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The systematics of the land crabs of the *Discoplax hirtipes* (Dana, 1851) species-group (Crustacea: Decapoda: Brachyura: Gecarcinidae), with description of a new species from the eastern Indian Ocean

Peter K. L. Ng[1] & Hsi-Te Shih[2*]

Abstract. The Indo-West Pacific gecarcinid *Discoplax hirtipes* (Dana, 1851) is one of the best known land crabs in the Indo-West Pacific, with a range spanning from the eastern Indian Ocean to Hawaii. Recently, the famous blue population of "*D. hirtipes*" from Christmas Island was described as a new species, *D. celeste* Ng & Davie, 2012. A revision of the *D. hirtipes* species-group using morphological and genetic data from mitochondrial 16S rRNA and COI (cytochrome oxidase subunit I) shows that the species can be divided into three distinct species; with the Indian Ocean population belonging to an undescribed taxon. The redescription of the taxa in the species-group as well as characterisation of the new species from the eastern Indian Ocean forms the basis of the present paper.

Key words. Crustacea, Brachyura, *Discoplax hirtipes* revision, Indo-West Pacific, *D. magna*, new species, morphology, 16S rRNA, COI genetic markers

INTRODUCTION

The Indo-West Pacific gecarcinid genus *Discoplax* A. Milne-Edwards, 1867, currently contains six species, *D. celeste* Ng & Davie, 2012, *D. gracilipes* Ng & Guinot, 2001, *D. hirtipes* (Dana, 1851), *D. longipes* A. Milne-Edwards, 1867, and *D. rotunda* (Quoy & Gaimard, 1824) (Ng et al., 2008; Ng & Davie, 2012).

Ng & Davie (2012) recently described *D. celeste* from Christmas Island in the eastern Indian Ocean, and discussed the taxonomy of *D. hirtipes* (Dana, 1851). They selected a neotype for *D. hirtipes* (Dana, 1851) from Fiji and commented that the species is actually restricted to the western Pacific and Southeast Asia. In addition to *D. celeste* that is endemic to Christmas Island, they noted that there was a third species (which they called *Discoplax* aff. *hirtipes*) from the Indian Ocean that was distributed from Christmas Island, Sumatra to the Andaman and Nicobar Islands. The present paper is intended to treat the taxonomy of *D. hirtipes* s. str. at length, document and discuss the variation across its range, as well as formally describe "*Discoplax* aff. *hirtipes*" as a new species (here named *Discoplax magna*) and compare it with congeners. The molecular relationships based on mitochondrial 16S rRNA and COI (cytochrome oxidase subunit I) between the members of the *D. hirtipes* species-group are presented and discussed.

MATERIAL AND METHODS

Specimens of *Discoplax hirtipes*, *D. celeste* and *D. magna* sp. nov. used were collected on the coastal area from the western Pacific and the eastern Indian Ocean, or loaned from various museums and institutions (Table 1). Specimens of *D. gracilipes*, *D. longipes*, *D. rotunda*, *Cardisoma carnifex* (Herbst, 1796) and *C. armatum* Herklots, 1851 were included as outgroups in phylogenetic analyses. Specimens collected were preserved in 70–95% ethanol after collection and illustrated with the help of a drawing tube attached to a stereomicroscope. The material examined is deposited in the Zoology Museum of the Chulalongkorn University (CUNHM), Bangkok, Thailand; Museum of Comparative Zoology (MCZ), Harvard University; Muséum national d'Histoire naturelle (MNHN), Paris; Museum Zoologicum Bogoriense (MZB), Java, Indonesia; Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); Queensland Museum (QM), Brisbane; Senckenberg Forschungsinstitut und Naturmuseum (SMF), Frankfurt am Main, Germany; and Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore.

The terminology used follows that used in Ng & Davie (2012). Measurements provided (in millimetres) are of the carapace width and length, respectively. The abbreviations G1 and G2 are used for the male first and second gonopods, respectively.

[1]Lee Kong Chian Natural History Museum, National University of Singapore, 6 Science Drive 2, Singapore 117546, Republic of Singapore; Email: dbsngkl@nus.edu.sg

[2]Department of Life Science, National Chung Hsing University, 250, Kuo Kuang Road, Taichung 402, Taiwan; Email: htshih@dragon.nchu.edu.tw (*corresponding author)

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Table 1. The haplotypes of 16S rRNA and COI genes of *Discoplax* spp. from West Pacific and Indian Oceans, and outgroups used in this study. For abbreviations of museums or universities, see Material and methods. "*" means the haplotype is a pseudogene (see text).

Species	Localities	No. of localities in Fig. 15	Catalogue no.	Sample size	Haplotypes of 16S	DDBJ accession no.	Haplotypes of COI	DDBJ accession no.
D. magna	India: Nicobar Islands	1	ZRC 1965.12.1.30	1	DSm-5	AB999604	—	
	Thailand: Similan	2	ZRC 2012.0011	1	DSm-1	AB999605	DSm-C1b	AB999624
		2	ZRC 2012.0011	1	DSm-4	AB999606	DSm-C1a	AB999625
		2	ZRC 2012.0010	1	DSm-3	AB999607	DSm-C3	AB999626
		2	ZRC 2012.0011	2	DSm-1	AB999605	DSm-C1	AB999627
	Indonesia: Pantai Cerocok, Painan, West Sumatra	3	ZRC 2008.0575	1	DSm-1	AB999605	DSm-C1	AB999627
	Indonesia: Pulau Siberut Sumatra	4	ZRC CRU 3752	1	DSm-1	AB999605	DSm-C1	AB999627
	Indonesia: Ujong Kulon National Park, West Java	5	ZRC CRU 3754	1	DSm-1	AB999605	—	
	Christmas Island	6	ZRC 2012.003	1	DSm-1	AB999605	DSm-C1a	AB999625
				2	DSm-2	AB999608	DSm-C2	AB999628
D. hirtipes	Indonesia: Pulau Dua, Serang, West Java	7	ZRC CRU 367	1	DSh-1	AB999609	DSh-C1	AB999629
	Malaysia: Pulau Pemangil, Johor	8	ZRC 2000.2583	1	DSh-1	AB999609	—	
	Taiwan: Hengchun Peninsula	9	ZRC 1998.452	1	DSh-1	AB999609	DSh-C1a	AB999630
	Taiwan: Hengchun Peninsula	9	ZRC 2002.0482	1	DSh-1	AB999609	DSh-C1	AB999629
	Ryukyus: Funaura jetty and beach, Iriomote Island	10	ZRC 2009.0154	1	DSh-3	AB999610	DSh-C1b	AB999631
	Philippines: Tawala Cave, Tawala, Panglao, Bohol	11	ZRC 2001.0310	1	DSh-1	AB999609	DSh-C1	AB999629
	Philippines: Momo beach, Panglao, Bohol	11	ZRC Panglao 2012: 107728, 107729	2	DSh-1	AB999609	DSh-C1	AB999629
	Philippines: Ginatilan, south of Matutinao, Cebu	11	ZRC 2008.0504	1	DSh-1	AB999609	DSh-C1b	AB999631
	Guam: Merizo Bay	12	ZRC 2001.0706	1	DSh-1	AB999609	DSh-C1	AB999629
	Guam: Pago Bay	12	ZRC 2001.2230	1	DSh-4	AB999611	DSh-C4	AB999632

Species	Localities	No. of localities in Fig. 15	Catalogue no.	Sample size	Haplotypes of 16S	DDBJ accession no.	Haplotypes of COI	DDBJ accession no.
	Palau: Central Pacific, Angaur Island, Angaur	13	ZRC 2000.1087	1	DSh-5	AB999612	DSh-C1b	AB999631
	Palau: Central Pacific, Angaur Island, Angaur	13	ZRC 2000.1087	1	DSh-1	AB999609	DSh-C1c	AB999633
	Palau: Angaur	13	ZRC 2000.1086	1	DSh-2	AB999613	DSh-C2	AB999634
	Indonesia: Gero-pok, Lombok	14	ZRC 2003.0582	1	DSh-2	AB999613	DSh-C2a	AB999635
	Fiji: Suva	15	ZRC 2010.0415 (neotype), 2010.0416	2	DSh-2	AB999613	DSh-C2b	AB999636
D. celeste	Christmas Island	6	ZRC 2011.0166, 2011.0168, 2011.0169, 2012.0028	14	DSc-1	AB999614	DSc-C1	AB999637
		6	ZRC 2012.0028	1	DSc-1	AB999614	DSc-C1a	AB999638
		6	ZRC	1	DSc-2	AB999615	DSc-C1	AB999637
		6	ZRC	1	—*		—*	
D. rotunda	Taiwan: Heng-chun		NCHUZOOL 13638	1	DSr-1	AB999616	DSr-C1a	AB999639
	Cocos (Keeling) Islands		ZRC	1	DSr-1	AB999616	DSr-C1	AB999640
	Indonesia: Kri Island, Papua		ZRC 2010.0423	1	DSr-1	AB999616	DSr-C1	AB999640
	Guam: Pago Bay		ZRC 2000.0566	1	DSr-2	AB999617	DSr-C1	AB999640
	Philippines: Bohol		ZRC 2001.0312	1	DSr-3	AB999618	DSr-C1b	AB999641
D. longipes	New Caledonia: Loyalty Island		ZRC 2001.1150	1	DSL-1	AB999619	DSL-C1	AB999642
			ZRC 2002.0050	1	DSL-2	AB999620	DSL-C2	AB999643
D. gracilipes	Philippines: Ka-wasan Fall, Cebu		ZRC 2003.0389	1	DSg	AB999621	DSg-C	AB999644
	Philippines: Bohol		ZRC 2003.0377, 2004.0461	2	DSg	AB999621	DSg-C	AB999644
Cardisoma carnifex	Taiwan: Cigu, Tainan		NCHUZOOL 13639	1	CDc	AB999622	CDc-C1	AB999645
C. armatum	Nigeria		ZRC	1	CDa	AB999623	CDa-C1	AB999646

Genomic DNA was isolated from the muscle tissue of legs, or the pleopods of females, by using the GeneMark tissue & cell genomic DNA purification kit (Taichung, Taiwan). A region of approximately 510–550 base pairs (bp) of the 5'-end of the 16S rRNA gene was selected for amplification with a polymerase chain reaction (PCR) using the primers 1471 (5'-CCTGTTTANCAAAAACAT-3') and 1472 (5'-AGATAGAAACCAACCTGG-3') (Crandall & Fitzpatrick, 1996). A portion of the COI gene was amplified with the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACC AAAAAATCA-3') (Folmer et al., 1994). The PCR conditions for the above primers were 40 cycles of denaturation for 50 s at 94°C, annealing for 70 s at 45–47°C, and extension for 60 s at 72°C, followed by a 72°C extension for 10 minutes. Sequences were obtained by automated sequencing (Applied Biosystems 3730) and were aligned with the aid of Clustal W (vers. 1.4, Thompson et al., 1994) and BioEdit (vers. 5.09, Hall, 2001), after verification with the complimentary strand. Sequences of the different haplotypes were deposited in the DNA Data Bank of Japan (DDBJ) database (accession numbers in Table 1).

For a combined analysis of 16S rRNA and COI, phylogenetic congruence among the two dataset partitions was tested under the maximum parsimony (MP) criterion using the incongruent length difference (ILD) test (Farris et al., 1994) implemented in the PAUP* programme (vers. 4.0b10, Swofford, 2003) as the partition homogeneity test. The parameters included 1000 reiterations of a heuristic search with 100 randomly added sequence replications, TBR branch swapping, using Steepest Descent, and the MULTREES option enabled. The topologies of the two data sets were congruent (P = 1.0) and so the sequences were combined.

For the combined 16S and COI dataset, the best-fitting models for sequence evolution of individual datasets were determined by jModelTest (vers. 0.1.1, Posada, 2008; Guindon & Gascuel, 2003), selected by the Bayesian information criterion (BIC). The obtained best models were HKY+G and TIM2+G, respectively, and were subsequently applied for the partitioned Bayesian inference (BI) analysis. The BI was performed with MrBayes (vers. 3.2.2, Ronquist et al., 2012) and the search was run with four chains for 10 million generations, with trees sampled every 1000 generations. The convergence of chains was determined by the effective sample size (ESS) (>200 as recommended) in Tracer (vers. 1.5, Rambaut & Drummond, 2009) and the first 500 trees were discarded as the burnin (determined by the average standard deviation of split frequency values below the recommended 0.01; Ronquist et al., 2005). Maximum likelihood (ML) analysis was conducted in RAxML (vers. 7.2.6, Stamatakis, 2006) for the combined dataset. The model GTR + G (i.e., GTRGAMMA) was used for all subsets with 100 runs, and found the best ML tree by comparing the likelihood scores. The robustness of the ML tree was evaluated by 1000 bootstrap pseudoreplicates under the model GTRGAMMA. A consensus MP tree was constructed using PAUP* with 2000 bootstrap replications of a simple heuristic search, tree bisection-reconnection (TBR) branch-swapping, and 100 random addition sequence replications. Gaps in MP tree construction were treated as missing. All characters were equally weighted. Other analyses, including the nucleotide composition, variable and parsimony informative positions, and Kimura 2-parameter (K2P) distance (Kimura, 1980) and p-distance between haplotypes were calculated using MEGA (vers. 5.2.2, Tamura et al., 2011).

TAXONOMY

Family Gecarcinidae Macleay, 1838

Discoplax A. Milne-Edwards, 1867

Discoplax A. Milne-Edwards, 1867: 284; Balss, 1957: 1671; Guinot, 1979: 152; Türkay, 1987: 145; Guinot, 1994: 168; Ng et al., 2001: 48; Ng & Guinot, 2001: 312; Ng et al., 2008: 214; Ng & Davie, 2012: 90

Type species. *Discoplax longipes* A. Milne-Edwards, 1867, by monotypy. Gender feminine.

Remarks. *Discoplax* A. Milne-Edwards, 1867, has long been synonymised with *Cardisoma* Latreille, in Latreille, Le Peletier, Serville & Guérin, 1828 (see Türkay, 1974). Türkay (1987) first treated it as a distinct genus but did not elaborate much on the reasons for this. Ng & Guinot (2001) showed that the two genera differed markedly in the form of their male thoracic sternum and both genera were distinct taxa.

