongsha Island, Taiwan.

analysis showed *P. bidens* is composed of several clades, but no obvious morphological differences can be found (personal observation). The species in the "*P. bidens*" group will need to be completely reappraised with material from the known range of all its members, and the taxonomic revision is now being done (C. D. Schubart, personal communication). *Parasesarma aurifrons*, *P. liho* (from the East Asian Arc to the Philippines and Sulawesi, Indonesia), and *P. paucitorum* (Sulawesi) form a main clade, sister to another main clade composed of *P. lenzii* and members of the *P. leptosoma* complex (see Li et al. 2018; Shahdadi et al. 2019b; Shih et al. 2019).

Komai et al. (2004) recorded "*P. semperi*" from Iriomote, Ryukyus, Japan, but its genetic relationship is different from the *P. semperi* s. str. (including types) and similar to *P. lividum* (*P*. nr. *lividum*; Shahdadi et al. 2018). In our study, the specimen from Ishigaki, Ryukyus also showed such a genetic pattern (Fig. 13). As such, we follow Shahdadi et al. (2018) and treat it as "*P*. nr. *lividum*" provisionally, and require further study to confirm its identity. *Parasesarma kuekenthali* (De Man, 1902) was described from the type locality in Halmahera, Indonesia (De Man 1902: 534), and Li (2015) reported it from southern Taiwan. This species is now also recorded from Dongsha Island in the northern South China Sea (male, 14.8 × 11.8 mm, NCHUZOOL 15702, coll. H.-T. Shih, 2 Sep. 2011 (identified as "*P. pictum*" in Shih 2012); male, 10.9 × 8.9 mm, NCHUZOOL 15703, coll. C.-Y. Chi et al., 12 Jun. 2019) (Table 1). The genetic data support the present identification of the two specimens (Fig. 13).

CONCLUSIONS

In our study, three new species, viz. *Parasesarma aurifrons* n. sp., *P. sanguimanus* n. sp., and *P. gemmatum* n. sp. described from Taiwan and the Philippines, which are also supported by the evidence

