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Research Article

A Review of the Widespread Indo-West Pacific Ghost Crab, *Ocypode ceratophthalmus* (Pallas, 1772) (Crustacea: Decapoda: Ocypodidae) Complex, With the Description of a New Species

Peter J. F. Davie,[1] **Peter K. L. Ng**,[2] **and Hsi-Te Shih**[3]

[1]*Queensland Museum, P.O. Box 3300, South Brisbane 4101, Queensland, Australia*
[2]*Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Singapore*
[3]*Department of Life Science and Global Change Biology Research Center, National Chung Hsing University, Taichung 402, Taiwan*

Correspondence should be addressed to Hsi-Te Shih; htshih@dragon.nchu.edu.tw

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The widespread Indo-West Pacific ghost crab, *Ocypode ceratophthalmus* (Pallas, 1772) is found to be a species-complex containing three distinct species. An Indian Ocean form, *O. celadon* sp. nov. occurs along the shores of East Africa, thence becoming an insular species spreading eastwards as far as Christmas Island. A central Indo-West Pacific species, *O. ceratophthalmus* is found from about Pakistan eastwards to Fiji, north to the southern part of the main islands of Japan and south down the coasts of Australia, and is the dominant species along the continental beaches throughout the region. *O. urvillii* Guérin, 1829, is newly raised from synonymy for an insular Pacific Ocean form that extends from Hawai'i and Clipperton Island in the central East Pacific, westwards into the northeastern Indian Ocean as far the Cocos (Keeling) Islands. A mitochondrial genetic study from cytochrome c oxidase subunit 1 (COI) supports the recognition of these three species. Each species can be relatively easily separated by claw characters, including the stridulatory crests on the major chela, the form of the male first gonopods (G1), the live colours and patterns, and other characters related to granulation and spination.

Keywords: Christmas Island; cytochrome c oxidase subunit 1 (COI); Indian Ocean; intertidal; new species; *Ocypode*; Ocypodidae; taxonomy; West Pacific

1. Introduction

During expeditions to Australia's Indian Ocean Territories of Christmas and Cocos (Keeling) Islands during 2010, 2011 and 2012, we were struck by the remarkable olive to gold colour of what has been previously considered just an Indian Ocean colour morph of the wide-spread *Ocypode ceratophthalmus* [1] (e.g., [2]). It particularly commanded our attention because living alongside this 'olive' colour form were the grey- and maroon-coloured crabs that we were most familiar with from living in the Western Pacific. Thus, we decided to investigate this phenomenon more thoroughly using an integrative taxonomic approach involving genetics and morphology. Our results show the olive-coloured Indian Ocean crabs to be a new species, *Ocypode celadon* sp. nov., that occurs from southeastern Africa west to Christmas Island. Unexpectedly, this study also revealed the presence of a hitherto 'forgotten' closely related species, *Ocypode urvillii* Guérin, 1829, that dominates on the islands of the Western Pacific, but which is also found in significant numbers in the eastern Indian Ocean. This species has similar colour and patterning to *O. ceratophthalmus*, in particular the strong characteristic H-shaped marking on the posterior carapace, and has been considered a synonym for around 100 years. A barcoding study with the mitochondrial cytochrome c oxidase subunit 1 (COI) was conducted to confirm the degree of separation of the three species, with specimens from extensive areas, including Tanzania, Mauritius, India, Cocos (Keeling), Christmas, Sumatra, Bali, West Australia, Kiribati, Fiji, Tonga and Hawaii. The presence of all three species co-occurring sympatrically on Christmas Island is conclusive evidence of their complete genetic separation and speciation.

Since the inception of this study, an important paper examining populational genetic structure in *O. ceratophthalmus* has been published [3]. Their results also found that this 'species' is not a genetically homogenous stock. They also reported three major genetically distinct clades—each largely geographically confined to either the eastern, central, or western parts of the Indo-Pacific. Using analyses of nuclear NaK intron sequences they also found evidence of a small fourth clade consisting solely of samples from the northeastern coast of New Guinea; however, this clade was not similarly separated using their COI sequences. We have not had specimens from northern Papua New Guinea available to us for study, and while we doubt that there will be species-level differences in this population, it is nevertheless an interesting avenue for further research.

Lucrezi and Schlacher [4] have given an extensive review of the ecology, biology and distribution of *Ocypode* species globally; however, it must be noted that their references to *O. ceratophthalmus* actually refer to a composite of three separate species separated in the present paper.

We have chosen to offer only diagnoses of each of the species highlighting the characters that are effective in separating them, rather than full exhaustive descriptions which would be largely superfluous. Also, we have mainly given primary synonyms for each species only, often because it would be difficult or impossible to unequivocally identify secondary records as belonging to one of the three species, and also because a complete synonymy for *O. ceratophthalmus* sensu lato has been given by Sakai and Türkay [2].

This work is dedicated to the late Max Orchard, Head Ranger of the Christmas Island National Park for 18 years. Max worked tirelessly for the conservation of the biota of Christmas Island and his support was pivotal to our success during our expeditions of 2010–2012, during which time we began the present research on *Ocypode*. Max also championed the documentation and conservation of the crabs of Christmas Island. His tangible legacy includes two books: Orchard (2012) [5] is an important publication fully detailing the crab diversity of Christmas Island with beautiful photographs and much information on the biology of each species and Orchard (2020) [6] details the famous annual Red Crab migrations. Max has helped carcinology push the frontiers of what we know about crabs on this remarkable island.

2. Material and Methods

Terminology follows Davie et al. [7]. Measurements provided, in millimetres, are of the maximum carapace width and length, respectively. Dates are formatted as day/month/year. Abbreviations: G1 = male first gonopod; P2–P5 = pereopods 2–5 (= first to fourth ambulatory legs).

Material examined is deposited in the Florida Museum of Natural History (FMNH or UF); Museum National d'Histoire Naturelle, Paris, France (MNHN); Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); Queensland Museum, Brisbane, Australia (QM); Senckenberg Museum of Natural History (SMNH or SMF); Western Australian Museum, Perth (WAM); Zoological Museum University of Copenhagen (ZMUC); and Zoological Reference Collection (ZRC), Lee Kong Chian Natural History Museum, National University of Singapore.

2.1. Genetic Methodology. Specimens used for molecular study are shown in Table 1. Genomic DNA was isolated from the tissue by using the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A portion of the COI gene was amplified with PCR using the primers LCO1490, HCO2198 [8], LCOB, HCOex3 [9], COH6 [10] and HCOex0 [11]. The PCR conditions for the above primers were denaturation for 50 s at 94°C, annealing for 70 s at 45–47°C and extension for 60 s at 72°C (40 cycles), followed by extension for 10 min at 72°C. Sequences were obtained by automated sequencing (Applied Biosystems 3730), after verification with the complementary strand, with 658-bp (base pair) segment of COI. Sequences were obtained by automated sequencing (Applied Biosystems 3730, USA) and deposited into the DNA Data Bank of Japan (DDBJ; Table 1), along with other sequences published in Shih et al. [12] (Table 1). A neighbour-joining tree was constructed with the programme MEGA (vers. 12, [13]), with Kimura 2-parameter (K2P) distance [14] and 2000 bootstrap reiterations. Other analyses, including nucleotide composition, variable and parsimony informative positions and K2P distance between haplotypes were also calculated using MEGA. The relationships of the COI haplotypes among the three species of *Ocypode* were examined using the programme PopART (vers. 1.7) [15].

3. Results

3.1. Genetic Results. A 658-bp segment of COI from 102 specimens representing the three *Ocypode* species was amplified, resulting in 43 different haplotypes (Table 1). The studied COI segment was AT rich (62.5%) (T, 34.8%; A, 27.7%; G, 16.8%; C, 20.7%). Within this gene fragment, 56 positions were variable and 35 were parsimoniously informative.

The neighbour-joining tree, based on 658 bp of COI (Figure 1), reveals that there are three distinct clades, corresponding to *O. ceratophthalmus*, *O. celadon* sp. nov. and *O. urvillii*. The clades of *O. ceratophthalmus* and *O. urvillii* are highly supported, whereas the *O. celadon* clade is moderately supported. These species were identified through morphological examination (Section 3.2). In the tree (Figure 1), the three clades form a highly supported major clade, with *O. ceratophthalmus* and *O. celadon* being more closely related, but the support value for their relationship is not high. The pairwise nucleotide divergences for COI with K2P distance are shown in Table 2. Three species are well separated by a minimum interspecific distance of 1.54% between *O. ceratophthalmus* and *O. celadon*, with a maximum intraspecific distance of 1.23% in both *O. ceratophthalmus* and *O. celadon*. A haplotype network for each of the three species was reconstructed based on 658-bp segments of their respective COI haplotypes

Table 1: The COI haplotypes of specimens of *Ocypode ceratophthalmus* species-complex from the Indo-West Pacific and the outgroups.