Discoplax hirtipes (Dana, 1851)

(Figs. 1, 2A–F, 5, 9A, B, 10, 12A–F, 13A–E)

Cardisoma hirtipes Dana, 1851: 253; Dana, 1852: 376; H. Milne-Edwards, 1853: 205; Dana, 1855: pl. 24 fig. 4; Stimpson, 1858: 100; Hess, 1865: 140; Heller, 1865: 35; Miers, 1876: 53; De Man, 1880: 34; Nauck, 1880: 26, pl. 1 figs. 9, 10; Hutton, 1882: 264; Filhol, 1886: 460; De Man, 1887: 349, pl. 14 fig. 3; Ortmann, 1894: 737 (part); Nobili, 1899: 271; Alcock, 1900: 447 (part); De Man, 1902: 548 (part); Doflein, 1904: 406; Stimpson, 1907: 111; Calman, 1909: 711; Tesch, 1918: 137 (part); Gordon, 1934: 5, fig. 1; Sakai, 1936: 174, pl. 14 fig. 4; Koba, 1936: 159, text fig. 1; Miyake, 1938: 108; Balss, 1938: 80; Esaki, 1938: 4, fig. 3; Miyake, 1939: 188, 220, pl. 15 fig. 1; Sakai, 1939: 704, pl. 111 fig. 1; Sakai, 1940: 32; Esaki, 1940: 412; Tweedie, 1950: 138, fig. 4g; Silas & Sankarankutty, 1960: 239; Shen & Liu, 1963: 141; Miyake, 1963: 69, pl. 1 fig. B; Johnson, 1965: 52 (part); Serène, 1968: 110; Bright & Hogue, 1972: 18 (part); Türkay, 1974: 229, text-figs. 2, 13; Sakai, 1976: 679, pl. 231; Türkay & Sakai, 1976: 14, 20, text-figs. 2, 6; pl. 1 figs. 3, 4; Takeda, 1982: 225; Miyake, 1983: 187, pl. 63(2); Guinot, 1985: 454; Dai et al., 1986: 518, pl. 74(6), text-fig. 295(2); Nagai & Nomura, 1988: 78; McLay & Ryan, 1990: 115; Dai & Yang, 1991: 568, pl. 74(6), text-fig. 295(2); Poupin, 1994: 53; Poupin, 1996: 65; Ng, 1998: 1151 (part); Minemizu, 2000: 291.

Cardisoma obesum – De Man, 1880: 35 (not *Cardisoma obesum* Dana, 1851 = *Cancer carnifex* Herbst, 1796).

Discoplax hirtipes – Türkay, 1987: 145; Ng et al., 2001: 48; Ng & Guinot, 2001: 334, 335 (part); Marumura & Kosaka, 2003: 63; Paulay et al., 2003: 507; Ho, 2003: 28–29; Poupin, 2005: 27; Shen & Jeng, 2005: 198, 3 unnumbered figs.; Naiyanetr, 2007: 108 (part); Ng & Richer De Forges, 2007: 323; Ng et

Fig. 1. Colours in life, *Discoplax hirtipes* (Dana, 1851). A, neotype male (64.2 × 53.0 mm) (ZRC 2010.0415) (photograph: D Huang), Fiji; B, male (not collected), Guam (photograph: G Paulay); C, male (in MNHN collections), Santo, Vanuatu (photograph: T-Y Chan); D, male (in MNHN collections), Loganville, Santo, Vanuatu (photograph: HH Tan); E, male (not collected), Siangjiaowan, Kenting National Park, Taiwan; F, male (not collected), Kenting National Park, Taiwan (photograph: H-C Liu); G, male (ZRC 2004.0462), Hinagdanan Cave, Panglao Island Nature Resort, Panglao, Bohol, Philippines (photograph: T-Y Chan); H, male (not collected), Panglao Island Nature Resort, Panglao, Bohol, Philippines (photograph: H-C Liu).

Fig. 2. Colours in life, *Discoplax* species. A–F, *D. hirtipes* (Dana, 1851); G, H, *D. celeste* Ng & Davie, 2012. A, male (ZRC 2000.2583), Pulau Pemangil, Malaysia (photograph: D Chia); B, male (not collected), Pulau Nikoi, Bintan Islands, Indonesia (photograph: N Lim, May 2012); C, male (not collected), Raja Ampat, West Papua, Indonesia (photograph: HH Tan, 25 December 2010); D, male (42.4 × 32.5 mm) (ZRC 2012.0712), Ambon, Indonesia; E, male (57.4 × 46.8 mm) (ZRC), Kumejima Island, Ryukyus, Japan; F, female (64.2 × 53.7 mm) (ZRC), Kumejima Island, Ryukyus, Japan; G, male (86.0 × 69.0 mm) (ZRC), Christmas Island (photograph: JC Mendoza, 4 February 2012); H, male (not collected), Waterfall Bay, Christmas Island (photograph: HH Tan, 2011).

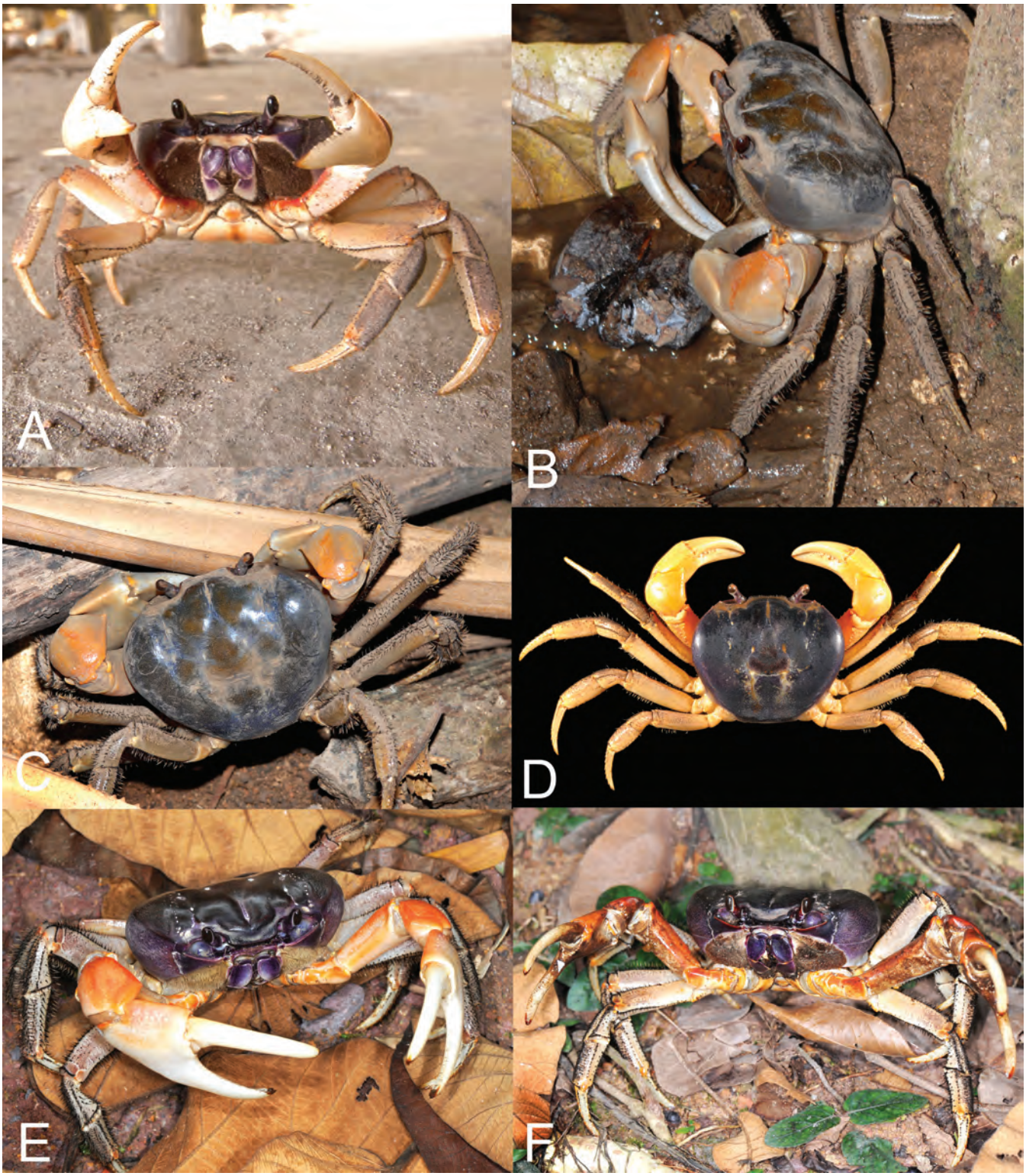

Fig. 3. Colours in life, *Discoplax magna* sp. nov. A, female (not collected), Narcodam Island, Nicobars (photograph: K Varma); B, C, male (not collected), Settlement Road, Christmas Island (photograph: HH Tan, 7 December 2007); D, female (47.1 × 39.7 mm) (ZRC 2012.0003), Christmas Island (photograph: HH Tan); E, F, paratype male (104.4 × 81.2 mm) (ZRC 2012.0011b), Similan Islands, Thailand (photograph: HH Tan).

al., 2008: 214 (part); Lee, 2008: 140; Lin et al., 2011: 36; Ng & Davie, 2012: 94 (part), figs. 5A, 6A, B, 7A–E; Shih, 2012: 106, figs. 150–152; Li & Chiu, 2013: 64; Shih, 2013: 27, fig. 7; Chen & Lo, 2014: 119; Ng & Clark, 2014: 596.

Cardisoma rotundum – Rathbun, 1906: 838; Sendler, 1923: 22; Edmondson, 1962: 23 (part) (not *Thelphusa rotunda* Quoy & Gaimard, 1824).

Material examined. Neotype: male (64.2 × 53.0 mm) (ZRC 2010.0415), Suva Municipal Market, obtained by Huang D, Fiji, 11 December 2010. Others: **Fiji** – 1 male (47.7 × 40.2 mm) (ZRC 2010.416), Suva, Fiji, Laucala Bay Road, outside outer campus of University of South Pacific, Huang D, 1 December 2010. **New Caledonia** – 1 male (61.4 × 78.0 mm) (MNHN–B 24813), Loyalty Islands, Lifou Island, We Cave, coll. Richer de Forges B, 14 July 1993; 1 male (61.0 × 79.0 mm) (MNHN–B 24811), Loyalty Islands. **Palau** – 1 male (79.5 × 63.1 mm), 1 female (ZRC 2000.1087), Angaur Island, coll. Tan SH, September 1998; 1 male (87.4 × 68.3 mm) (ZRC 2000.1086), Angaur Island, coll. Tan SH, September 1998; 1 male (86.4 × 68.5 mm) (ZRC 2000.1088), Angaur Island, coll. Tan SH, September 1998. **Solomon Islands** – 1 male (54.2 × 45.3 mm) (QM-W15247), Tulagi Island, coll. Covacevich J, 15 December 1976; 1 male (46.5 × 39.2 mm), 1 female (57.0 × 49.0 mm) (QM-W15248), on road leaving Honiara, Guadalcanal, coll. Covacevich J, 15 December 1976; 1 male, 2 females (SMF 5865), Buka, Hanseatischen Südsee-Expedition, coll. Wolff E, 1909. **South Seas** – 1 male (SMF 5864), Maitland Island, Hanseatischen Südsee-Expedition, coll. Wolff E, 26 April 1909; 1 male, 1 female (SMF 5859), Südsee, don. Godeffroy Museum; 1 female (SMF 5863), Nissan Atoll, Pinipal, Hanseatischen Südsee-Expedition, coll. Wolff E, 8 May 1909. "**Hawaii**" – 1 male (33.1 × 28.1 mm) (MCZ Cru 5769) [photographs], "Oahu Island", coll. Mann H, 1 January 1864 – 31 December 1864. **Guam** – 1 male (93.5 × 73.4 mm) (ZRC 2001.2230), Pago Bay, coll. Louie, 31 July 2001; 1 male (66.6 × 54.0 mm) (ZRC 2001.0704), Merizo Bay, coll. Ng PKL, 1 August 2001; 1 female with zoeae (ZRC 2001.705), Merizo Bay, coll. Ng PKL, 1 August 2001. **Philippines** – 1 male (QM-W26690), in forest just outside of Virata Cave, Libaong, Panglao, Bohol, coll. Ng PKL et al., 18 December 2000; 1 male (ZRC 2001.310), Panglao, Bohol, coll. Ng PKL, 17 December 2000; 1 male (ZRC 2001.2308), Panglao, back beaches, coll. Liu H-C, 29 November 2001; 1 male (ZRC 2004.0462), Hinagdanan Cave vicinity, near Panglao Island Nature Resort, Panglao, Bohol, coll. Ng PKL, 3 March 2004; 2 females (SMF-ZMG 114), Manila, Luzon, or Bohol, coll. Semper K, 1876. **Taiwan** – 1 male (68.5 × 55.5 mm) (ZRC 1999.1039), 1 female (ZRC 1998.411), Hengchun Peninsula, Pingtung County, coll. Liu H-C & Tan SH, 22 May 1998; 2 males, 2 females (ZRC 1998.398, 439, 452, 472), Hengchun Peninsula, Pingtung, coll. Liu H-C et al., 19 May 1998; 2 males (larger 76.7 × 59.5 mm) (ZRC 1998.424), Hengchun Peninsula, Pingtung, coll. Liu H-C et al., 19 May 1998; 1 female (ZRC), Hengchun Peninsula, Pingtung County, coll. Liu H-C et al., May 1998; 1 male (ZRC 1999.203), Hengchun Peninsula, Pingtung County, coll. Ng PKL, 30 May 1997; 1 male (ZRC 1998.531), Hengchun Peninsula, Pingtung County, coll. Ng PKL, 13 May 1998; 1 male (NCHUZOOL 13640), Dongsha (= Pratas) Island, Kaohsiung City, coll. Shih H-T et al., 26 May 2012. **Japan** – 1 male (ZRC 1999.239), Yaeyama, Ryukyus, coll. 19 August 1969; 1 male (57.4 × 46.8 mm), 2 females (larger 64.2 × 53.7 mm), Kumejima Island, Ryukyus, coll. Ng PKL, November 2009; 1 female (ZRC 2009.0154), Funaura jetty and beach, Iriomote Island, Ryukyus, coll. Ng NK & Cai Y, 15 June 2000; 1 male (SMF 6372), Tokashiki, Ryukyus, coll. Sakai T, 24 September 1973; 1 male (SMF 6383), mangrove, Ishigaki Island, Ryukyus, coll. Sakai T; 1 male, 1 female (SMF 7709), Ishigaki Island, Ryukyus, coll. Watabe T; 1 male (SMF 6374), Tokashiki-Smaren, coll. Sakai T, 24 September 1973. **Indonesia** – 1 male (65.9 × 53.3 mm) (MZB Cru 112), Batavia, north Java, coll. Dammerman, November 1919; 1 male (88.9 × 68.0 mm) (MZB Cru 364), Pulau Dua, north of Jakarta, north Java, coll. Sabar F, 23 June 1970; 1 male, 1 female (ZRC 1965.12.1.11–12), Pulau Panjang, South Natuna Island, August 1931; 1 juvenile female (19.9 × 15.8 mm) (SMF 12012), Goa Peleug, cave, Leuggiling, Bukit Peninsula, Bali, coll. Dobat K, 12 August 1984; 1 male (54.5 × 44.1 mm) (ZRC 2003.0582), Geropok, Lombok, coll. local fisherman, 12 February 2002; 1 male (42.4 × 32.5 mm) (ZRC 2012.0712), Ambon, coll. Rahayu DL, 12–20 August 2012; 1 male (60.3 × 50.7 mm) (SMF 5623), Batjan (=Bacan), Moluccas, coll. Kükenthal Expedition; 1 male (SMF 5860), Ternate, coll. Kükenthal Expedition; 1 female (SMF 5862), Ternate, coll. Kükenthal Expedition. **Vanuatu** – 3 males, 3 females (ZRC), Loganville Market, from around Santo Island, coll. Ng PKL, 14 September 2006; 1 male (ZRC), near rocky areas at Maritime Centre, Santo, Vanuatu, coll. Ng PKL, 10 September 2006. **Vietnam** – 1 male (ZRC 1973.10.31.275), Vietnam, coll. Nhathrang Oceanographic Institute, 9 April 1971. **Malaysia** – 2 males (ZRC 2000.2583), Pulau Pemanggil, Johor, coll. Chia DGB, 11 September 1991. **Singapore** – 1 female (ZRC 1965.12.1.10), Paya Lebar, July 1938.