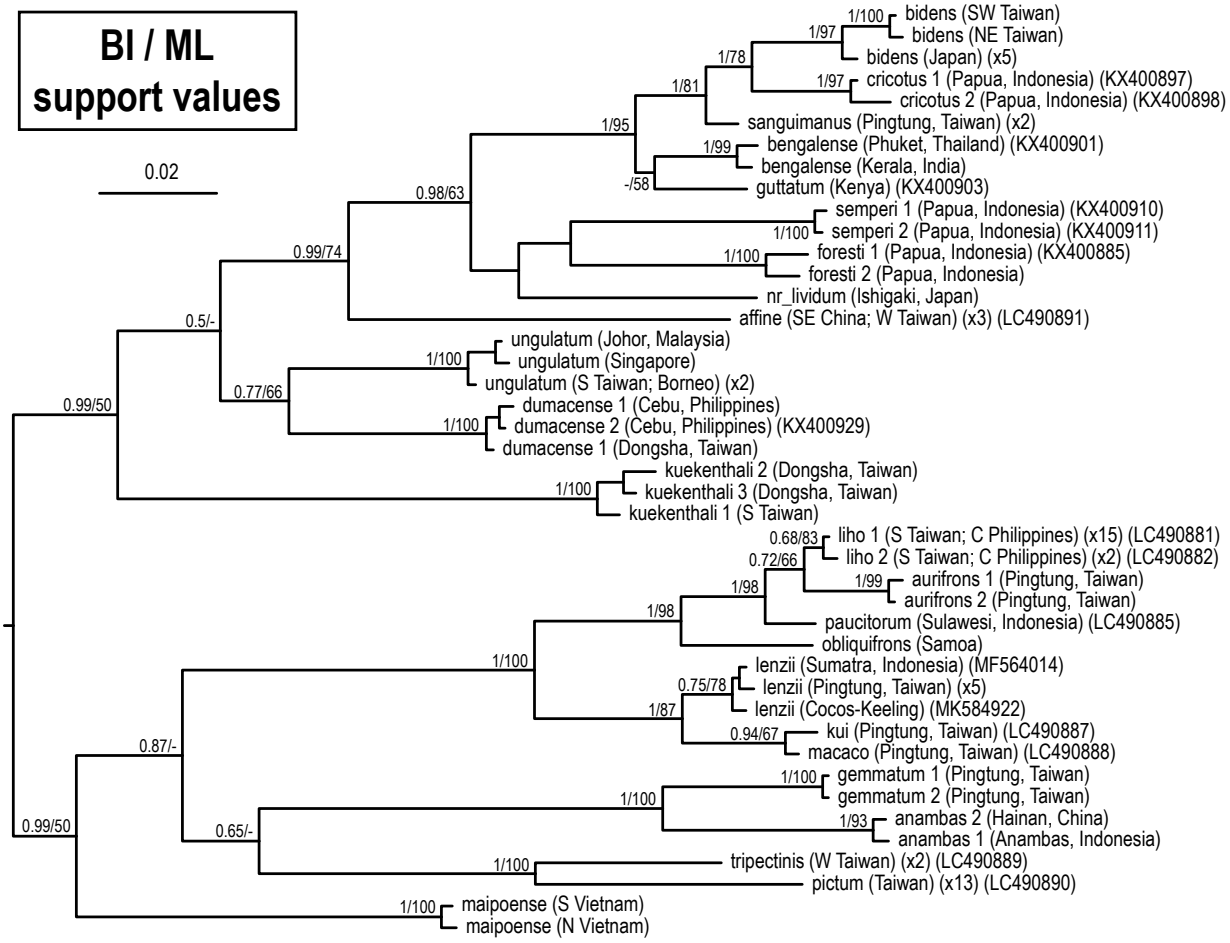

Fig. 13. A Bayesian inference (BI) tree for species of *Parasesarma*, based on the cytochrome *c* oxidase subunit I (*COI*) gene. Probability values at the nodes represent support values for BI and maximum likelihood (ML). For haplotype names, see table 1.

from *COI*. In addition, *P. lenzii* (Pingtung, Taiwan) and *P. dumacense* (Dongsha Island, Taiwan) are also newly recorded from Taiwan.

Acknowledgments: This work and the reinstated species name have been registered with ZooBank under urn:lsid:zoobank.org:pub:C41DA00E-A4B5-42F1-8BBC-A172AAE46012. This study was supported by grants from the Ministry of Science and Technology (MOST 105-2621-B-005-002-MY3; 108-2621-B-005-002-MY3), Executive Yuan, Taiwan, to HTS; and research grants from Kenting National Park and Kaltis International Co., Ltd. to JJL. We wish to thank Pei-Yi Hsu, Jung-Hsiang Lee and Chung-Yu Chi helping specimen collection in the field; to Ping-Ho Ho (National Taiwan Ocean University), Hsiu-Chin Lin and Te-Yu Liao (National Sun Yat-sen University) for providing equipment for specimen examination; and to Pei-Yi Hsu for measuring specimens and some of the molecular work. Special thanks to Adnan Shahdadi (University of Hormozgan, Iran) for valuable comments on earlier version of manuscript and kindly sharing his *COI* sequences of *P. anambas* and *P. obliquifrons* for comparison. We acknowledge two anonymous referees, who greatly improved the manuscript.

Authors' contributions: JJL collected and processed the samples, performed the ecological observation, and drafted the manuscript. HTS conceived the study, performed molecular analysis, and drafted the manuscript. PKLN performed the morphological comparison and drafted the manuscript. All authors read and approved the final manuscript.

Competing interests: The authors declare that they have no conflict of interest.

Availability of data and materials: Sequences generated in the study have been deposited in the DNA Data Bank of Japan (DDBJ) database (accession numbers in Table 1 in manuscript).

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Bürger O. 1893. Beiträge zur Kenntniss der Gattung *Sesarma*. Zool Jahrb Syst **7:**613–632, pl. 21.

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. Zool Anz **269:**89–99. doi:10.1016/j.jcz.2017.08.002.