Species	Localities	Catalogue number	COI haplotypes	DDBJ accession number
Ocypode ceratophthalmus	India: Karwar	NCHUZOOL 15319	Oc1	LC900931
	India: Karwar	NCHUZOOL 15320	Oc1	LC900932
	India: Tamil Nadu	ZRC unreg	Oc2	LC900933
	Thailand: Similan	ZRC unreg	Oc3	LC900934
	Thailand: Similan	ZRC unreg	Oc1	LC900935
	Thailand: Phangnga	NCHUZOOL 15321	Oc4	LC900936
	Thailand: Chalong Bay, Phuket	NCHUZOOL 15322	Oc5	LC900937
	Thailand: Phuket	NCHUZOOL 15323	Oc3	LC900938
	Cocos-Keeling: Direction Island	ZRC 2019.1532	Oc6	LC900939
	Christmas: Greta Beach	QM-W55077	Oc7	LC900940
	Christmas: Greta Beach	QM-W55095	Oc1	LC900941
	Christmas: Ethel Beach	QM-W55074	Oc1	LC900942
	Christmas: Greta Beach	QM-W55080	Oc1	LC900943
	Christmas: Greta Beach	ZRC 2019.1528	Oc3	LC900944
	Christmas: Greta Beach	QM-W55086	Oc3	LC900945
	Christmas: Greta Beach	QM-W55094	Oc3	LC900946
	Christmas: Ethel Beach	QM-W55089	Oc3	LC900947
	Christmas: Ethel Beach	ZRC unreg	Oc3	LC900948
	Christmas: Ethel Beach	QM-W55072	Oc3	LC900949
	Christmas: Flying Fish Cove	ZRC 2019.1529	Oc8	LC900950
	Christmas: Greta Beach	QM-W55092	Oc9	LC900951
	Christmas: Ethel Beach	QM-W55093	Oc10	LC900952
	Christmas: Greta Beach	QM-W55076	Oc11	LC900953
	Christmas: Greta Beach	QM-W55079	Oc12	LC900954
	Christmas: Ethel Beach	QM-W55073	Oc13	LC900955
	Indonesia: Sumatra: Pantai Carocok, Painan	ZRC unreg	Oc1	LC900956
	Indonesia: Sumatra: Pantai Carocok, Painan	ZRC unreg	Oc14	LC900957
	Indonesia: Lovina, Bali	NCHUZOOL 15324	Oc15	LC900958
	Malaysia: Tioman Island	NCHUZOOL 15325	Oc16	LC900959
	Vietnam: Phu Quoc	NCHUZOOL 15326	Oc17	LC900960
	Vietnam: Phu Quoc	NCHUZOOL 15326	Oc5	LC900961
	Hong Kong: New Territories: Sai Wan	ZRC unreg	Oc16	LC900962
	Taiwan: Yilan	NCHUZOOL 15327	Oc2	LC900963
	Taiwan: Anping, Tainan	NCHUZOOL 14916	Oc16	LC150410
	Taiwan: Penghu	NCHUZOOL 15328	Oc18	LC900964
	Taiwan: Dongsha Island	NCHUZOOL 15329	Oc19	LC900965
	Taiwan: Dongsha Island	NCHUZOOL 15330	Oc1	LC900966
	Taiwan: Taiping Island	NCHUZOOL 15331	Oc1	LC900967
	Borneo	ZRC unreg	Oc2	LC900968
	Borneo	ZRC unreg	Oc20	LC900969
	West Australia: Ningaloo	ZRC unreg	Oc21	LC900970
	Fiji	UF 1479	Oc22	LC900971
Ocypode celadon	Tanzania: Zanzibar I.	UF 2141	Oe1	LC900972
	Madagascar	UF 14179	Oe2	LC900973
	Madagascar	UF 14179	Oe3	LC900974
	Madagascar	UF 14218	Oe4	LC900975
	Mauritius: Cap Malheureux	UF 4982	Oe5	LC900976
	Maldives: Laamu Atoll	ZRC unreg	Oe6	LC900977
	Maldives: Laamu Atoll	ZRC unreg	Oe1	LC900978
	Cocos-Keeling	ZRC unreg	Oe1	LC900979

Table 1: Continued.

Species	Localities	Catalogue number	COI haplotypes	DDBJ accession number
	Cocos-Keeling	ZRC unreg	Oe1	LC900980
	Cocos-Keeling	ZRC unreg	Oe1	LC900981
	Cocos-Keeling	ZRC unreg	Oe1	LC900982
	Cocos-Keeling	ZRC unreg	Oe1	LC900983
	Cocos-Keeling	ZRC unreg	Oe1	LC900984
	Cocos-Keeling	ZRC unreg	Oe1	LC900985
	Cocos-Keeling	ZRC unreg	Oe1	LC900986
	Cocos-Keeling	ZRC unreg	Oe1	LC900987
	Cocos-Keeling	ZRC unreg	Oe7	LC900988
	Cocos-Keeling	ZRC 2019.1504	Oe7	LC900989
	Cocos-Keeling	ZRC unreg	Oe7	LC900990
	Cocos-Keeling	ZRC unreg	Oe7	LC900991
	Cocos-Keeling	ZRC unreg	Oe7	LC900992
	Cocos-Keeling	ZRC unreg	Oe7	LC900993
	Cocos-Keeling: North Keeling	ZRC unreg	Oe8	LC900994
	Cocos-Keeling	ZRC unreg	Oe8	LC900995
	Cocos-Keeling	ZRC unreg	Oe9	LC900996
	Cocos-Keeling	ZRC unreg	Oe10	LC900997
	Cocos-Keeling	ZRC unreg	Oe11	LC900998
	Cocos-Keeling	ZRC unreg	Oe12	LC900999
	Christmas	ZRC unreg	Oe7	LC901000
	Christmas	ZRC 2010.0008	Oe1	LC150411
	Christmas	QM-W55065	Oe1	LC901001
	Cocos-Keeling	ZRC 2019.1504	Ou1	LC901002
	Cocos-Keeling	ZRC unreg	Ou1	LC901003
	Christmas	ZRC unreg	Ou2	LC901004
	Christmas: Greta Beach	QM-W55087	Ou1	LC901005
	Christmas	ZRC 2010.0007	Ou3	LC150412
	Christmas: Ethel Beach	QM–W55070	Ou3	LC901006
	Christmas: Ethel Beach	ZRC 2019.1525	Ou1	LC901007
	Christmas: Ethel Beach	QM-W55088	Ou4	LC901008
	Christmas: Ethel Beach	ZRC 2019.1526	Ou1	LC901009
	Christmas: Ethel Beach	QM–W55071	Ou5	LC901010
	Christmas: Ethel Beach	QM-W55059	Ou3	LC901011
	Christmas: Ethel Beach	QM-W55060	Ou3	LC901012
	Christmas: Ethel Beach	QM-W55064	Ou3	LC901013
	Christmas: Ethel Beach	QM-W55063	Ou3	LC901014
Ocypode urvillii	Indonesia: Bali	NCHUZOOL 15332	Ou1	LC901015
	Philippines: Camiguin	NCHUZOOL 15333	Ou3	LC901016
	New Caledonia: Loyalty Island	ZRC unreg	Ou3	LC901017
	Kiribati: Kiritimati: Line Islands	ZRC unreg	Ou3	LC901018
	Kiribati: Kiritimati	ZRC unreg	Ou3	LC901019
	Tonga Island	UF 2681	Ou2	LC901020
	Hawaii: Oahu	ZRC 2000.0420	Ou3	LC901021
	Polynesia: Marquesas	MNHN-IV-2011-8922	Ou3	LC901022
	Polynesia: Marquesas	MNHN-IV-2011-8943	Ou3	LC901023
	Polynesia: Marquesas	MNHN-IV-2011-8922	Ou3	LC901024
	Polynesia: Marquesas	MNHN-IV-2011-8911	Ou6	LC901025
	Polynesia: Marquesas	UF 9805	Ou6	LC901026
	Polynesia: Marquesas	MNHN-IV-2011-8922	Ou7	LC901027
	Polynesia: Society	UF 15702	Ou8	LC901028
	Polynesia: Society	UF 9812	Ou9	LC901029

Table 1: Continued.

Species	Localities	Catalogue number	COI haplotypes	DDBJ accession number
Outgroups				
Ocypode stimpsoni	Taiwan: Hsinchu: Ganna	NCHUZOOL 14921	—	LC150428
Ocypode rotundata	Iran: Qeshm	SMF 40586	—	LC150424
Ocypode cf. nobili	Malaysia: Kuching: Santubong	NCHUZOOL 14918	—	LC150417

Note: Abbreviations for the museum and genetic sequence repositories are detailed in Section 2.

(Figure 2). In this study, *O. ceratophthalmus* is well separated from *O. celadon* and *O. urvillii* by ≥9 and ≥11 steps, respectively.

3.2. Taxonomy. Ocypodidae Rafinesque, 1815

Ocypode ceratophthalmus (Pallas, 1772) [1]

(Figures 3; 4; 5A; 6A,B; 7A,B,G; 8A,B; 9A,D,G; 10)

Cancer ceratophthalmus Pallas, 1772 [1]:83, pl. 5 figs 7, 8. [Opinion 712]

Cancer arenarius Toreen in Osbeck, 1765 [16]:479 [a *nomen oblitum*, a subjective synonym of *O. ceratophthalmus* (Pallas, 1772) [1]; see Low and Ng, 2012 [17]:[43–46].

Cancer caninus Herbst, 1782 [18]:78.

Ocypoda Macleayana Hess, 1865 [19]:143 pl. 6 Figure 8; Haswell, 1882 [20]:95.

Ocypoda macleayana—De Man, 1887 [21]:696.

[?] *Ocypode ceratophthalma*—Balss, 1934 [22]:226 [Dolly Beach, Christmas Island—no description].

Ocypode ceratophthalmus—Ng et al., 2008 [23]:240, 242; Orchard, 2012 [5]:233–235; Murniati et al., 2022 [24]:264–265, Figure 2.