Diagnosis. In life, adult carapace with dorsal surfaces grey to various shades of brown, sometimes purplish-brown; ventral surfaces cream to dirty white or pale yellow; third maxillipeds with median parts dark purple to brown; cheliped pale purple and brown to orange and yellow to completely white, fingers orange, yellow to white (Figs. 1, 2A–F). Carapace with dorsal surface evenly convex tranversely and longitudinally, regions demarcated; epigastric regions swollen but margins defined, separated from frontal margin by transversely narrow concavity, just separated from postorbital cristae, without shallow furrow or groove; postorbital region gently swollen without trace of cristae, cervical groove distinct; postorbital and branchial regions clearly separated, especially from frontal view (Figs. 1, 2A–F, 5, 9A, B). In large adult males, chela very stout, broad; fingers elongated, subcylindrical (Figs. 1, 2A–F). Ambulatory legs in adults usually relatively slender, especially merus and propodus (Fig. 12A–F). Male abdomen relatively broader; somite 6 with lateral margin strongly convex, much broader than long; distal margin gently concave; telson triangular, longer than broad, lateral margins gently concave to almost straight, tip rounded (Fig. 10). G1 almost straight, relatively slender; G1 almost straight, relatively stouter; distal part relatively longer, bent laterally at angle of about 80° from vertical;

Table 2. Matrix of percentage pairwise nucleotide divergences with K2P distance (lower left) and mean number of differences (upper right) based on 658 bp of COI within and between species of *Discoplax*. Values of range are shown in parentheses.

	Intraspecific		Interspecific					
	Nucleotide divergence	Mean nucleotide difference	*D. hirtipes*	*D. rotunda*	*D. magna*	*D. celeste*	*D. longipes*	*D. gracilipes*
D. hirtipes	0.67 (0–1.7)	4.34 (0–11)	—	20.95 (17–24)	27.6 (20–31)	23.93 (20–27)	70.2 (68–72)	65.13 (64–66)
D. rotunda	0.12 (0–0.3)	0.8 (0–2)	3.29 (2.65–3.79)	—	26.6 (25–29)	25.73 (25–28)	70.4 (70–71)	64.4 (64–65)
D. magna	0.27 (0–0.61)	1.78 (0–4)	4.37 (3.12–4.93)	4.2 (3.93–4.6)	—	6.93 (6–10)	71.8 (71–73)	67.8 (67–69)
D. celeste	0.08 (0–0.61)	0.5 (0–4)	3.76 (3.13–4.27)	4.06 (3.94–4.43)	1.06 (0.92–1.54)	—	75 (—)	71 (—)
D. longipes	0.3 (—)	0 (—)	11.82 (11.4–12.17)	11.86 (11.78–11.98)	12.09 (11.93–12.33)	12.71 (12.7–12.72)	—	10 (—)
D. gracilipes	—	—	10.88 (10.67–11.04)	10.74 (10.67–10.85)	11.35 (11.2–11.57)	11.95 (—)	1.54 (—)	—

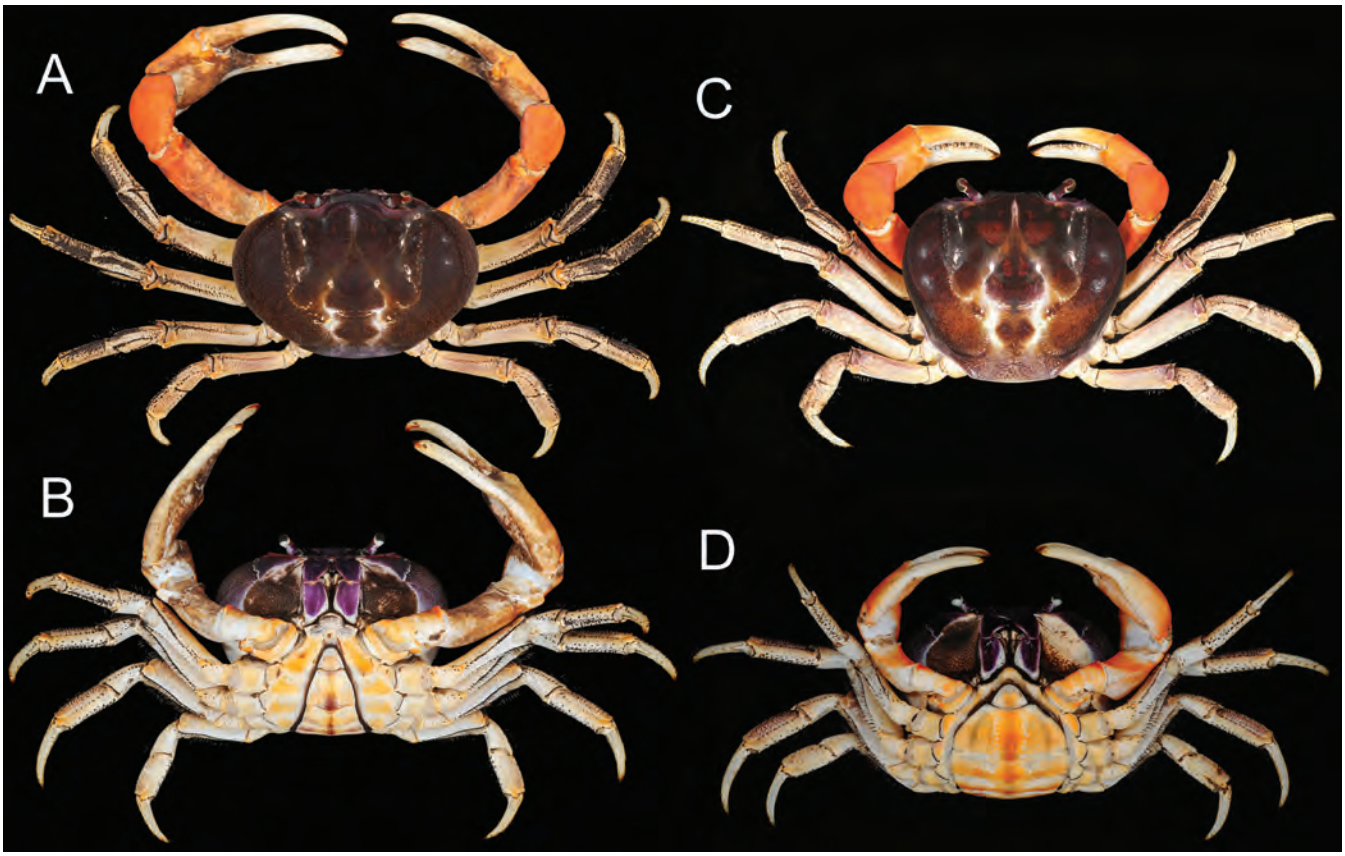

Fig. 4. Colours in life, *Discoplax magna* sp. nov. A, B, paratype male (104.4 × 81.2 mm) (ZRC 2012.0011); C, D, paratype female (83.8 × 72.4 mm) (ZRC 2012.0011). Both specimens from Similan Islands, western Thailand (photographs: HH Tan).

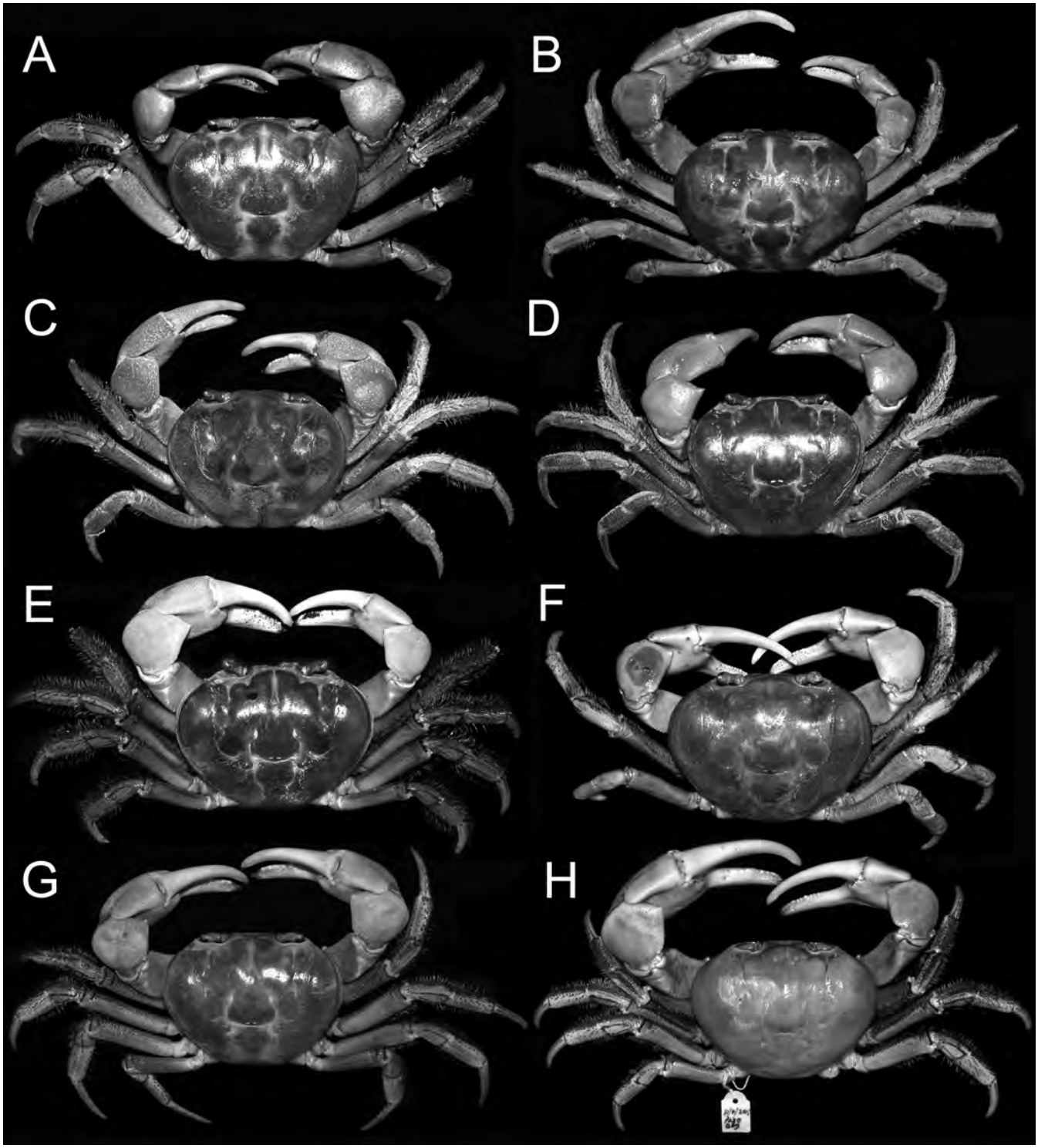

Fig. 5. Overall dorsal views, *Discoplax hirtipes* (Dana, 1851). A, neotype male (64.2 × 53.0 mm) (ZRC 2010.0415), Fiji; B, male (87.4 × 68.3 mm) (ZRC 2000.1086), Angaur Island, Palau; C, male (54.5 × 44.1 mm) (ZRC 2003.0582), Lombok; D, male (57.4 × 46.8 mm), Kumejima Island, Japan; E, male (68.8 × 52.0 mm) (ZRC 2004.462), Panglao, Philippines; F, male (76.7 × 59.5 mm) (ZRC 1998.424), Taiwan; G, male (73.5 × 58.4 mm) (ZRC 2001.0706), Merizo Bay, Guam; H, male (93.5 × 73.4 mm) (ZRC 2001.2230), Pago, Guam.