Davie PJF. 2010. A new species of *Perisesarma* (Brachyura, Sesarmidae) from Western Australia. Crust Monogr **14:**195–207. doi:10.1163/9789047427759_012.

Hsu PY, Shih HT. 2018. A new record crab of *Parasesarma lepidum* (Decapoda: Brachyura: Sesarmidae) from southern Taiwan. Coll Res **31:**85–90.

Koller P, Liu HC, Schubart CD. 2010. A new semiterrestrial species of the genus *Parasesarma* De Man, 1895, from Taiwan (Crustacea: Decapoda: Brachyura: Sesarmidae). Crust Monogr **14:**357–368. doi:10.1163/9789047427759_024.

Komai T, Nagai T, Yogi A, Naruse T, Fujita Y, Shokita S. 2004. New records of four grapsoid crabs (Crustacea: Decapoda: Brachyura) from Japan, with notes on four rare species. Nat Hist Res **8:**33–63.

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B. 2017. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol Biol Evol **34:**772–773. doi:10.1093/molbev/msw260.

Li JJ. 2015. Two new records of *Parasesarma* De Man, 1895 and Ptychognathus Stimpson, 1858 (Decapoda: Brachyura: Grapsoidea) from Taiwan. Taiwan J Biodivers **17:**49–57. (in Chinese)

Li JJ, Chiu YW. 2013. Land crabs of Hengchun Peninsula. National Museum of Marine Biology & Aquarium, Pingtung, Taiwan, 91 pp. (in Chinese)

Li JJ, Hsu JW, Ng NK, Shih HT. 2019. Eight new records of crabs (Decapoda: Brachyura: Sesarmidae, Varunidae) from the coasts of Taiwan. Crustaceana **92:**1207–1230. doi:10.1163/15685403-00003935.

Li JJ, 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. doi:10.11646/zootaxa.4482.3.2.

Maenosono T, Naruse T. 2015. Morphological characteristics and taxonomical problems of the genus *Parasesarma* De Man, 1895 (Crustacea: Decapoda: Brachyura: Sesarmidae) from the Ryukyu Archipelago, Japan. Fauna Ryukyuana **23:**1–41. (in Japanese)

Man JG de. 1895. Man, J. G., De (1895) 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. Zweiter Theil. Zool Jahrb Syst **9:**75–218.

Man JG de. 1902. Die von Herrn Professor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden. Abh Senckenb Naturforsch Ges **25:**467–929, pls. 19–27.

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). Raffles Bull Zool **64:**257–268.

NG PKL, Guinot D, Davie PJF. 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bull Zool **Suppl 17:**1–286.

Ng PKL, Hoang NK, Rahayu DL. 2010. On the taxonomy and ecology of the mangrove crab *Perisesarma maipoense* (Soh, 1978) (Crustacea: Decapoda: Brachyura: Sesarmidae) from Vietnam. Raffles Bull Zool **58:**239–243.

Ng PKL, Schubart CD. 2017. On the taxonomy of *Pseudosesarma edwardsii* (De Man, 1887) and *P. crassimanum* (De Man, 1887) (Crustacea: Decapoda: Brachyura: Sesarmidae), with description of a new species from Sri Lanka. Raffles Bull Zool **65:**655–669.

Ng PKL, Shih HT, Ho PH, Wang CH. 2017. An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). J Nat Taiwan Mus **70:**1–208. doi:10.6532/JNTM.201712_70(3;4).01.

Ng PKL, Wang CH, Ho PH, Shih HT. 2001. An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). Nat Taiwan Mus Spec Publ Ser **11:**1–86.

Rahayu DL, Davie PJF. 2002. Two new species and a new record of *Perisesarma* (Decapoda, Brachyura, Grapsidae, Sesarminae) from Indonesia. Crustaceana **75:**597–607. doi:10.1163/156854002760095624.

Rahayu DL, Ng PKL. 2009. Two new species of *Parasesarma* De Man, 1895, from Southeast Asia (Crustacea: Decapoda: Brachyura: Sesarmidae). Zootaxa **1980:**29–40. doi:10.5281/zenodo.185266.