Material Examined

Types: Neotype of *Cancer ceratophthalmus*, ZRC-2023.066, male (44.9 mm × 40.6 mm), Changi Beach, adjacent Carpark 7, Singapore, 1°22′27.81″N, 104°0′23.01″E, coll. S. Tan et al., 3.08.2012. Holotype of *Ocypoda macleayana* Hess [19], ZMG-126 1 juvenile (now transferred to SMF). Type locality: Sydney.

Additional material: India: ZRC 1965.7.20.124, male (42.6 mm × 37.0 mm), Madras (Chennai), India, 10.03.1967, R. Serene. Cocos (Keeling) Islands: ZRC 2019.1532, female, Cocos (Keeling) Islands: southern beach of Direction Island, CK-12, 21.03.2011. Thailand: ZRC 2019.1531, 8 specs., Similan Islands, Thailand, SM-03, 2.02.2012; ZRC 2019.1534, two males (19.0, 16.3 mm cw), two females (30.4, 30.4 mm cw), Phuket, Thailand, PHU-16, 29.05.2012; ZRC 2019.1536, two females (16.1 mm × 13.6 mm; 29.6 mm × 25.6 mm), Phuket, Thailand, PHU-03, 24.05.2012. Christmas Island: QM-W55072, female (31.2 mm × 26.0 mm), Ethel Beach, Christmas I., 27°27.805'S, 105°40.443'E, 25.01.2010, P. Davie and P. Ng; QM-W55073, male (28.7 mm × 23.6 mm), Ethel Beach, Christmas I., 29.01.2010, P. Davie and P. Ng; QM-W55074, male (34.1 mm × 30.7 mm), Ethel Beach, Christmas I., 22.01.2010, P. Davie and P. Ng; QM-W55082, two males (26.7 mm × 22.6 mm; 28.1 mm × 23.2 mm), CI-20, Dolly Beach, Christmas Island, 10° 25.815' S, 105° 40'.18' E, 29.01.2010; QM-W55081, male (29.6 mm × 22.6 mm), CI-09, Waterfall Bay, Christmas Island, 23.01.2010; QM-W55085, male (37.3 mm × 31.9 mm), CI-05, Flying Fish Cove, Christmas I., 20.03.2011; QM-W55091, three subadult male, three juvenile female (unmeasured), CI-17, Waterfall Bay, Christmas Island, 10° 27.54′ S, 105° 42.30′ E, 23.03.2011; QM-W55086, female (34.2 mm × 30.2 mm), CI-33, Greta Beach, Christmas Island, 10° 30.127' S, 105° 40.475′ E, 27.03.2011; QM-W55090, male (26.0 mm × 21.7 mm), data as for QM-W55086; QM-W55092, male (28.4 mm × 24.4 mm), data as for QM-W55086; QM-W55094, male (24.9 mm × 21.0 mm), data as for QM-W55086; QM-W55095, female (24.7 mm × 20.9 mm), data as for QM-W55086; QM-W55089, female (35.3 mm × 31.5 mm), CI-38, Ethel Beach, Christmas Island, 10°27.805' S, 105°42.443' E, 28.03.2011; QM-W55093, male (30.9 mm × 26.9 mm), data as for QM-W55089; QM-W55076, female (35.7 mm × 29.5 mm), CI-40, Greta Beach, Christmas Island, 10° 30.127' S, 105° 40.475' E, 27.03.2011; QM-W55077, male (39.0 mm × 34.9 mm), data as for QM-W55076; QM-W55078, three subadult male, four subadult female (unmeasured), data as for QM-W55076; QM-W55079, male (24.5 mm × 20.5 mm), data as for QM-W55076; QM-W55080, male (35.2 mm × 30.7 mm), data as for QM-W55076; QM-W55084, male (38.0 mm × 34.7 mm), data as for QM-W55076; QM-W55083, female (38.9 mm × 33.4 mm), CI-13, Flying Fish Cove, Christmas Island, 10.429863' S, 105.667135'E, intertidal, 08.02.2012; ZRC 2019.1530, male, Greta Beach, Christmas Island, evening, CI3-29, 10°30.127'S, 105°40.475'E, 15.02.2012; ZRC 2019.1529, male, Flying Fish Cove, Christmas Island, (intertidal), C03-13,10°25.792'S, 105°40.028'E, Christmas Island and Pulu Keeling Expeditions 2010–2012, 8.02.2012; ZRC 2019.1528, two males, Christmas Island: Greta Beach, morning, CI-03-05, 10°30.127'S, 105°40.475'E, 5.02.2012; ZRC 2019.1535, one male, one female, Flying Fish Cove, Christmas Island, CI-03-13, 10°25.792'S, 105°40.028'E, 8.02.2012; ZRC 2020.0520, 11 males, eight females, Greta Beach, Christmas Island, CI-03-05, 10°30.127'S, 105°40.475'E, 5.02.2012. Malaysia: WAM-C33971, male (40.6 mm × 35.2 mm), Pelangi Beach Resort, Langawi I., W. Malaysia; ZRC 2019.1538, two males (38.5 mm × 32.5 mm; 42.5 mm × 37.7 mm), female, Kuantan, Pantai Batu Hitam, Malaysia, Z. Jaafar, 5.11.2002, [tissue extracted by KJH Wong]; ZRC 2001.1024, male, two females, N.E. Sabah, near Kota Kinabalu, E. Malaysia, T.S.H., P.K.L. Ng, Nov. 2000. Sabah: WAM-209-73, juv. female (20.2 mm × 16.3 mm), two males (27.0 mm × 22.4 mm; 29.1 mm × 25.0 mm), Agal Bay, NW Sabah, B.R. Wilson, 12.03.1964; WAM-218-73, female (20.7 mm × 17.1 mm), three males (24.0 mm × 20.4 mm; 23.9 mm × 20.7 mm; 27.3 mm × 23.3 mm), Usukan Bay, NW Sabah, 6°22'N, 116°20'E, B.R. Wilson, 13.03.1964. Singapore: ZRC 1989.2105, female, Singapore, Sentosa Island, P. K. L. Ng, Mar. 1988. Philippines: ZRC

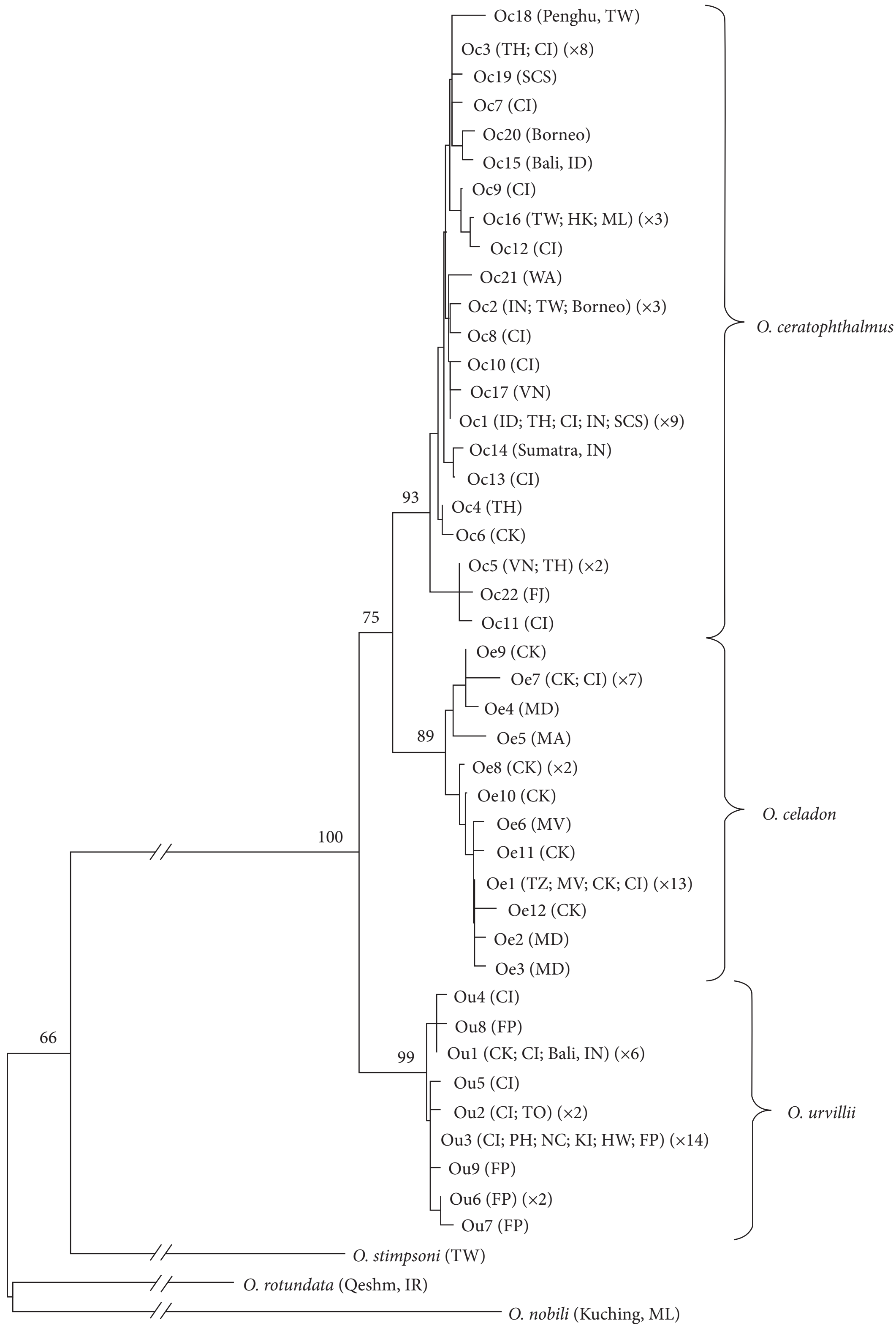

FIGURE 1: A neighbour-joining COI tree of the *Ocypode ceratophthalmus* species complex and other related congeneric species based on the COI marker. Only bootstrap values > 50% are show on nodes. For haplotype names, see Table 1. CI, Christmas Island; CK, Cocos (Keeling); FJ, Fuji; FP, French Polynesia; HK, Hong Kong; HW, Hawaii; ID, Indonesia; IN, India; IR, Iran; KI, Kiribati; MA, Mauritius; MD, Madagascar; ML, Malaysia; MV, Maldives; NC, New Caledonia; PH, Philippines; SCS, South China Sea; TH, Thailand; TO, Tonga; TW, Taiwan; VN, Vietnam; WA, Western Australia.