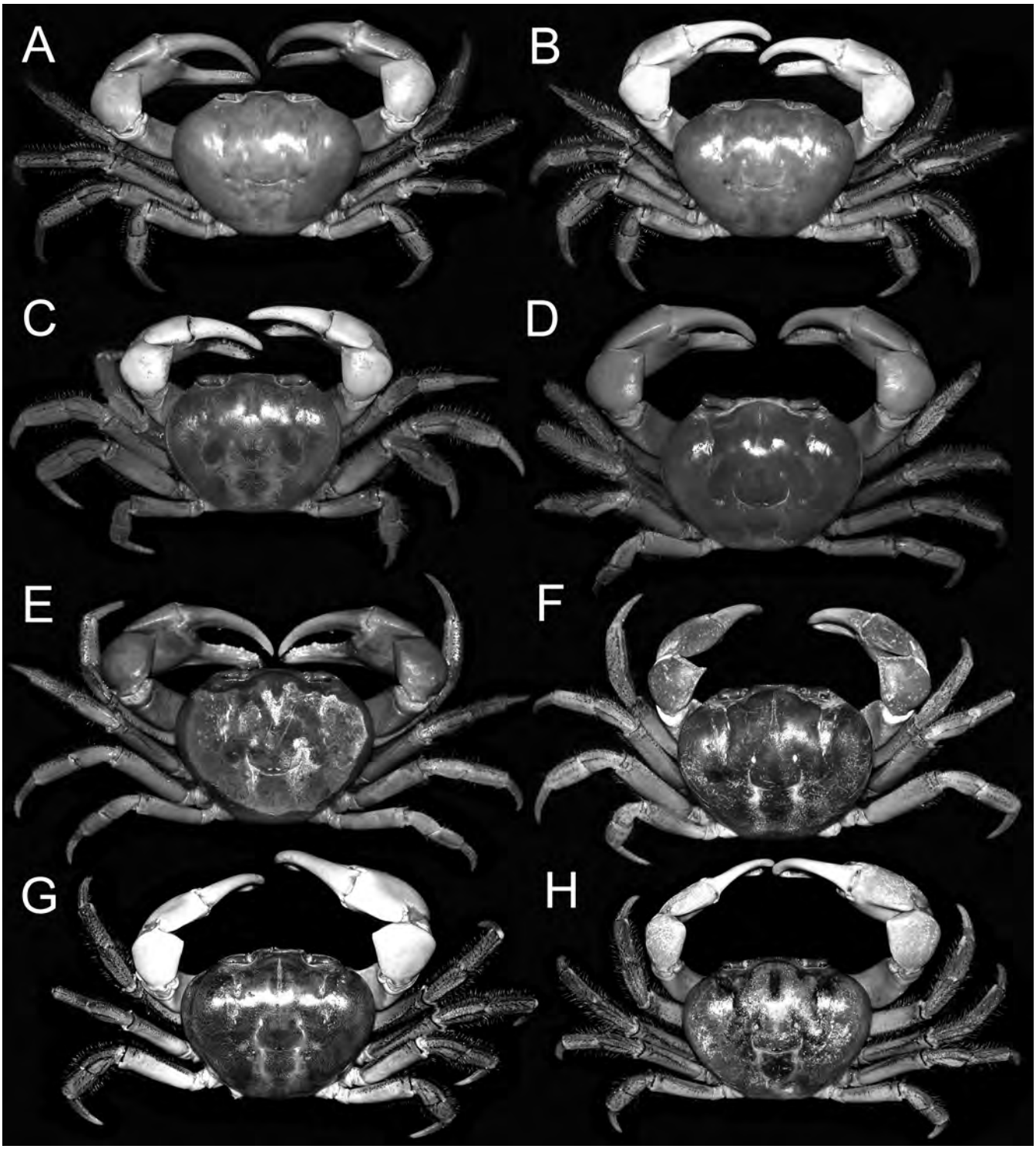

Fig. 6. Overall dorsal views of *Discoplax* species. A–C, *D. celeste* Ng & Davie, 2012; D–H, *D. magna* sp. nov. A, holotype male (106.0 × 83.6 mm) (ZRC 2011.0168), Waterfall Bay, Christmas Island; B, paratype male (84.3 × 65.7 mm) (ZRC 2011.0166), Waterfall Bay, Christmas Island; C, paratype male (52.0 × 44.0 mm) (ZRC), Christmas Island; D, male (74.6 × 61.9 mm) (ZRC 1965.12.1.30–39), Nicobar Islands; E, male (69.7 × 55.5 mm) (ZRC 1965.12.1.25), Mentawei Islands; F, male (51.1 × 42.5 mm) (ZRC 2008.0575), Pantai Cerocok, Sumatra; G, male (77.8 × 60.5 mm) (MZB Cru 3753), Pantai Permisan, Java; H, male (83.1 × 68.1 mm) (ZRC 2012.0004), Waterfall Bay, Christmas Island.

distal-most part pectinated, upper part sharply tapering to acute tip, lower part angular (Fig. 13A–E).

Description. Carapace transversely ovate to subovate, broader than long; dorsal surface evenly convex tranversely and longitudinally, surface smooth, glabrous; regions not well demarcated but discernible; cervical groove distinct, not distinctly joining H-shaped gastro-cardiac median depression prominent (Figs. 1, 2A–F, 5). Epigastric regions prominent but margins poorly defined, not cristate, separated from each other by deep, median Y-shaped furrow which bifurcates posteriorly; prominently anterior to and distinctly separated from postorbital cristae by cervical groove (Figs. 1, 2A–F, 5). Postorbital region gently swollen without cristae, separated submedially by short longitudinal furrow, proximal part almost reaching cervical groove (Figs. 1, 2A–F, 5). Subhepatic and suborbital regions smooth, glabrous; pterygostomial region covered with dense short setae which completely obscure surface, setae just reaching inner suborbital surface (Figs. 1D, F, H, 2A, C).

Frontal region gently upturned to form shallow concave shelf between it and epigastric regions; front deflexed downwards; frontal margin almost straight to slightly sinuous from dorsal and frontal views; margin deflexed inwards to form relatively broad subtrapezoidal plate which joins proepistome (Figs. 1, 2A–F, 5, 9A, B). Epistome longitudinally narrow; posterior margin with sharp triangular median lobe, lateral margins concave (Figs. 1F, 2A, 9A, B). Supraorbital margin gently sinuous, cristate, smooth (Figs. 1, 2A–F, 5); suborbital margin gently curved, not fusing with supraorbital margin laterally, leaving large gap. Orbit large, subovate; eye filling about half of orbit; eye peduncle short; cornea large (Figs. 5, 9A, B). External orbital tooth broadly triangular, low, tip not over-reaching orbit, not extending beyond frontal margin, outer margin almost straight, almost confluent with anterolateral margin (Fig. 5). Anterolateral margin strongly convex, rounded, smooth, without distinct cristae in adults, ridges or granules; gradually curving to meet posterolateral margin (Fig. 5). Posterolateral margin gently convex to slightly sinuous, smooth, rounded; strongly converging towards gently sinuous posterior carapace margin (Fig. 5). Basal article of antenna subquadrate, separated from frontal margin by distinct gap; article 4 small, not closing hiatus between frontal margin and ocular peduncle (Fig. 9A, B). Antennules relatively small, folding sub-obliquely (Fig. 9A, B). Buccal cavity relatively broad, third maxillipeds not closing anterior part, visible as distinct transverse gap (Figs. 1F, 2A, 9A, B). Third maxillipeds relatively elongate, meri and ischia forming rhomboidal gape when closed; merus subquadrate, anterior and outer lateral margins concave, median surface gently depressed; ischium subquadrate with distinct oblique submedian sulcus; exopod slender, tip reaching to about half length of merus, flagellum long (Fig. 9A, B).

Chelipeds subequal; surfaces smooth to gently rugose (Figs. 1, 2A–F, 5). Merus short, dorsal margin rugose or with striae, not serrated or granular; ventral margin with low granules. Carpus rounded, with large broadly triangular inner subdistal tooth (Figs. 1, 2A–F, 5). Chela large, swollen, surfaces

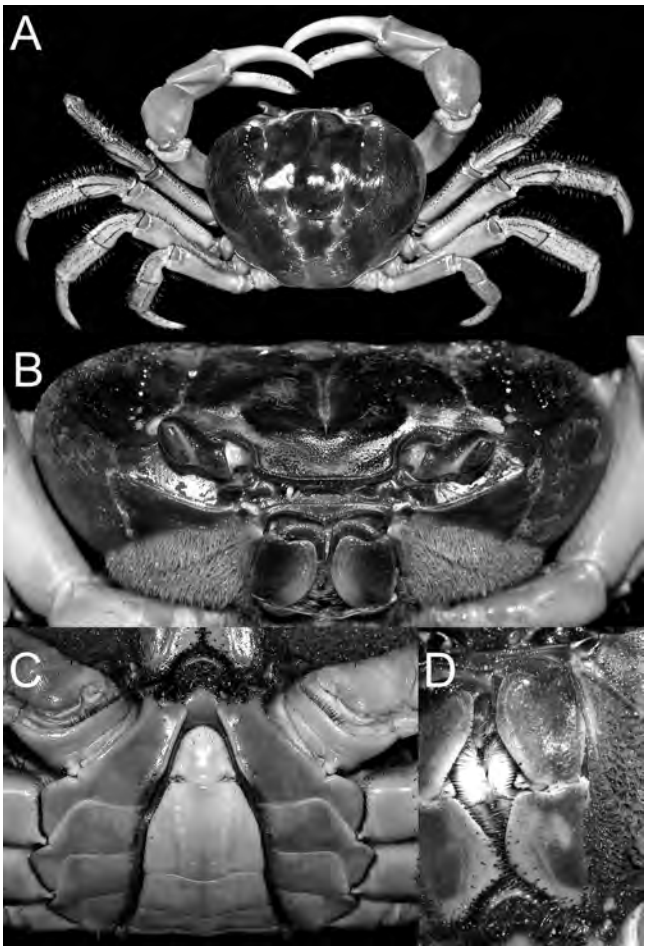

Fig. 7. *Discoplax magna* sp. nov., holotype male (96.7 × 80.1 mm) (ZRC 2012.0010), Similan Islands, western Thailand. A, overall dorsal view; B, frontal view of carapace; C, anterior male thoracic sternum and male abdominal somites 4–6 and telson; D, left third maxilliped.

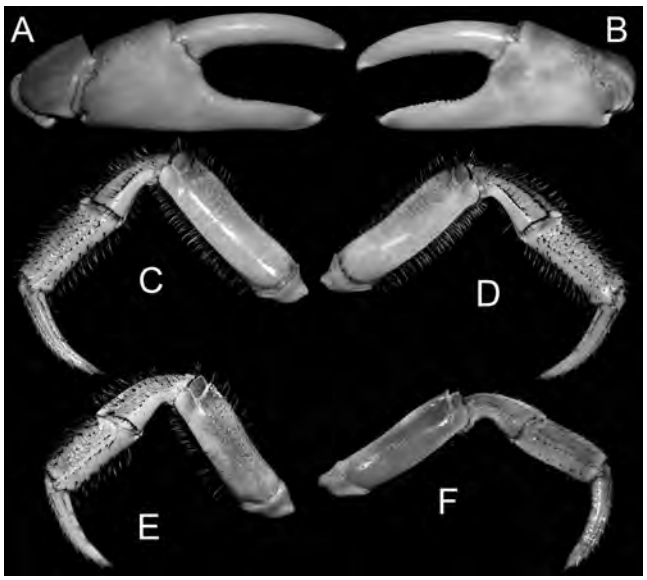

Fig. 8. *Discoplax magna* sp. nov., holotype male (96.7 × 80.1 mm) (ZRC 2012.0010), Similan Islands, western Thailand. A, outer view of right chela; B, outer view of left chela; C, left third ambulatory leg; D, right third ambulatory leg; E, left fourth ambulatory leg; F, right fourth ambulatory leg (regenerated).

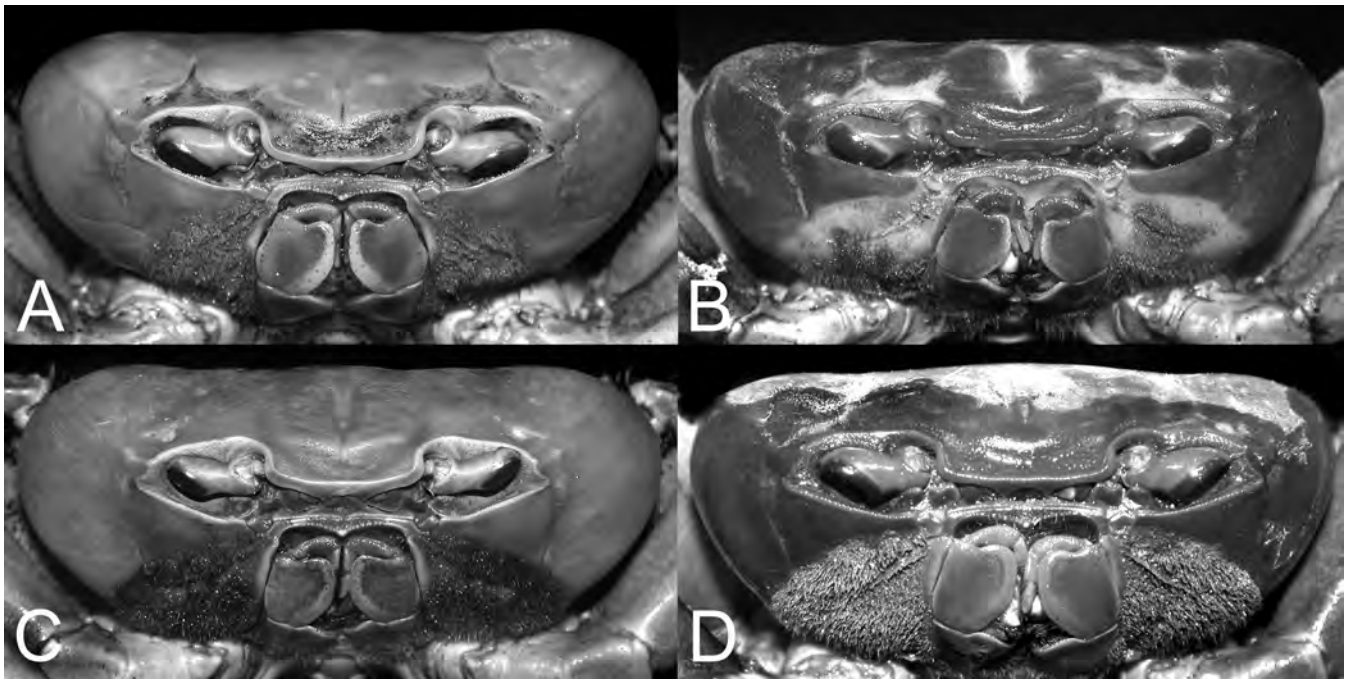

Fig. 9. Frontal carapace views of *Discoplax* species. A, B, *D. hirtipes* (Dana, 1851); C, *D. celeste* Ng & Davie, 2012; D, *D. magna* sp. nov. A, male (93.5 × 73.4 mm) (ZRC 2001.2230), Pago, Guam; B, male (87.4 × 68.3 mm) (ZRC 2000.1086), Angaur Island, Palau; C, holotype male (106.0 × 83.6 mm) (ZRC 2011.0168), Waterfall Bay, Christmas Island; D, male (74.6 × 61.9 mm) (ZRC 1965.12.1.30–39), Nicobar Islands.

smooth to gently rugose; lower margin of palm sinuous; fingers slender, curved, longer than palm; cutting margins with low denticles along length, distal-most part pectinated, tip gently recurved; fingers in adults subcylindrical, forming large gape between them when closed (Figs. 1, 2A–F, 5).

Ambulatory legs not elongated, second pair longest, last pair shortest; segments relatively long, slender (especially merus and propodus); surfaces slightly rugose (Figs. 1, 2A–F, 5, 12A–F). Merus relatively slender, laterally flattened, cross-section subovate; dorsal margin usually uneven, covered with striae or rugose, not granulated or serrate, subdistal angle low, not dentiform; margins lined with dense, long, stiff setae that partially obscure margins (Fig. 12A–F). Carpus slender; outer surface with 2 low, subparallel carinae; margins and carinae lined with dense long, stiff setae (Fig. 12A–F). Propodus rectangular; lateral margins subparallel or gently tapering distally, lined with dense stiff setae, outer median surface with longitudinal row of short stiff setae; anterior distal margin with rounded lobe into which dactylus fits (Fig. 12A–F). Dactylus elongate, styliform, gently curving, subquadrate in cross-section, margins lined with strong short spines and scattered short setae; tip corneous (Fig. 12A–F).