Rahayu DL, Ng PKL. 2010. Revision of the *Parasesarma plicatum* (Latreille, 1803) species-group (Crustacea: Decapoda: Brachyura: Sesarmidae). Zootaxa **2327:**1–22. doi:10.11646/zootaxa.2327.1.1.

Rahayu DL, Setyadi G. 2009. Mangrove estuary crabs of the Mimika Region, Papua, Indonesia. PT Freeport Indonesia, Timika, Papua, Indonesia, i–viii, 1–154 pp.

Rathbun MJ. 1914. New species of crabs of the families Grapsidae and Ocypodidae. Scientific Results of the Philippines Cruise of the fisheries Steamer "Albatross" 1907–1910. Proc US Nat Mus **47:**69–85.

Rathbun MJ. 1924. New species of crabs from Samoa. Proc Biol Soc Wash **37:**127–128.

Ronquist F, Huelsenbeck JP, Teslenko M, Nylander JAA. 2019. MrBayes 3.2 manual. Available at http://mrbayes.csit.fsu.edu/manual.php. Accessed 9 Sep. 2019.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MRBAYES 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol **61:**539–542. doi:10.1093/sysbio/sys029.

Serène R. 1968. The Brachyura of the Indo-West Pacific region. *In*: Serène R (ed) Prodromus for a check list of the non-planctonic marine fauna of South East Asia. UNESCO, Singapore National Academy of Science. Singapore, Specieal Publication No. 1, Fauna III CC3.: pp. 33–112.

Shahdadi A, Davie PJF, Schubart CD. 2018. Systematics and phylogeography of the Australasian mangrove crabs *Parasesarma semperi* and *P. longicristatum* (Decapoda: Brachyura: Sesarmidae) based on morphological and molecular data. Invertebr Syst **32:**196–214. doi:10.1071/is17040.

Shahdadi A, Mvogo Ndongo PA, Suess T, Schubart CD. 2019a. 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. doi:10.1163/15685403-00003863.

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. Zool J Linn Soc **182:**517–548 (printed in 2018). doi:10.1093/zoolinnean/zlx032.

Shahdadi A, Schubart CD, Ng PKL. 2019b. 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. doi:10.1163/15685403-00003901.

Shanij K, Praveen VP, Suresh S, Oommen MM, Nayar TS. 2016. Tree climbing and temporal niche shifting: an anti-predatory strategy in the mangrove crab *Parasesarma plicatum* (Latreille, 1803). Curr Sci **111:**1201–1207. doi:10.18520/cs/v111/i7/1201-1207.

Shih HT. 2012. Warrior – The seashore crabs of Dongsha Island. Marine National Park, Kaohsiung, Taiwan, 159 pp. (in Chinese)

Shih HT, Hsu PY, Shahdadi A, Schubart CD, Li JJ. 2019. The synonymy of the supratidal crab 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. Zool Stud **58:**21. doi:10.6620/ZS.2019.58-21.

Shih HT, Ng PKL, Davie PJF, Schubart CD, Türkay M, Naderloo R, Jones DS, Liu MY. 2016. Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, sensu lato and its subgenera. Raffles Bull Zool **64:**139–175.

Soh CL. 1978. On a collection of sesarmine crabs (Decapoda, Brachyuran, Grapsidae) from Hong Kong. Mem Hong Kong Nat Hist Soc **13:**9–22, pls. 1–4.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics **22:**2688–2690. doi:10.1093/bioinformatics/btl446.

Tesch JJ. 1917. Synopsis of the genera *Sesarma*, *Metasesarma*, *Sarmatium* and *Clistocoeloma*, with a key to the determination of the Indo-Pacific species. Zool Meded Leiden **3:**127–269, pls. 15–17.

Tweedie MWF. 1950. The fauna of the Cocos-Keeling Islands, Brachyura and Stomatopoda. Bull Raffles Mus **22:**105–148, pls. 16–17.

Yeo DCJ, Rahayu DL, Ng PKL. 2004. Brachyura (Crustacea) of the Anambas Expedition 2002. Raffles Bull Zool Suppl **11:**79–88.