Table 2: Matrix of percentage of pairwise nucleotide divergences with Kimura 2-parameter (K2P) distances based on the cytochrome c oxidase subunit I (COI) gene within and between species of the *Ocypode ceratophthalmus* complex.

Species	**Intraspecific**	**Interspecific**		
		Ocypode ceratophthalmus	***Ocypode celadon***	***Ocypode urvillii***
Ocypode ceratophthalmus	0.42 (0–1.23)	—	—	—
Ocypode celadon	0.5 (0–1.23)	2.12 (1.54–2.81)	—	—
Ocypode urvillii	0.16 (0–0.61)	2.41 (2.01–2.97)	3.06 (2.65–3.6)	—

Note: Range of values is given in parentheses.

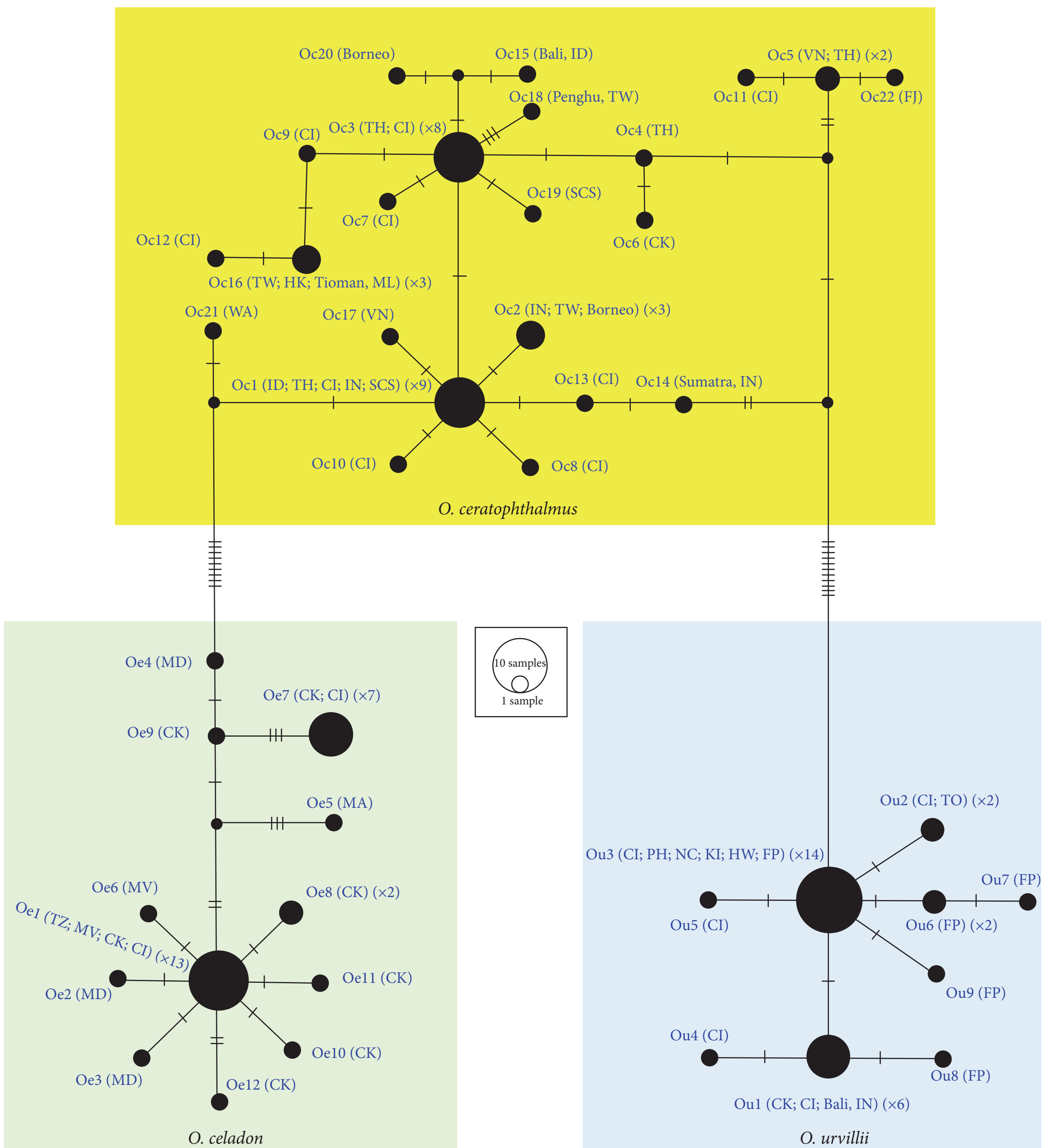

Figure 2: Genealogical network for the COI haplotypes observed from the *Ocypode ceratophthalmus* species complex. The unlabelled nodes indicate inferred haplotypes that were not identified in the sampled populations. See Table 1 for haplotype names and Figure 1 legend for abbreviation of country/area.

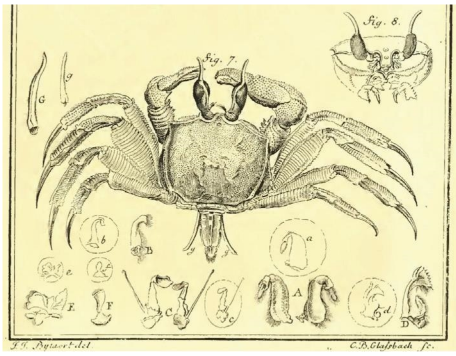

Figure 3: *Ocypode ceratophthalmus* (Pallas, 1772), reproduction of original figures (Pallas, 1772, plate 5, Figures 7 and 8).

2001.2319, female, Panglao Beach, Bohol, Philippines, P. K. L. Ng, H.C. Liu, 27.11.2001; WAM-unreg., two males (29.5 mm × 25.0 mm; 20.0 mm × 16.4 mm), sand cay, Cataoyan Reef, SE Polillo I., Philippines, B.R. Wilson, 8.08.1965; WAM-unreg., five males (17.8 mm × 14.5 mm–29.4 mm × 23.9 mm), three females (27.4 mm × 22.5 mm–35.0 mm × 29.8 mm), Villa Carmen, Cabcabon, Bataan, Philippines, B.R. Wilson, 23.07.08.1965. Indonesia: ZRC 2010.0422, male (33.4 mm × 28.8 mm), Kri Is., Papua, Indonesia, Dec. 2010, H.H. Tan; ZRC 2016-0708, male (24.7 mm × 20.8 mm), female (25.3 mm × 21.9 mm), Makawidey Village, Makawidey Bay, Bitung, Menado, N. Suluwesi, Indonesia, H.H. Tan, 30.07.2016. Papua New Guinea: FMNH-2330, two males (27.6 mm × 23.3 mm; 35.2 mm × 31.3 mm), Louisades Arch., Papua New Guinea, shore, mangroves and reef flat, G. Paulay, 04.06.1998. Australia (continental): WAM-C8334, male (40.6 mm × 35.3 mm), Theyenard I., 15 miles WNW of Onslow, Western Australia; WAM-C8336, male (38.9 mm × 33.3 mm), Long I., North-West Cape, Western Australia; WAM-C8501, male (41.4 mm × 36.2 mm), Hospital Beach, Bernier I., Shark Bay, Western Australia; WAM-C202-73, male (41.0 mm × 35.8 mm), Monkey Mia, Shark Bay, Western Australia, B.R. Wilson, 28.09.1963; WAM-C22533, male (33.9 mm × 28.8 mm), Neds Camp., Cape Range National Park, Western Australia; WAM-C41922, three males (36.3 mm × 31.2 mm–41.3 mm × 35.4 mm), five females (29.8 mm × 25.6 mm–41.8 mm × 35.8 mm), Broome, NW Western Australia; QM-W55075, male (42.8 mm × 37.6 mm), Roebuck Bay, nr Crab Creek, NW Western Australia, in burrows in sand behind mangroves, 24.06.2007, P. Davie; QM-W12350, female (38.6 mm × 33.6 mm), Pellew Group, Northern Territory; WAM-unreg., two females (28.5 mm × 23.9 mm; 36.6 mm × 32.2 mm), Buffalo Creek, Nhulubuy, Gove Peninsula, Northern Territory, 2.07.1976; QM-W29036, male (43.2 mm × 38.3 mm), Bramble Cay, 09°08’S, 143°53’E; QM-W28309, female (45.9 mm × 36.1 mm), Mon Repos Beach, nr Bundaberg, SE Queensland, 24°48’S, 152°26’E, 27.03.1975, B. Mackness; WAM-C8335, female (38.1 mm × 32.6 mm), Heron I., Queensland; QM-W12346, female (41.1 mm × 35.4 mm), Moreton Bay, SE Queensland; QM-W12349, male (41.4 mm × 34.7 mm), one ovig. female (38.7 mm × 33.3 mm), Moreton Island, 18.11.1907, H.B. Taylor; QM-W12351, male (42.8 mm × 36.5 mm), two females (37.1 mm × 31.8 mm; 40.8 mm × 33.5 mm), Woody Point,

Figure 4: *Ocypode ceratophthalmus* (Pallas, 1772), neotype, ZRC-2023.066, male (44.9 mm × 40.6 mm), Changi Beach, adjacent Carpark 7, Singapore, coll. S. Tan et al., 3.08.2012. (A) Dorsal view; (B) ventral view; (C) frontal view.