Thoracic sternites 1 and 2 completely fused, forming small semi-circular plate, surface covered with dense short setae that may obscure surface (especially in smaller specimens); anterior margin with rounded cristae; separated from sternite 3 by gently convex suture; sternites 3 and 4 completely fused without trace of suture; sternite 3 longitudinally narrow, sternite 4 large (Fig. 10). Sterno-abdominal cavity relatively broad, reaching almost to approximate position between sternites 3 and 4, level with imaginary line joining anterior edges of coxae of chelipeds (Fig. 10).

Male abdomen relatively broad, all somites and telson free; lateral margins of somites lined with short setae (Fig. 10). Somite 1 longitudinally very narrow; somite 2 similar in shape to somite 1 but relatively broader longitudinally; somites 1 and 2 completely occupying space between coxae of last ambulatory leg, thoracic sternite 8 not visible; somites 3–5 increasingly trapezoidal in shape, all lateral margins convex; somite 6 trapezoidal, distinctly wider than long, lateral margins distinctly convex especially along distal part, distal margin gently concave (Fig. 10). Telson triangular, wider than long, lateral margins gently concave to almost straight or sinuous, tip rounded (Fig. 10).

G1 almost straight, relatively stout; distal surfaces adjacent to pectinated tip densely lined with long, stiff setae which completely obscure structure and margins except for tip, rest of surface with scattered long, short soft setae; tip bent laterally at angle of about 80° from vertical; outer surface of distal part deeply concave; distal part of inner margin prominently convex, forming hump-like structure; subdistal part of dorsal (sternal) surface with elongated ovate flap which is appressed to main structure, distal margin convex, lined with dense stiff setae; distal part relatively longer, pectinated, beak-like, upper part sharply tapering to sharp tip, lower part angular (Fig. 13A–E). G2 short, ca. 0.2 times length of G1; tip spatulate.

Remarks. The original description of *Discoplax hirtipes* by Dana (1851, 1852) is relatively brief but has enough characters to conclusively identify his taxon and differentiate it from congeners at the time. In his first diagnosis of the species, Dana (1851: 253) wrote: "CARDISOMA HIRTIPES.—

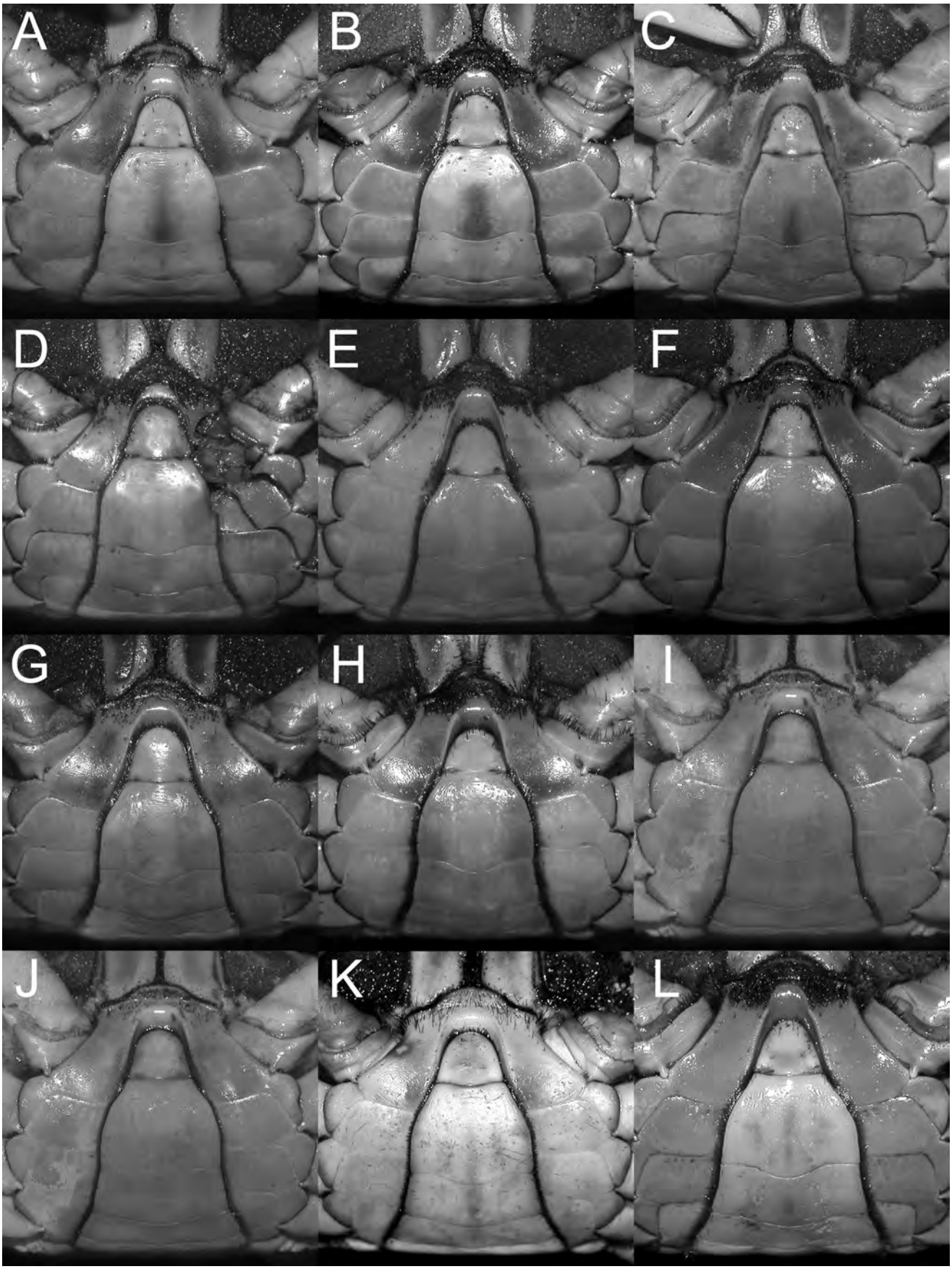

Fig. 10. Male anterior thoracic sternums and male abdomens, *Discoplax hirtipes* (Dana, 1851). A, neotype male (64.2 × 53.0 mm) (ZRC 2010.0415), Fiji; B, male (79.5 × 63.1 mm) (ZRC 2000.1087), Palau; C, male (87.4 × 68.3 mm) (ZRC 2000.1086), Angaur Island, Palau; D, male (54.5 × 44.1 mm) (ZRC 2003.0582), Lombok; E, male (73.5 × 58.4 mm) (ZRC 2001.0706), Merizo Bay, Guam; F, male (93.5 × 73.4 mm) (ZRC 2001.2230), Pago, Guam; G, male (57.4 × 46.8 mm), Kumejima Island, Japan; H, male (68.8 × 52.0 mm) (ZRC 2004.462), Panglao, Philippines; I, male (76.7 × 59.5 mm) (ZRC 1998.424), Taiwan; J, male (68.5 × 55.5 mm) (ZRC 1999.1039), Taiwan; K, male (42.4 × 32.5 mm) (ZRC 2012.0712), Ambon; L, male (88.9 × 68.0 mm) (MZB Cru 364), Pulau Dua, north Java.

Carapax longitudinaliter convexus, margine laterali antice notatus, prope dentem post-orbitalem minute apiculato, areolâ praemedianâ antice juxta frontem paulo abruptâ, regione pterygostomianâ pilosâ. Processus praeorbitalis orbitam antennamque externam sejungens triangulatus, trihedricus. Articulus antennae externae 1mus rectangulatus apice recte truncatus. Pedes *maris* antici crassi, subaequi, sat breves, manu punctatâ, digitis late hiantibus. Pedes postici hirti. *Long*. carapacis *maris* 22½"; lat. 28"; long. frontis 7½"; lat. areae buccalis antice 5⅜", postice 8¼". *Hab*. insulis 'Viti.'"

In his more detailed treatment a year later, Dana (1852: 376–377), with figures, expanded on the diagnosis as follows: "*Carapax longitudinaliter convexus, margine laterali anticè notatus, prope dentem post-orbitalem minutè apiculato, areolâ praemedianâ antice juxta frontem paulo abruptâ, regione pterygostomianâ pilosâ. Processus praeorbitalis orbitam antennamque externam sejungens triangulatus, trihedricus. Articulus antennarum externarum 1mus rectangulatus apice rectè truncatus. Pedes* maris *antici crassi, subaequi, sat breves, manu punctatâ, breviore quam latitudo carapacis, parte manus ante digitos breviore quam altiore, digitis late hiantibus. Pedes postici hirti.* [Carapax longitudinally convex, lateral margin having a border anteriorly and a minute point near the postorbital angle, praemedian areolet near margin of front quite abrupt, pterygostomian region pilose. Process between orbit and outer antennas triangular, trihedral. First joint of outer antennas rectangular, truncate across above. Anterior feet of *male* short but stout, subequal, hand punctate, shorter than breadth of carapax, along upper margin to finger much shorter than high, fingers much gaping. Posterior feet rough hairy.] Plate 24, fig. 2 *a*, male, natural size; *b*, male abdomen and sternum; *c*, base of outer antennae and the adjoining process between it and orbit; *d*, tarsus of fourth pair, enlarged. Feejee Islands, Pacific. Length of carapax of male, twenty-two and a half lines; breadth, twenty-eight lines; length of front, seven and a half lines; breadth of buccal area anteriorly, five and two-thirds lines; posteriorly, eight and one-fourth lines; length of upper margin of hand to finger, eight lines; height, thirteen and a half lines; whole length of hand, twenty-three lines. The angle on the lateral margin is continued through nearly half the length of the sides. The third joint of the eight posterior legs forms an edge above, which edge is hairy as well as the lower margin. Carpus entire and smooth, nearly rectangular and subacute on inner side. The line between the medial and posterior regions of the carapax, is situated much posterior to the middle of the carapax. *C. hirtipes*, DANA, Proc. Acad. Nat. Sci. Philad., v. 253."

Evans (1967: 410) reported there was a dried type specimen of *Cardisoma hirtipes* in the British Museum (Natural History) (present NHM) with the catalogue number 61.44. Ng & Clark (2014) showed that this specimen is not a type specimen of the species, and that it may have been accidentally and/or incorrectly labelled in the past. In any case, the specimen figured by Dana (1855: pl. 24 fig. 4) agrees very well with what is here defined as *Discoplax hirtipes* and not *Cardisoma carnifex*. Ng & Davie (2012), in describing a sister species from Christmas Island, believed that the type of *Cardisoma hirtipes* Dana, 1851, was no longer extant, and argued a neotype male was necessary. To this effect, they selected a fresh male specimen with colour and molecular data from Fiji measuring 64.2 × 53.0 mm (ZRC 2010.0415) (Figs. 1A, 5A) as the neotype of *Cardisoma hirtipes* Dana, 1851. This specimen remains as the neotype in view of the supposed type in NHM not been the syntype of the species.

Türkay's (1974: 233) records of "*Cardisoma hirtipes*" include all three species. His material from Fiji, New Hebrides, Bismarck Archipelago, New Britain, Caroline Islands, Solomon Islands, New Guinea, Moluccas, northern Java and Japan are clearly *D. hirtipes* s. str. His material from Christmas Island has been referred to *D. celeste* by Ng & Davie (2012). Türkay's (1974) records from southern Java, Mentawei, Andaman and Nicobar Islands should now be referred to *D. magna* sp. nov. The specimen figured by Türkay (1974: 231, fig. 12) is a large male (92.4 × 72.0 mm, SMF 4147) collected from an unspecified location in Java by S. Strubell. Its carapace, male abdominal structure (Fig. 11K) and G1 structures agree with *D. magna* sp. nov., and it was probably collected from the southern part of the island.

The records of *D. hirtipes* from Madagascar (cf. Alcock, 1900: 448) and New Zealand (cf. Heller, 1865: 35; see also Hutton, 1882; Filhol, 1886) are clearly erroneous and have been discussed at length by Türkay (1974: 234). The only record of this species from Madagascar was by Alcock (1900: 448) who indicated he had specimen(s) from there. However, there are no other records of *Discoplax hirtipes* (or its sister species discussed here) west of Christmas Island, and we agree with Türkay (1974) this record should be discounted. In any case, the species is no longer regarded as part of the fauna of New Zealand (see Hutton, 1882: 264). The record from Hawaii is also almost certainly wrong, as the species is not known from that far in the east. Türkay (1974) examined a specimen supposedly from Hawaii and accepted the dubious record. In his review of the Hawaiian fauna, Castro (2011: 113) commented that "Rathbun (1906: 838) listed two specimens of *Discoplax rotunda* (Quoy & Gaimard, 1824) (as *Cardisoma rotundum*) collected in Oahu in 1864 and deposited in MCZ (lot 5769) [Museum of Comparative Zoology, Harvard University]. No additional Hawaiian Is. records of gecarcinid land crabs exist [see Edmondson (1962), who lists Rathbun's record as *C. hirtipes* Dana, 1852, a distinct species]. *Discoplax rotunda* occurs in other Pacific islands, including the Line Islands, but there are no known subsequent records from the Hawaiian Islands. Both *D. hirtipes* and *D. rotunda* were nevertheless listed as occurring in the archipelago by Sakai (1976, both as species of *Cardisoma*) and *D. rotunda* questionably by McLaughlin et al. (2005). P.K.L. Ng (personal communication) agrees that these records are 'almost certainly the result of mislabelling'. Paulay & Starmer (2011) similarly concluded that the MCZ lot most probably did not originate in the Hawaiian Is." The authors managed to examine one of specimens in question in the MCZ—it is a small specimen of *D. hirtipes* without any doubt. The original data in the bottle in MCZ states there was also a female specimen but it cannot be found.

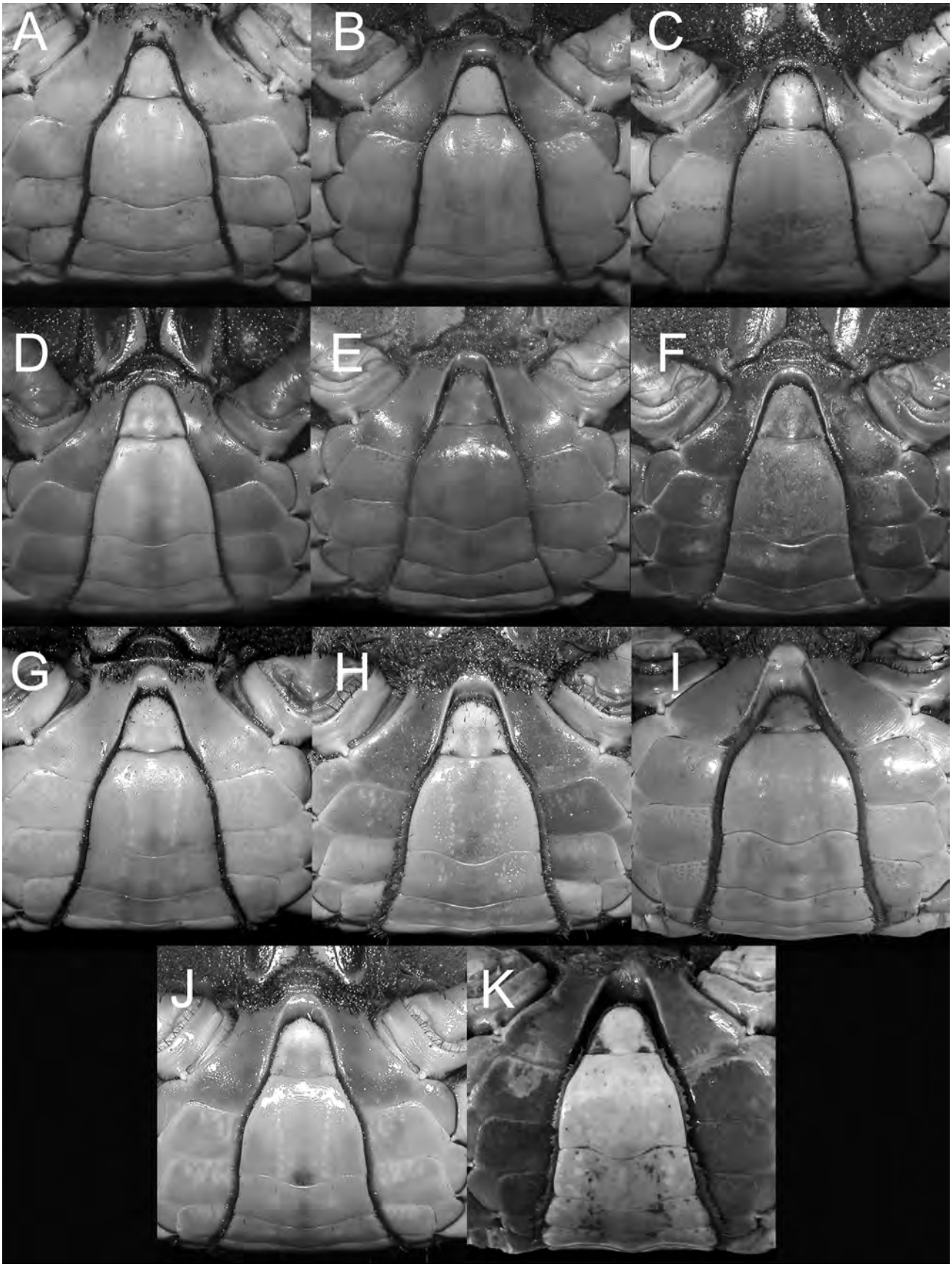

Fig. 11. Male anterior thoracic sternums and male abdomens, *Discoplax* species. A–C, *D. celeste* Ng & Davie, 2012; D–I, *D. magna* sp. nov. A, holotype male (106.0 × 83.6 mm) (ZRC 2011.0168), Waterfall Bay, Christmas Island; B, paratype male (84.3 × 65.7 mm) (ZRC 2011.0166), Waterfall Bay, Christmas Island; C, paratype male (52.0 × 44.0 mm) (ZRC), Christmas Island; D, male (51.1 × 42.5 mm) (ZRC 2008.0575), Pantai Cerocok, Sumatra; E, male (69.7 × 55.5 mm) (ZRC 1965.12.1.25), Mentawei Islands; F, male (74.6 × 61.9 mm) (ZRC 1965.12.1.30–39), Nicobar Islands; G, male (77.8 × 60.5 mm) (MZB Cru 3753), Pantai Permisan, Java; H, male (83.1 × 68.1 mm) (ZRC 2012.0004), Waterfall Bay, Christmas Island; I, paratype male (97.4 × 79.1 mm) (CUNHM), Similan Islands, western Thailand; J, paratype male (74.2 × 63.4 mm) (ZRC 2012.0011), Similan Islands, western Thailand; K, male (92.4 × 72.0 mm) (SMF 4147), Java.

The sole record of this species from Tahiti in French Polynesia was based also on Heller (1865: 35) but this is also very doubtful as the species has not been found there since, even though it was accepted as valid by Türkay (1974) and has been included in the faunal lists by Guinot (1985) and Poupin (1994, 1996, 2005). Guinot (1985) expressed doubt but retained this record with reservation. Interestingly, it is not listed by Poupin & Juncker (2010), although three other gecarcinids are known from that area (see also Ng et al., 2011). In addition, there is also no record from Wallis & Futuna (Poupin, 2008), so the easternmost distribution is Fiji (Fig. 15). In any case, the problems with the collection data of Heller have been discussed at length by Pretzmann (1964), who noted that the mistakes in localities are always towards the east; with the real locality invariably to the west (see also McLaughlin & Dworschak, 2001). This may suggest that his "Tahiti" is probably closer to Australia.

Discoplax celeste Ng & Davie, 2012
(Figs. 2G, H, 6A–C, 9C, 11A–C, 12G–I, 13F–J)

Cardisoma carnifex – Andrews, 1900: 164 (not *Cancer carnifex* Herbst, 1796).

Cardisoma hirtipes – Balss, 1934: 236; Gibson-Hill, 1947: 48; Tweedie, 1947: 35; Türkay, 1974: 229 (part); George, 1978: 6; Hicks et al., 1984: 54; Hicks et al., 1990: 54; Ng, 1998: 1151 (part); Morgan, 2000: 123 (not *Cardisoma hirtipes* Dana, 1851).

Discoplax hirtipes – Ng & Guinot, 2001: 334, 335 (part); Davie, 2002: 185 (not *Cardisoma hirtipes* Dana, 1851).

Discoplax celeste Ng & Davie, 2012: 90, figs. 1–4, 6C, 6D, 7F–J; Orchard, 2012: 13, 130–143, 25 unnumbered figs. Shih, 2013: 26, fig. 5.

Diagnosis. In life, adult carapace with dorsal surfaces blue to bluish-white; ventral surfaces white to dirty white; third maxillipeds with median parts blue; cheliped pale blue to completely white, fingers white (Fig. 2G, H). Carapace with dorsal surface evenly convex tranversely and longitudinally, regions poorly demarcated; epigastric regions swollen but margins poorly defined, separated from frontal margin by transversely narrow concavity, barely separated from postorbital cristae, without distinct furrow or groove; postorbital region gently swollen without trace of cristae, cervical groove shallow; postorbital and branchial regions appear more confluent, especially from frontal view (Figs. 2G, H, 6A–C, 9C). In large adult males, chela very stout, broad; fingers elongated, subcylindrical (Fig. 2G, H). Ambulatory legs in adults relatively stout, short, especially merus and propodus (Fig. 12G–I). Male abdomen relatively broad; somite 6 with lateral margin strongly convex, just broader than long; distal margin gently concave; telson triangular, longer than broad, lateral margins gently concave to almost straight, tip rounded (Fig. 11A–C). G1 almost straight, relatively slender; G1 almost straight, relatively slender; distal part relatively short, bent laterally at angle of about 80° from vertical; distal-most part pectinated, upper part sharply tapering to acute tip, lower part subtruncate (Fig. 13F–J).

Material examined. Holotype: male (106.0 × 83.6 mm) (QMW-29123 ex ZRC 2011.0168), Waterfall Bay, near Christmas Island Resort, Christmas Island, 30 January 2010. Paratypes: 1 male (41.9 × 36.5 mm) (QM-W8258), coll. Covacevich J, February 1980; 1 male, 3 females (ZRC 1965.12.1.21–24), Ross Hill, coll. Gibson-Hill CA, August–September 1932; 1 male (ZRC 2012.0026), Ross Hill Spring, coll. Orchard M, 30 May 2005; 7 males, 1 female (ZRC 1965.12.1.13–20), coll. Tweedie MWF, 1932; 1 male (68.3 × 50.2 mm), 3 females (largest 75.5 × 60.0 mm) (ZRC 1965.12.1.21–24), coll. Tweedie MWF, August–September 1932; 3 females (ZRC 2012.0020), station CI 11, Hosnie's Springs, freshwater spring, uplifted *Bruguiera* patch, sandy and limestone bedrock, 10°28.650'S, 105°41.491'E, coll. CI 2010 expedition team, 24 January 2010; 5 males (largest 103.9 × 80.5 mm), 3 females (largest 81.3 × 60.3 mm) (ZRC 2012.0015), station CI 11, Hosnie's Springs, freshwater spring, uplifted *Bruguiera* patch, sandy and limestone bedrock, 10°28.650'S, 105°41.491'E, coll. CI 2010 expedition team, 24 January 2010; 6 males (ZRC 2012.0027), station CI 11, Hosnie's Springs, freshwater spring, uplifted *Bruguiera* patch, sandy and limestone bedrock, 10°28.650'S, 105°41.491'E, coll. CI 2010 expedition team, 24 January 2010; 1 male (44.4 × 38.7 mm), 4 females (15.9 × 14.1 mm, 22.3 × 19.0 mm, 27.5 × 23.5 mm, 39.0 × 34.0 mm), 1 juvenile (7.9 × 7.1 mm) (ZRC 2012.0028), station CI 32, Hugh's Dale, freshwater springs, gravel muddy substrate and limestone blocks, 10°28.716'S, 105°33.556'E, coll. CI 2010 expedition team, 3 February 2010; 3 young males, 4 young females, 1 juvenile (ZRC 2012.0019), 2 males (ZRC 2012.0017), station CI 32, Hugh's Dale, freshwater springs, gravel muddy substrate and limestone blocks, 10°28.716'S, 105°33.556'E, coll. CI 2010 expedition team, 3 February 2010; 2 males (larger 103.9 × 77.8 mm) (ZRC 2012.0025), The Dales, coll. CI 2010 expedition team, 3 February 2010; 2 males (ZRC 2012.0016), station CI 14, Whip Cave, along road to Waterfall Bay, in anchialine cave, loamy substrate, limestone bedrock, 10° 25.377'S, 105° 42.081'E, coll. CI 2010 expedition team, 27 January 2010; 2 females (42.4 × 35.8 mm, 47.1 × 39.2 mm) (ZRC 2012.0018), 2 males (99.3 × 80.8 mm, 60.9 × 51.1 mm), 2 females (75.4 × 61.4 mm, 80.6 × 66.1 mm) (QM-W29121), station CI 23, Waterfall Bay, near Christmas Island Resort, freshwater stream, sandy beach, limestone base rock, 10°27.54'S, 105°42.30'E, coll. CI 2010 expedition team, 30 January 2010; 1 male (84.3 × 65.7 mm) (ZRC 2011.0166), stream near Waterfall Bay, before entrance of Christmas Island Resort, coll. Ng PKL, January 2010; 1 female (82.7 × 66.3 mm) (ZRC 2011.0167), stream near Waterfall Bay, before entrance of Christmas Island Resort, coll. CI 2010 expedition team, January 2010; 5 males, 1 female (ZRC 2011.0169), station CI 07, stream near Waterfall Bay, before entrance of Christmas Island Resort, 23 January 2010; 4 males (largest 103.5 × 80.5 mm), 1 female (98.0 × 85.0 mm) (ZRC 2012.0022), Waterfall Bay, February 2010; 1 male (104.9 × 82.7 mm) (ZRC 2012.0023), stream near Waterfall Bay, before entrance of Christmas Island Resort, coll. CI 2010 expedition team, March 2010; 1 female (82.6 × 65.7 mm) (ZRC 2012.0024), Waterfall Bay, coll. CI 2010 expedition team January–February 2010; 2 males (larger 112.7 × 88.5 mm) (ZRC 2012.0014), stream near Waterfall Bay, before entrance of Christmas Island Resort, coll. CI 2011 expedition team, March 2011; 3 males (99.3 × 80.8 mm, 103.8 × 80.4 mm, 111.2 × 85.6

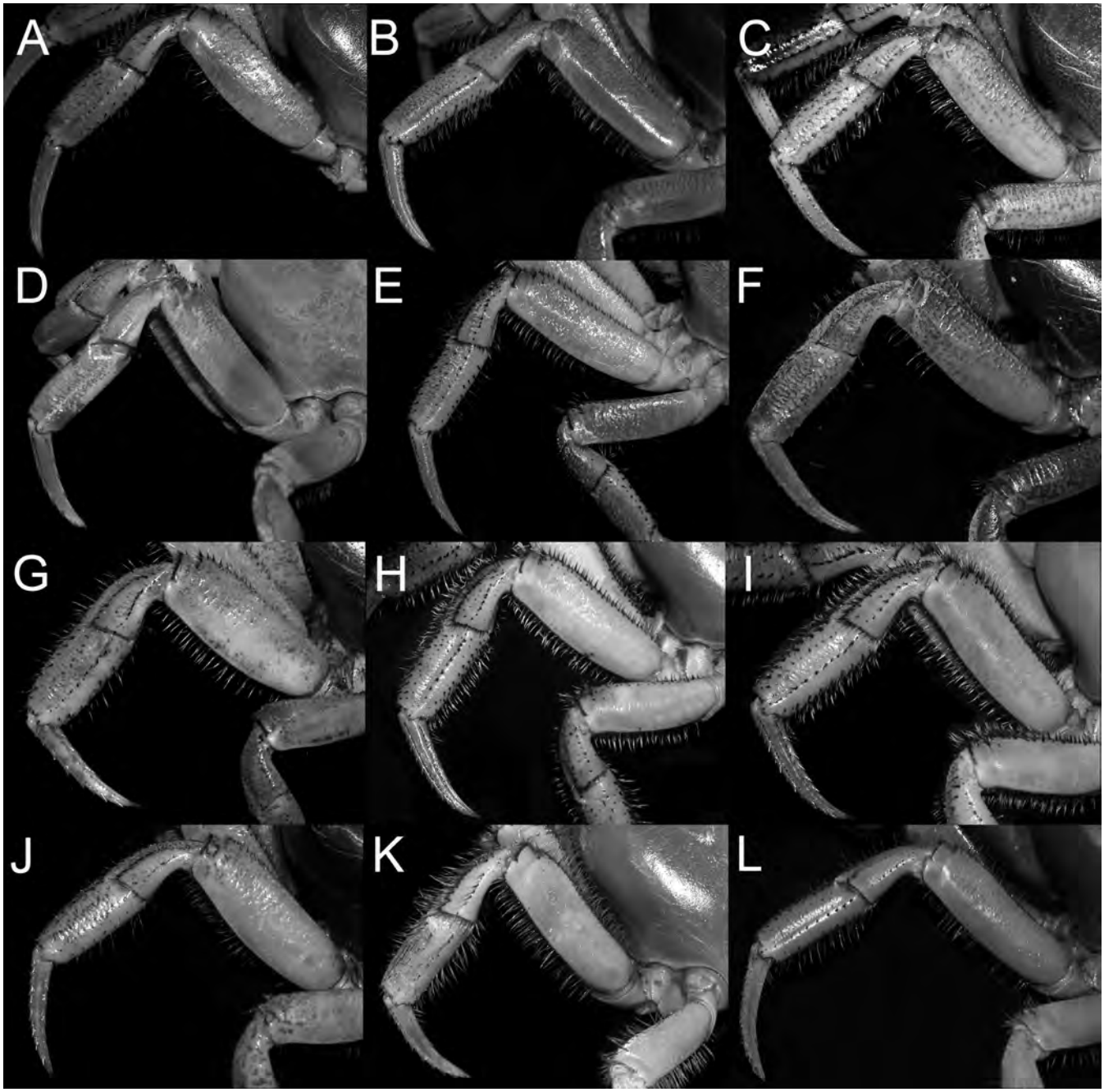

Fig. 12. Left fourth ambulatory legs, *Discoplax* species. A–F, *D. hirtipes* (Dana, 1851); G–I, *D. celeste* Ng & Davie, 2012; J–L, *D. magna* sp. nov. A, neotype male (64.2 × 53.0 mm) (ZRC 2010.0415), Fiji; B, male (87.4 × 68.3 mm) (ZRC 2000.1086), Angaur Island, Palau; C, male (54.5 × 44.1 mm) (ZRC 2003.0582), Lombok; D, male (68.5 × 55.5 mm) (ZRC 1999.1039), Taiwan; E, male (73.5 × 58.4 mm) (ZRC 2001.0706), Merizo Bay, Guam; F, male (57.4 × 46.8 mm), Kumejima Island, Japan; G, paratype male (52.0 × 44.0 mm) (ZRC), Christmas Island; H, paratype male (84.3 × 65.7 mm) (ZRC 2011.0166), Waterfall Bay, Christmas Island; I, holotype male (106.0 × 83.6 mm) (ZRC 2011.0168), Waterfall Bay, Christmas Island; J, male (51.1 × 42.5 mm) (ZRC 2008.0575), Pantai Cerocok, Sumatra; K, male (69.7 × 55.5 mm) (Z RC 1965.12.1.25), Mentawei Islands; L, male (74.6 × 61.9 mm) (ZRC 1965.12.1.30–39), Nicobar Islands.