Moreton Bay, J.T. Jamieson. Lord Howe Island: QM-W26881, male (36.8 mm × 32.1 mm), Ned’s Beach, Lord Howe Island, 26.10.2003, G. Kelly. New Caledonia: QM-W52508, two males (39.9 mm × 34.4 mm; 40.7 mm × 36.5 mm), beach at du Cap, west coast New Caledonia, 21°30’S, 165°30’E, 03.12.1993; ZRC 2019.1537, male (43.1 mm × 38.3 mm), Loyalty Islands, New Caledonia, Stn OU86, KiwA3, 14.08.2010. Vanuatu: ZRC 2019.1533, male (40.1 mm × 35.4 mm), Vanuatu, intertidal, VM34, 15°29.4’S, 167°15.2’E, SANTO 2006 Expedition, 23.09.2006; ZRC 2010.0015, female (36.7 mm × 31.8 mm), Vanuatu, Stn VM31, 15°28.9’S, 167°15.5’E, SANTO 2006 Expedition, 22.09.2006. Fiji: FMNH-1479, female (19.9 mm × 17.3 mm), Stn LAK-21, in front of Mike’s Dive Centre, sand flat, coll. L. Kirkendale and V. Bonito, 16.10.2001.

Diagnosis

Carapace (Figures 4A and 5A) slightly wider than long (1.1–1.2 times), finely granular over dorsal surface. Eyestalks prolonged distally beyond cornea in a long stylus in mature adults. Carapace marginally broadest at exorbital angles in larger specimens or at about anterior third in smaller. Exorbital angles broadly triangular and weakly directed

Figure 5: Dorsal views of male *Ocypode* species: (A) *O. ceratophthalmus*, neotype, ZRC-2023.066 (44.9 mm × 40.6 mm), Changi Beach, Singapore; (B) *Ocypode celadon* sp. nov., holotype, QM-W55057, Cocos (Keeling): North Keeling Island, male (42.3 mm × 38.7 mm); (C) *O. urvillii*, neotype, ZRC-2014.0250 (40.1 mm × 37.2 mm), Tahiti, French Polynesia.

laterally in large specimens. Supraorbital margin with inner part lateral to base of rostrum relatively flat to weakly concave, not forming marked concave cup; outer lateral margin oblique, relatively straight and to exorbital angle. Palm of major chela appears longer; height subequal to length (length in midline from base of gape to indent of articulation versus maximum vertical height); fingers also appear longer and narrower than other species in this complex; granulation on

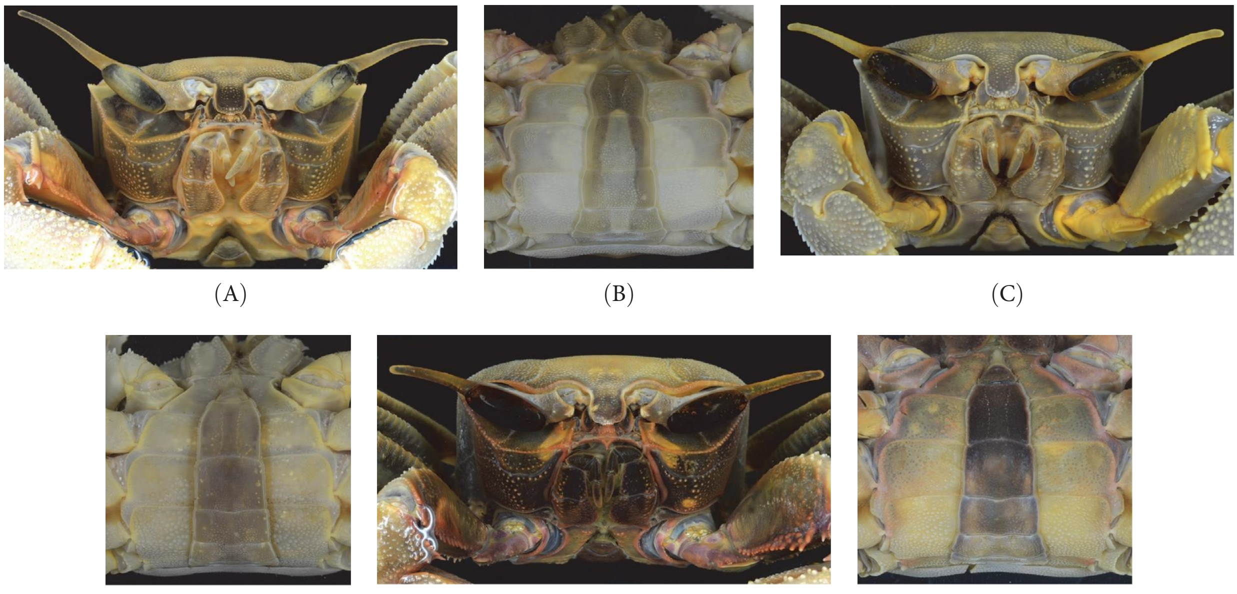

Figure 6: (A, C, E) Frontal views of male *Ocypode* species showing frontal margins, orbits and pterygostome. (B, D, F) Ventral view of male pleon of same. (A, B) *Ocypode ceratophthalmus*, neotype, ZRC-2023.066, (44.9 mm × 40.6 mm), Changi Beach, Singapore; (C, D) *Ocypode celadon* sp. nov., holotype, QM-W55057, Cocos (Keeling): North Keeling Island, male (42.3 mm × 38.7 mm); (E, F) *O. urvillii*, neotype, ZRC-2014.0250 (40.1 mm × 37.2 mm), Tahiti, French Polynesia.

outer face of major chela mostly relatively small, taller and narrower near superior margin; finer and more rounded ventrally; spination of lower margin strong and sharp, directed more vertically downwards; obviously alternating in size. Stridulatory crest (Figure 7G) with superior half composed of c. 17 widely spaced chitinous tubercles, mostly subglobular, but ventral 5–6 widening into narrower transverse striae. Ventral half marked by c. 30–33 much finer broader, more closely set striae, that maintain same interspacing over entire length; slightly narrower anteriorly but without obviously defined waist at transition point; relatively even in width over most of its length. Minor chela (Figure 8A,B) with very sharp spines along upper and lower margins, distally pointed spines more upright; proximal half of dactyl with row of strong sub-conical spines with blunt corneous tips; lower margin weakly concave under base of fingers; relatively straight over distal half. G1 apically broadly rounded, corneous tip directed laterally, not projecting; subapical thumb strongly developed, hooked and projecting distally (Figure 9A,D,G).

Colour (Figures 4 and 10)

Adults with dorsal carapace and pereiopods pale sandy cream, but with strong maroon/brown marking on lower back framing mesogastric, cardiac and intestinal regions; lower surfaces of carapace and pereiopods dark maroon to reddish brown from orbital socket to level of thoracic somite 6, then transitioning to pale cream posteriorly. Chelae typically white; without marked indication of darker colour over superior margin of palm or base of dactyl; upper face of carpus pale creamy white. Walking legs without obvious banding over superior face.

Stevens et al. [25] showed that individual crabs change colour according to a circadian rhythm, becoming lighter during the day and darker at night, thus, significantly improving their camouflage against the sand background according to prevailing light conditions. As an overlay to this, crabs living on darker sand backgrounds are also typically darker than those found on lighter coloured sand. This has similarly been reported from Hawai'i for *O. urvillii* (see later).

Distribution

From about Pakistan [3] and Cocos (Keeling) east to Fiji, north to the southern part of the main islands of Japan and southwards along the coasts of Australia (to Shark Bay, WA, on the west Coast and Jervis Bay, NSW, in the east). Widely distributed in the Indonesian Archipelago, e.g., Sumatra, Java, Sulawesi, the Lesser Sunda Islands, the Moluccas, the Aru Islands and Papua [24] (Figure 11).

Ecology

These crabs, like other *Ocypode* species, are fleet-footed scavengers and predators. They prefer open sandy beaches below frontal dunes. In Hong Kong, this species is abundant above high water on both dissipative and reflective sandy shores and extending onto sheltered sand flats [26, 27]. It also occurs sympatrically with the Chinese endemic *O. mortoni* George, 1982, showing no clear habitat/niche distinction between the two species, although *O. ceratophthalmus* is much more widespread and abundant [27].