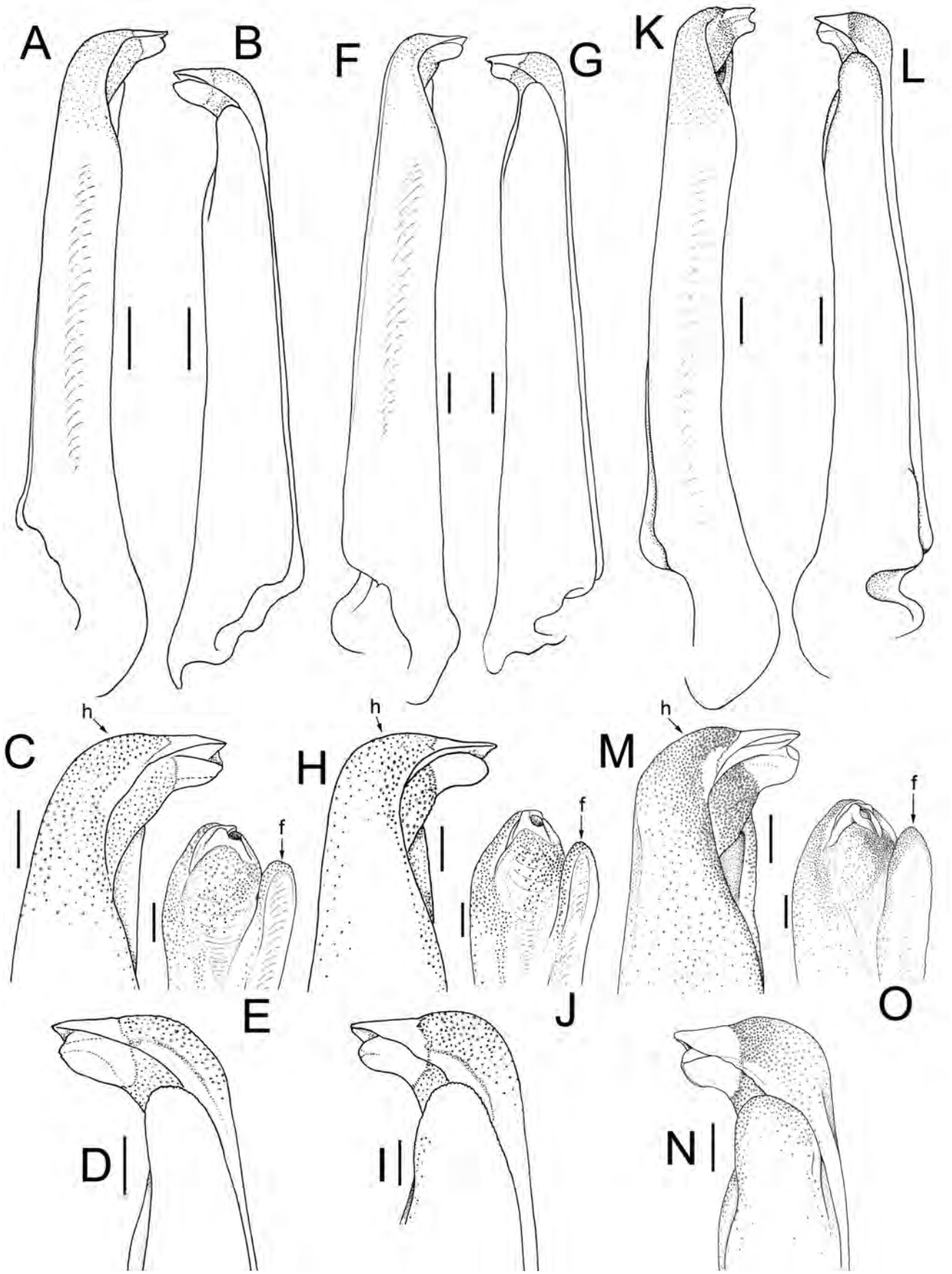

Fig. 13. Left G1s (denuded), *Discoplax* species. A–E, *D. hirtipes* (Dana, 1851), neotype male (64.2 × 53.0 mm) (ZRC 2010.0415), Fiji; F–J, *D. celeste* Ng & Davie, 2012, holotype male (106.0 × 83.6 mm) (ZRC 2011.0168), Waterfall Bay, Christmas Island; K–O, *D. magna* sp. nov., holotype male (96.7 × 80.1 mm) (ZRC 2012.0010), Similan Islands, western Thailand. A, F, K, ventral views of left G1s; B, G, L, dorsal views of left G1s; C, H, M, ventral views of distal parts of left G1s; D, I, N, dorsal views of distal parts of left G1s; E, J, O, lateral views of distal parts of left G1s. h = hump on subdistal part of G1; f = distal flap on sternal surface of G1. Scale bars = 2.0 mm (A, B, F, G); 1.0 mm (C–E, H–J).

mm), 1 female (79.5 × 64.5 mm) (QM-W29122), 4 males (largest 106.2 × 83.4 mm) (ZRC 2012.0021), station CI 08, on path to Dolly Beach, 10°31.272'S, 105°40.512'E, coll. CI 2010 expedition team, 23 January 2010. Others: 1 male (86.0 × 69.0 mm), 1 female, 1 juvenile (ZRC), station CI 13, stream near Waterfall Bay, before entrance of Christmas Island Resort, coll. CI 2012 expedition team, 4 February 2012. All localities in Christmas Island.

Remarks. The taxonomy of this species and its differences with *D. hirtipes* s. str. have been discussed at length by Ng & Davie (2012).

Discoplax magna sp. nov.

(Figs. 3, 4, 6D–H, 7, 8, 9D, 11D–K, 12J–L, 13K–O)

Cardisoma hirtipes – Gibson-Hill, 1947: 48 (part); Tweedie, 1947: 35 (part); Türkay, 1974: 229 (part), fig. 12; Naiyanetr, 1998: 95 (not *Cardisoma hirtipes* Dana, 1851).

Discoplax hirtipes – Ng & Guinot, 2001: 334, 335 (part); Ng & Davie, 2002: 380; Naiyanetr, 2007: 108 (part) (not *Cardisoma hirtipes* Dana, 1851).

Cardisoma carnifex – Thamrongnawasawat et al., 2009: 432 (not *Cancer carnifex* Herbst, 1796).

Discoplax aff. *hirtipes* – Ng & Davie, 2012a: 91; Ng & Davie, 2012b: 13; Orchard, 2012: 144–147; Raman et al., 2013: 351, fig. 4e.

Material examined. Holotype: male (96.7 × 80.1 mm) (ZRC 2012.0010), on trail, northern part of Ko Miang 4, Similan Islands, western Thailand, Andaman Sea, coll. Lai JCY & Tan SK, 2–5 January 2012. Paratypes: **Thailand** – 3 paratype males (104.4 × 81.2 mm, 99.1 × 80.6 mm, 74.2 × 63.4 mm), 1 paratype female (83.8 × 72.4 mm) (ZRC 2012.0011), same data as holotype; 1 paratype male (97.4 × 79.1 mm) (CUNHM), Ko Muang (Island No. 4), Similan Archipelago, Phangnga Province, western Thailand, coll. students, 22 November 1991. Others: **Indonesia** – 1 male (38.1 × 32.5 mm) (MZB), Ujung Kulon Reserve, westernmost Java, coll. Stewart C, August 1993; 1 male (58.2 × 49.4 mm) (MZB Cru 2239), Sancang (probably Leuweung Sancang, Garut area, southern Java, coll. Iskandar D, 3 December 1977; 1 male (77.8 × 60.5 mm) (MZB Cru 3753), Pantai Permisan, Permisan coast, Nusa Kambangan, Cilacap area, southern Java, coll. Hadiaty RK, 18 August 2002; 1 male, 1 female (ZRC 1965.12.1.28–29), Sumatra, old museum exhibit; 2 males (ZRC 1965.12.1.26–27), west Sumatra, coll. Rostados GE, 1897; 1 male (51.1 × 42.5 mm) (ZRC 2008.0575), Pantai Cerocok, Painan, West Sumatra, coll. Lai JCY & Ng NK, 6 July 2003; 1 male (69.7 × 55.5 mm) (ZRC 1965.12.1.25), South Pagi, Mentawei Island, west Sumatra, December 1902; 1 male (72.9 × 58.4 mm) (MZB Cru 3751), Taileleo, Sumbar, Siberut Selatan, west Sumatra, coll. Saim

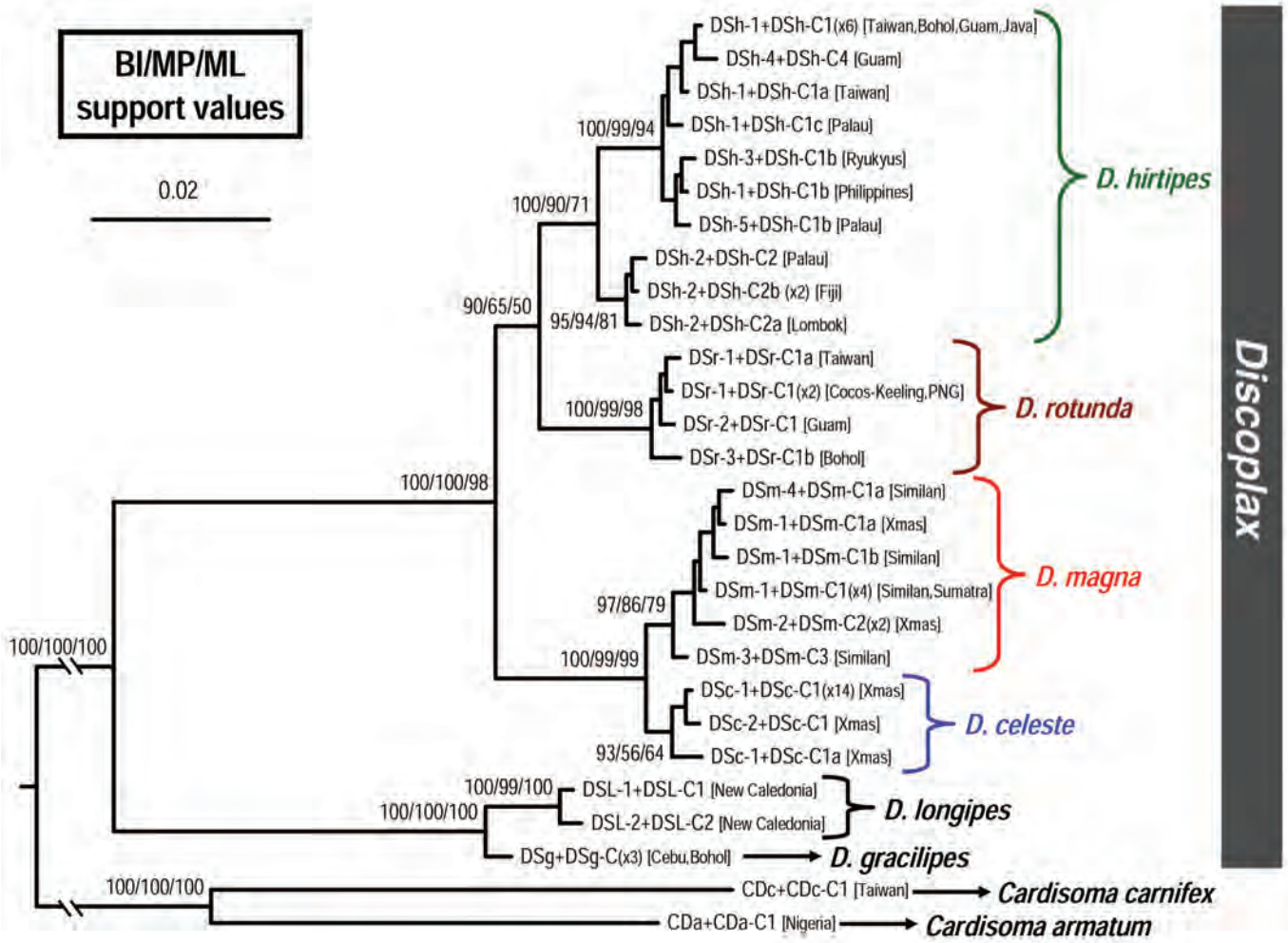

Fig. 14. A Bayesian Inference (BI) tree for *Discoplax* spp., and outgroup *Cardisoma carnifex* and *C. armatum*, based on combined 16S rRNA and cytochrome oxidase I genes. Probability values at nodes represent support values for BI, maximum parsimony (MP) and maximum likelihood (ML). For haplotype names, see Table 1.

A, 21 July 1995; 1 male (92.4 × 72.0 mm) (SMF 4147), Java, coll. Strubell S. **Nicobar Islands** – 12 males (largest 86.9 × 72.3 mm), 2 females (larger 66.4 × 55.1 mm) (ZRC 1965.12.1.30–39), Nicobar Islands, coll. Gibson–Hill CA, October 1950. **Christmas Island** – 1 female (47.1 × 39.7 mm) (ZRC 2012.0003), station CI 16, in beach forest, along road towards Dolly Beach, coll. Ng PKL, 23 January 2010; 1 male (83.1 × 68.1 mm) (ZRC 2012.0004), stream near Waterfall Bay, before entrance of Christmas Island Resort, coll. Ng PKL, 31 March 2011.

Diagnosis. In life, adult carapace with dorsal surfaces brown to greyish-brown; ventral surfaces orangish-white to yellow; third maxilliped with median parts purple; chelipeds orange to red; distal part of fingers white (Figs. 3, 4). Carapace with dorsal surface evenly convex tranversely and longitudinally, regions demarcated; epigastric regions swollen but margins poorly defined, separated from frontal margin by transversely narrow concavity, separated from postorbital cristae, with shallow or barely discernible furrow or groove; postorbital region gently swollen without trace of cristae, cervical groove shallow; postorbital and branchial regions appear somewhat confluent, especially from frontal view (Figs. 3, 4A, C, 6D–H, 7A, B, 9D). In large adult males, chela not especially enlarged in proportion to long fingers; fingers elongated, partially flattened laterally, sometimes appearing almost blade-like (Figs. 3B, E, F, 4A, B, 8A, B). Ambulatory legs in adults relatively stout, short to slender (Figs. 8C–F, 12J–L). Male abdomen relatively narrower; somite 6 with lateral margin gently convex except sometimes in very large males, just broader than long; distal margin gently concave; telson triangular, longer than broad, lateral margins gently concave to almost straight, tip rounded (Figs. 4B, 7C, 11D–K). G1 almost straight, relatively slender; distal part relatively short, bent laterally at angle of about 80° from vertical; distal-most part pectinated, upper part sharply tapering to acute tip, lower part subtruncate (Fig. 13K–O).

Morphological variation. The carapace gets proportionately more swollen in very large specimens, with the lateral cristae becoming indiscernible (e.g., Fig. 4A). However, the relative strengths of the postorbital and epigastric cristae remain relatively unchanged. The fingers of the chela get relatively more laterally flattened in large males (e.g., Figs. 3E, F, 4A, B) being relatively more cylindrical in smaller males (e.g., Fig. 6F) and females (Fig. 3D). The form of the male abdomen is relatively constant, with the lateral margins of somite 6 usually just gently convex (Fig. 11D–H, J), although in very large males, it may vary slightly and sometimes appear more convex (Fig. 11I, K). The G1 structure is relatively constant, being consistently the most slender among the three species treated here.

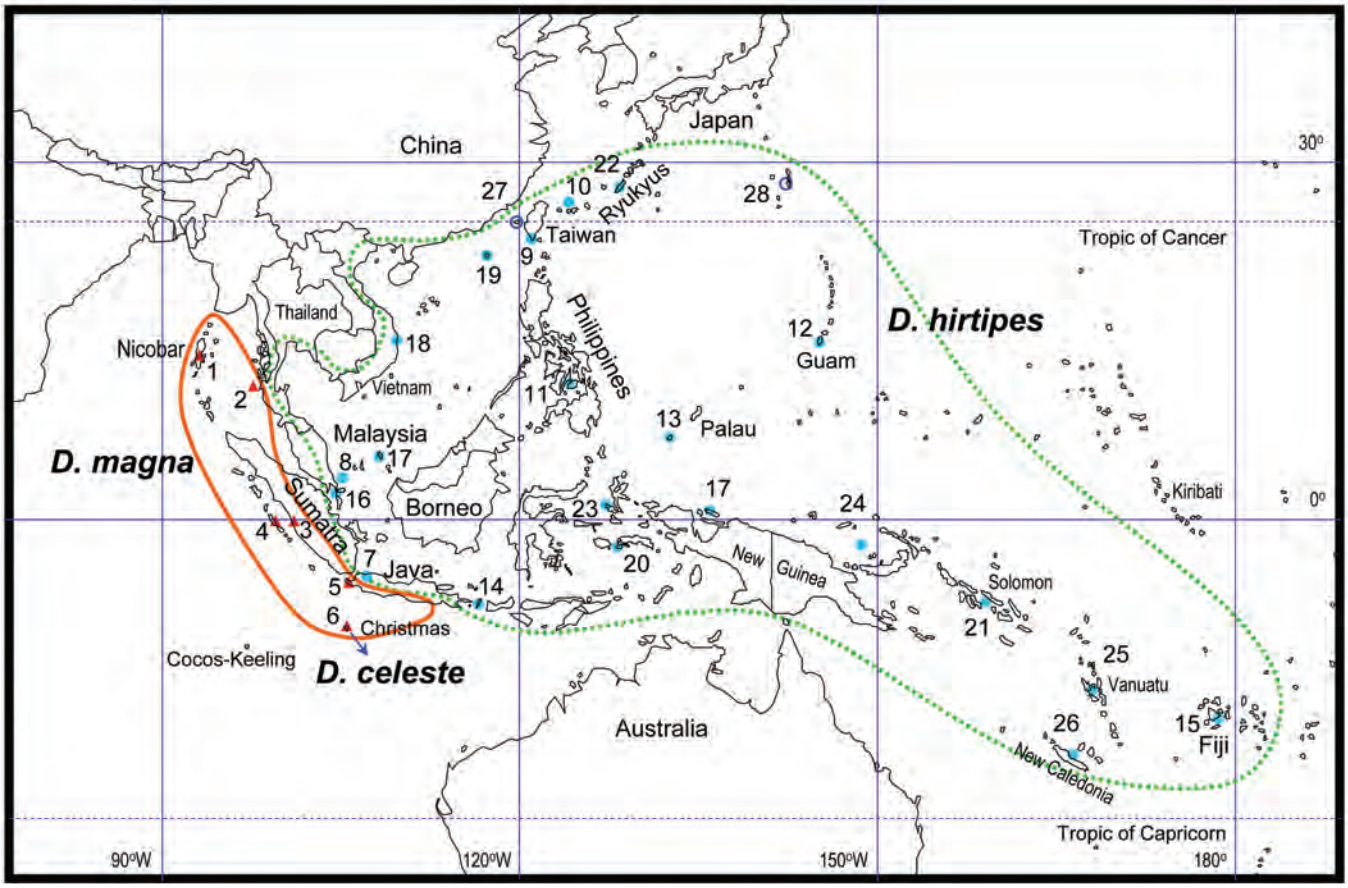

Fig. 15. Collection sites for *D. hirtipes*, *D. magna* and *D. celeste* used in molecular study [red triangles (nos. 1–6) for *D. magna* and blue circles (nos. 7–15) for *D. hirtipes*] (Table 1) and material examined of *D. hirtipes* [16, Singapore; 17, Natuna Island; 18, Vietnam; 19, Dongsha Island; 20, Ambon Island; 21, Solomon, 22, Okinawa, the Ryukyus; 23, Bacan Islands, Maluku, Indonesia; 24, islands in Bismarck Sea; 25, Vanuatu; 26, New Caledonia]. Empty blue circles (with nos. 27–28) mean the additional records of *D. hirtipes* from other references: 27, Penghu Islands, Taiwan (Shen & Jeng, 2005); 28, Ogasawara (Bonin) Islands, Japan (Türkay, 1974). Different lines indicate the updated range of the *D. hirtipes* and *D. magna*.

Etymology. The name is derived from the Latin "*magna*" for large.

Remarks. With regard to the morphology of the carapace (dorsal surfaces more swollen with the epigastric and postorbital regions relatively less inflated, more rounded and the grooves between them more shallow) and G1 (relatively more slender and elongate, with the distal part relatively shorter) (Figs. 9D, 13K–O), *D. magna* sp. nov. is closer to *D. celeste* than *D. hirtipes* (Figs. 9C, 13F–J). The G1 structure of *D. magna* sp. nov., however, is proportionately even more slender (Fig. 13K–O) when similarly sized specimens are compared (cf. Fig. 13F–J). In addition, the male abdomen of *D. magna* sp. nov. is relatively more slender with somite 6 proportionately longer (Figs. 7C, 11D–K) than *D. celeste* (Fig. 11A–C) or *D. hirtipes* (Fig. 10). Interestingly, the form of the chelae of large male specimens of *D. magna* sp. nov. is also different, being relatively more elongate and the fingers distinctly more flattened laterally, appearing almost blade-like from dorsal view (Figs. 3E, F, 6D–H, 8A, B). In *D. celeste* and *D. hirtipes*, the fingers of the chelae of even very large males are not as elongate or flattened (Figs. 1, 2, 5, 6A–C).

The material on hand from Andaman Sea, western Sumatra, southwestern and southern Java, all localities facing the Indian Ocean are clearly *D. magna* sp. nov. Java is significant as a location as specimens from northern Java are clearly *D. hirtipes* instead. Naiyanetr (1998) listed "*Cardisoma hirtipes*" from Ko Surin, Phangnga, in the Andaman Sea, so his record is clearly *D. magna* sp. nov. Naiyanetr's (2007) record of "*Discoplax hirtipes*", however, also has locations in the Gulf of Thailand, so his list may include both *D. magna* sp. nov. and *D. hirtipes* s. str. Thamrongnawasawat et al.'s (2009: 432) record of "*Cardisoma carnifex*" depicts a specimen almost identical to the colour and form of *D. magna*, and they cited their records from western Thailand.

There is also a difference in colour. Alcock (1900: 448) remarked: "In life the carapace is dark violet and the chelae bright cinnabar red." This is very evident on most of the specimens from western Thailand examined (Figs. 3E, F, 4). The long-preserved specimens from Nicobars have also retained this colouration. The western Sumatran specimen (ZRC 2008.0575) was purplish-brown with bright reddish-orange chelae when alive (Lai JCY, pers. comm.).

Biology. *Discoplax magna* is a fully terrestrial crab, and similar to *D. hirtipes* in its habitat preferences. It lives in well forested karst areas sometimes up to a kilometre or more from the sea; and the habitats are always outside water although the ground is usually moist or damp. They dig burrows by the side of trees and rocks, usually in moist areas or where there are substantial accumulations of rotting vegetation. Its habits and habitat are in contrast to those of *D. celeste*, which has much more aquatic habits, and prefers swampy areas, streams and sites with at least some standing water (see Ng & Davie, 2012; Orchard, 2012).

DNA ANALYSES AND DISCUSSION

A total of 12 specimens of *D. magna* sp. nov., 17 *D. hirtipes* and 16 *D. celeste* were used in the molecular phylogenetic analysis. One specimen of *D. celeste* was not included because the 16S and COI sequences are apparently pseudogenes (Table 1, see below). A 554-bp segment of 16S was amplified and aligned. Of these, 37 positions were variable and 23 parsimoniously informative, and 13 different haplotypes were distinguished (Table 1). The studied segment of the 16S rRNA sequences was AT rich (69.2%) (T, 35.2%; A, 34.0%; G, 19.6%; C, 11.2%). For the COI gene, a 658-bp segment was compared, resulting in 24 different haplotypes (Table 1). The studied segment of the COI sequences was also AT rich (62.7%) (T, 34.4%; A, 28.3%; G, 17.2%; C, 20.0%). Two specimens of *D. magna* and one specimen of *D. hirtipes* were not included in subsequent analyses because the COI sequences were not successfully obtained (Table 1).

The phylogenetic tree, based on 1212 bp of the combined 16S and COI, was constructed using BI, with the support values from BI, MP and ML analyses (Fig. 14). The genus *Discoplax* is monophyletic with strong support from all three methods, with one major clade composed of the "long-legged" group (*D. gracilipes* and *D. longipes*) and the remaining species forming another major clade. This major clade includes the three species within the *D. hirtipes* species-group and *D. rotunda*. Unexpectedly, *D. hirtipes* is closer to *D. rotunda* than to *D. celeste* and *D. magna*, which are sister species. Although the available data shows *D. rotunda* to be closer to *D. hirtipes*, the support values are not high. There are also subclades seen within *D. hirtipes*, with one distributed in northwestern range and another in southeastern range. However, both subclades occur in Palau; and we did not observe any major morphological differences (not even live colour) between the specimens. As such, we treat them as one species for the time being.

The pairwise nucleotide divergences for COI with K2P distance (and differences in the total bp numbers) are shown in Table 2. The mean interspecific K2P distance of *D. magna* is 1.23% (8 bp) with the closest *D. celeste*, which is 3.1 times greater than the mean intraspecific distance of *D. magna*, at 0.4% (2.6 bp) (Table 2). In addition, the lowest interspecific K2P distance of *D. magna* is 0.92% with *D. celeste*, which is 1.5 times greater than the largest intraspecific distance of *D. magna* at 0.61%. The minimum interspecific divergence is relatively small, compared with other intertidal crabs: 4.74% for *Helice tridens* vs. *H. latimera* clade (Varunidae, cf. Shih & Suzuki, 2008); 3.62 % for *Mictyris guinotae* vs. *M. brevidactylus* (Mictyridae, cf. Davie et al., 2010); 11.95% for *Mictyris thailandensis* vs. *M. guinotae* (cf. Davie et al., 2013); 4.43 % for *Scopimera ryukyuensis* vs. *S. globosa* (Dotillidae, cf. Wong et al., 2011); 5.44% for *Ocypode mortoni* vs. *O. stimpsoni* (Ocypodidae, cf. Wong et al., 2012); 4.77% for *Uca jocelynae* vs. *U. neocultrimana* (Ocypodidae, cf. Shih et al., 2010); and 2.49% for *Uca splendida* vs. *U. crassipes* (cf. Shih et al., 2012). As the *D. magna* and *D. celeste* form two well-supported reciprocally monophyletic clades (Fig. 14), have consistent morphological differences

and are sympatric in Christmas Island, they can be recognised as separate species. The small divergence, however, suggests that both species speciated recently. If the substitution rate of COI at 1.66%/10^6 years for marine sesarmids (Schubart et al., 1998) is applied, the two species separated only about 0.7 million years ago (with the p-distance 0.73%).

Both Buhay (2009) and Schubart (2009) have reported the occurrence of non-functional nuclear copies of mtDNA (numts), pseudogenes, in crustaceans. In our study, one female specimen of *D. celeste* having a combined 16S and COI sequence located outside the major clade composed of the *D. hirtipes* species-group and *D. rotunda*. It seems not uncommon for pseudogene to occur in gecarcinids, based on the study of the American *Cardisoma* spp. (Schubart, 2009). To avoid the occurrence of pseudogenes, Buhay (2009) suggested using mitochondrial-rich tissue and more than three individuals for each species, while Schubart (2009) considered the best way is the use of optimised primers.

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