Adults are typically crepuscular and nocturnal in habit, though juveniles are often seen during daylight hours, apparently emerging more regularly to renew respiratory water [28, 29]; PJFD pers. obs.). Younger smaller crabs typically construct burrows lower on the beach, with the burrows of larger adults found higher up towards high water mark (PJFD pers. obs.).

Burrow structure is varied and has been reported to be J-, U- and Y-shaped, as well as spiral and single tubes [29]. According to Chan et al. [29], differences in depth and shape

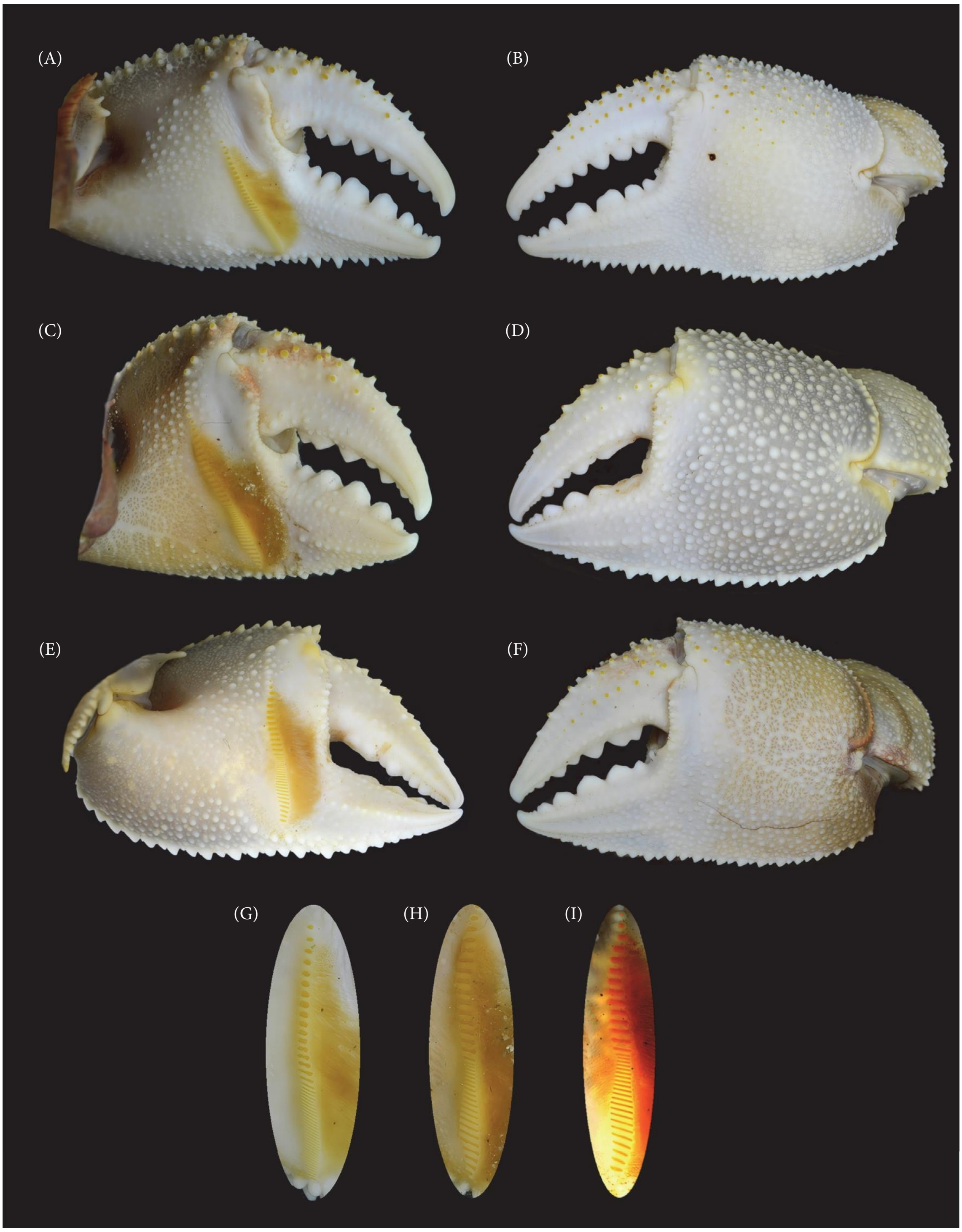

Figure 7: (A–F) Inner and outer faces of major chela of male *Ocypode* species: (A, B) *O. ceratophthalmus*, neotype, ZRC-2023.066 (44.9 mm × 40.6 mm), Changi Beach, Singapore; (C, D) *Ocypode celadon* sp. nov., holotype, QM-W55057, Cocos (Keeling): North Keeling Island, male (42.3 mm × 38.7 mm); (E, F) *O. urvillii*, neotype, ZRC-2014.0250 (40.1 mm × 37.2 mm), Tahiti, French Polynesia. (G–I) Magnified view of stridulatory ridges.

are a factor of age and size. In Hong Kong, juveniles produced shallow J-shaped burrows, which incline vertically to a depth of about 160 mm; medium-sized adults prefer Y-shaped and spiral burrows to a depth of about 360 mm; while the largest crabs lived in simple, inclined, single tube burrows to a mean depth of 320 mm. Chan et al. [29] speculate that smaller crabs replenish respiratory water more frequently, and thus, prefer to keep to shallower depths, while larger crabs need more complex burrows for mating and refuge.

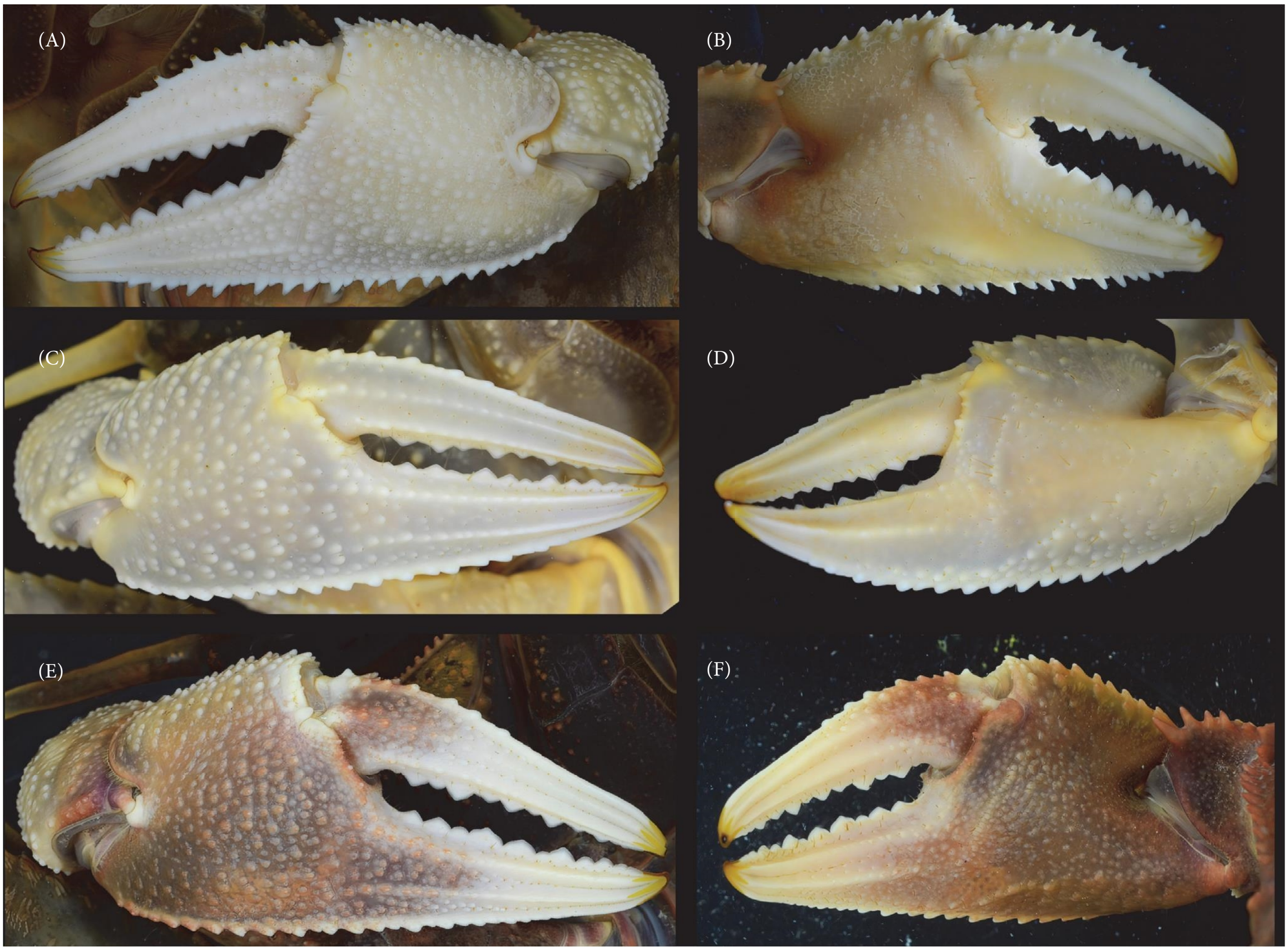

Figure 8: (A–F) Inner and outer faces of minor chela of male *Ocypode* species: (A, B) *O. ceratophthalmus*, neotype, ZRC-2023.066 (44.9 mm × 40.6 mm), Changi Beach, Singapore; (C, D) *Ocypode celadon* sp. nov., holotype, QM-W55057, Cocos (Keeling): North Keeling Island, male (42.3 mm × 38.7 mm); (E, F) *O. urvillii*, neotype, ZRC-2014.0250, (40.1 mm × 37.2 mm), Tahiti, French Polynesia.

(A) (B) (C) (D) (E) (F) (G) (H) (I)

Figure 9: Three views of distal part of male G1 of *Ocypode* species: (A, D, G) *O. ceratophthalmus*, neotype, ZRC-2023.066 (44.9 mm × 40.6 mm), Changi Beach, Singapore; (B, E, H) *Ocypode celadon* sp. nov., holotype, QM-W55057, Cocos (Keeling): North Keeling Island, male (42.3 mm × 38.7 mm); (C, F, I) *O. urvillii*, neotype, ZRC-2014.0250 (40.1 mm × 37.2 mm), Tahiti, French Polynesia.

On Japanese beaches, this species is dominant from summer to autumn, while newly settled juveniles arrive on the beaches from June to August and continue to grow until late autumn [30]. However, the population does not persist over winter, suggesting that it is too cold and thus close to their northern distribution limit.

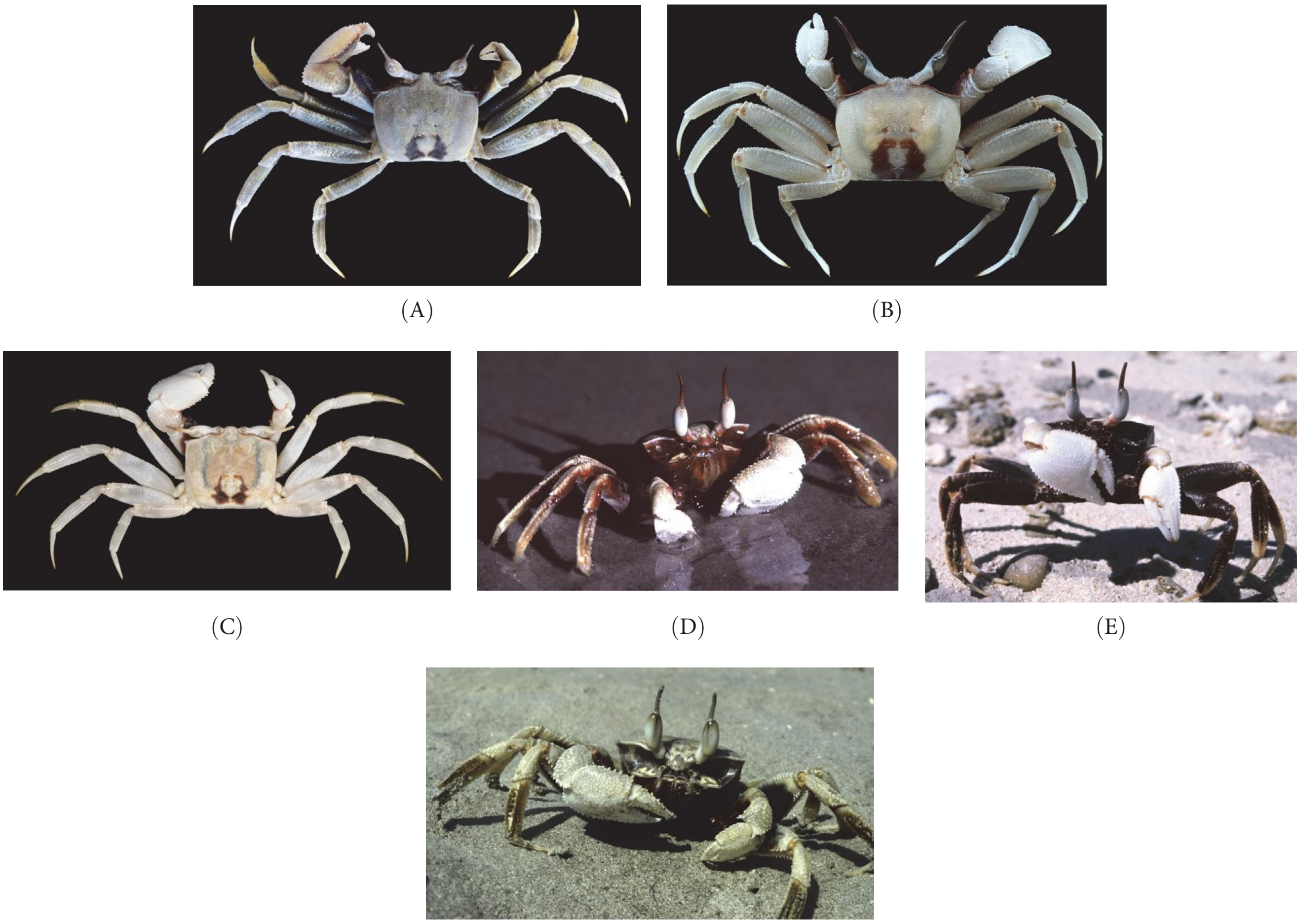

FIGURE 10: Live photos to show the variation in colour of *Ocypode ceratophthalmus*. (A) Philippines (Ondrej Radosta); (B) Thailand (Mos Nattapat); (C) Ethel Beach, Christmas Island, CI-13, 25.01.2010; (D) Hervey Bay, SE Qld, Australia (Qld Museum, Andrew Elliot); (E) Heron Island, Qld Australia (Qld Museum, Neville Coleman Collection); (F) Moreton Bay, SE Qld, Australia (P. Davie).

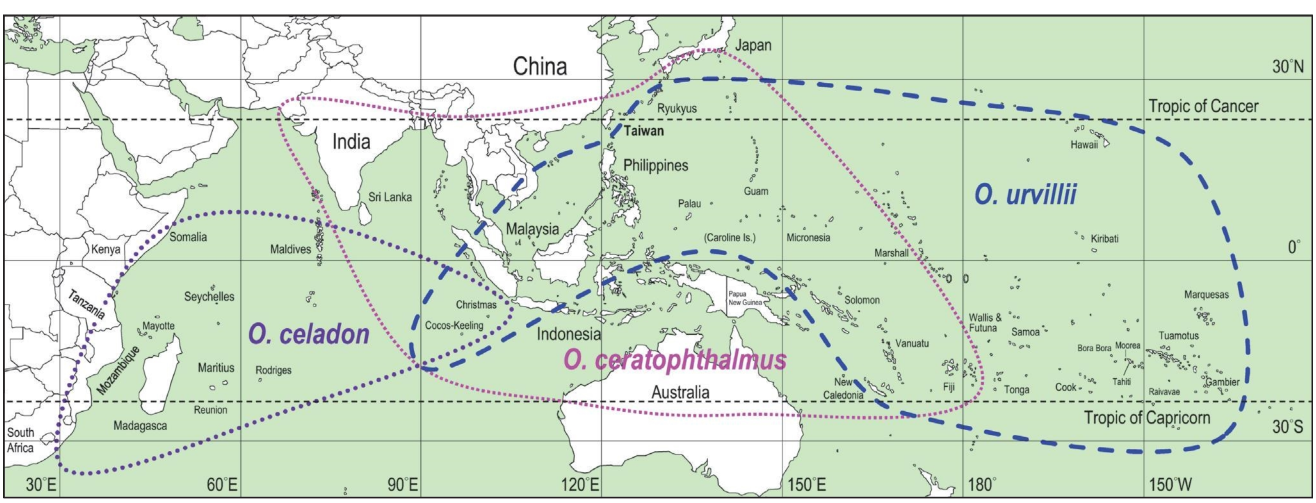

FIGURE 11: Map of the distributions of *Ocypode ceratophthalmus*, *O. celadon* sp. nov., and *O. urvillii*.

Remarks

The numerous characters that separate this species from its two sibling sister species are given in Section 4.

The type material *Cancer ceratophthalmus* Pallas, 1772, cannot be located. Pallas had not undertaken any expeditions to the Indo-West Pacific region prior to the description of this species, and he did not indicate in his original account any locality information. In his Latin description, however, Pallas made mention of 'The work of the famous Voet Coleopterist' and 'A Belgian name was given to the Cancer found (Hondskrabbe)'. So this would imply that the specimen he described came from the collection of Johannes Eusebius Voet (1706–1778). Voet was a physician cum naturalist known for having a large collection of insects and shells, and as the author/artist of the 1806 posthumous publication '*Catalogus Systematicus Coleopterorum*'. His hometown Dordrecht is in the southern part of the Netherlands, relatively close to the Belgian border where Flemish is commonly spoken, so this would have been why the vernacular name Hondskrabbe (dog-crab) would have been given, perhaps in reference to the crab's fast running across the beach. As it happens, 'hond' is the same name used for dog in Belgian, Flemish and Dutch. We have little information on how Voet's collections were dispersed; however, such collections were commonly sold to a number of European museums. Based on the movements of Pallas during this period, he would most likely have encountered the specimen of the 'Hondskrabbe' in either the Netherlands or Berlin. Pallas worked in The Hague during the early 1760s, during which time he wrote his Miscellanea Zoologica (1766), including descriptions of some new species he had discovered in the Dutch museum collections. So it is feasible that this is also where he may have encountered some of Voet's collections, including the new *Ocypode*. The type however cannot now be found in the Naturalis Biodiversity Center, Leiden (previously Rijksmuseum van Natuurlijke Historie). It could also have been acquired by the Berlin Museum, where Pallas worked prior to becoming a professor at the Russian Academy of Sciences in St Petersburg after 1767. Dr. Oliver Coleman examined the Berlin Museum collections on our behest and found no specimens of this species that could have been sufficiently old to have been examined by Pallas, and therefore, we have to draw the inevitable conclusion that the type has been lost and a neotype is required to establish the identity of *O. ceratophthalmus*.

The type locality is sometimes cited as India (see [31]), however, our close scrutiny of the original Latin description gives no indication of a locality. The word 'indica' is mentioned in the second sentence of the first paragraph under the main heading, and it seems that this was taken as an indication that the locality was India; however, in the context of the paragraph, we understand that 'indica' means 'show' or 'indicate' rather than being a geographic reference.

The spelling of the species epithet '*ceratophthalmus*' has often been contentious, with Sakai and Türkay [2], in their revision of the genus, arguing that '*ceratophthalma*' is necessary to be in agreement with the feminine gender of genus *Ocypode*. The species was originally described by Pallas [1] as *Cancer ceratophthalmus* with *Cancer* being masculine in gender. Whether the ending '-ophthalmus' changes in gender depending on the gender of the genus, however, depends on how it was originally used, that is, whether as a noun or an adjective, and this was not explicitly stated by Pallas [1]. As such, following Article 31.2.2 of the Code, the name '*ceratophthalmus*' is here treated as a noun in apposition.

The identity of *Cancer caninus* Herbst [18], has been problematic. The issues were discussed in Ng et al. ([23]:242): 'Herbst ([18]:78) cited and repeated the description of Rumphius (1705) from Indonesia. However the description is peculiar and seems to be a composite of two different species. Holthuis suggested to Beekman (1999: 400) that one might be a species of *Cardisoma* (Gecarcinidae), and the other the well-known ocypodid *O. ceratophthalmus*. From the description (translated by Beekman, 1999: 33), the gecarcinid is either *Cardisoma carnifex* or *Discoplax hirtipes*, but the description of *Ocypode* is more precise and we agree that it must be *O. ceratophthalmus*. There are no types and no figures (see also Sakai [32]), but the name is available under the Code'. To deal with this situation Ng et al. ([23]:242) acted as first revisors, and selected the *Ocypode* part of the description to represent *Cancer caninus* Herbst [18]. As such, *Cancer caninus* Herbst [18], is now a junior subjective synonym of *Cancer ceratophthalmus* Pallas, 1772.

Ocypode rhombea Fabricius, 1798, was placed into the synonymy of *O. ceratophthalmus* by Sakai and Türkay [2]. Until that time, it had been most commonly treated as a junior subjective synonym of *Ocypode quadratus* (Fabricius, 1787) (see Ng et al. [23]:240). Sakai and Türkay [2] stated that they had examined a putative 'juvenile type specimen in the ZMUC, and … we are confident that *O. rhombea* Fabricius, 1798, is a junior synonym of *O. ceratophthalmus* (Pallas, 1772) [1]'. It is true that a young male dry syntype of *O. rhombea* does still exist in Copenhagen; however, it is in poor condition, the ventral surface is glued to a card, and it is missing all pereiopods except the right cheliped, and the lower half of this is hidden by its position on the mounting card. That being said, our interpretation of its identity is at odds with that of Sakai and Türkay [2]. We still consider it to be a juvenile of *O. quadratus* based on the shape of the carapace, particularly the degree of divergence of the lateral margins, and the fact that the cornea of the eye is identical with that species. Even at such a small size the calcareous lateral dorsal extension of the ocular peduncle is wider and more swollen in *O. ceratophthalmus*, and the presence of an incipient horn is at least indicated. Sakai and Türkay (2013:694) further erroneously stated that *O. rhombea* was described from the Indo-West Pacific, although they earlier listed the type specimen they examined as having an 'unknown locality'. In fact Fabricius did not state the locality in his original description, and it is known that he had other crab species in his collection from the Atlantic coast of the Americas, just as he had numerous specimens from Asian seas. Therefore, we are convinced that the small existing syntype in the ZMUC is actually a subadult *O. quadratus* as formerly believed, and we return *O. rhombea* to the synonymy of that species.

Ocypode celadon sp. nov.

(Figures 5B; 6C,D; 7C,D,H; 8C,D; 9B,E,H; 12)

Ocypode ceratophthalmus—Jackson, Smale and Berry, 1991 [33]:280–286

Ocypode urvillei—Stebbing, 1917 [34]:11.

Ocypoda Urvillei—Bouvier, 1921 [35]:57.

Ocypode aegyptiaca—Hoffmann, 1874 [36]:13. [not *Ocypode aegyptiaca* Gerstaecker, 1856]

Ocypoda ceratophthalma—Ward, 1942 [37]:103; Fourmanoir, 1954 [38]:1, Figure 1.

Ocypode ceratophthalma—Barnard, 1950 [39]:86, Figure 17c,d; Fourmanoir, 1953 [40]:88; Berry, 1976 [41]:35–37, 1 unnumbered text-figure.

Ocypode ceratophthalmus—Stebbing, 1910 [42]:326; Barrass, 1963 [43]:73; Michel, 1964 [44]:11; Day, Millard and Broekhuysen, 1954 [45]:140, 153; Millard and Harrison, 1954 [46]:166; Taramelli, 1955 [47]:31; Crosnier, 1965 [48]:93, Figures. 152, 160, 167–168, pl. 8, Figure 1, pl. 10, Figure 3; Kensley, 1970 [49]:104; Emmerson, 2017 [50]:345–353.

Ocypode sp.—Orchard, 2012 [5]:237–239.

Material Examined

HOLOTYPE: QM-W55057, male (42.3 mm × 38.7 mm), Cocos (Keeling): North Keeling Island, sandy beach, 11°49.782'S 96°49.039'E, Stn CK:2-17, 8.02.2012.

PARATYPES: South Africa: WAM-C44845, five females (30.9 mm × 27.7 mm; 34.5 mm × 30.3 mm; 28.8 mm × 26.2 mm; 31.6 mm × 28.2 mm; 30.6 mm × 27.2 mm); five males (36.3 mm × 32.9 mm; 33.3 mm × 29.3 mm; 33.5 mm × 31.0 mm, 33.3 mm × 29.6 mm; 29.4 mm × 26.7 mm); South Africa, Natal, Banga Nek, Kosi Bay, coll. R.W. George, 2.06.1970.

Mozambique: WAM-unreg., eight females (23.4 mm × 19.9 mm–38.5 mm × 33.1 mm), Casuamine I., Mozambique, G. Hughes, 9.08.1970. WAM-219-73, male (40.5 mm × 36.0 mm), Pomene, Mozambique, P.F. Berry, 25.04.1970. Kenya: WAM-unreg., female (32.5 mm × 27.4 mm), Manda I., Kenya, East Africa, coll. A.J. Bruce, 21.04.1959. Comores: FMNH-UF13661, male (33.7 mm × 29.5 mm), N'Goija, Mayotte, Comores, 12.9642°S, 45.0864°E, reef flat, MAY08-241, A. Anker and F. Michonneau, 7.06.2008 [Photographed]. Mauritius: FMNH-4973, female (29.5 mm × 25.8 mm), Cape Malheureux, by Les Carcasailles Apartments, Mascarene Is., Mauritius, 19°59.15'S, 57°37.61'E, near-shore reef flat, Stn MAU-010, J. Starmer, no date. FMNH-4570, three females (18.9 mm × 16.3 mm; 22.1 mm × 18.6 mm; 25.8 mm × 22.8 mm), three males (15.9 mm × 12.8 mm; 17.0 mm × 14.9 mm; 17.7 mm × 15.7 mm), Cape Malheureux, by Les Carcasailles Apartments, Mascarene Is., Mauritius, 19°59.15'S, 57°37.61'E, near-shore reef flat, Stn MAU-146, J. Starmer, no date. Tanzania: FMNH-2361, one male (19.4 mm × 16.8 mm), three females (20.6 mm × 17.5 mm; 24.5 mm × 21.3 mm; 38.2 mm × 33.4 mm), Bawe I., Zanzibar, Tanzania, C. Meyer, 15.01.2000. Seychelles: SMNH-Decapoda 13766, one male (30.3 mm × 26.4 mm), three females (21.5 mm × 18.4 mm; 33.0 mm × 28.2 mm; 37.2 mm × 33.0 mm), Long Island, Seychelles, H. Sundberg, Feb.–April 1935. SMNH-Decapoda 13767, male (40.3 mm × 35.9 mm), female (41.8 mm × 35.6 mm), Long Island, Seychelles, H. Sundberg, 3.04.1935. SMNH-14370 [= Decapoda 13751], two male (44.0 mm × 38.3 mm; 42.9 mm × 37.8 mm), Frigate Island, Seychelles, H. Sundberg, 11.04.1935. Cocos (Keeling) Islands: QM-W55068, male (42.3 mm × 38.5 mm), Cocos (Keeling) Islands: North Keeling Island, west to southwest coast, intertidal area, CK2-17, 11°49.782'S 96°49.039'E, 8 Feb. 2012. ZRC 2019.1574, three males (32.1 mm × 27.7 mm; 36.9 mm × 31.7 mm; 39.5 mm × 35.1 mm), two females (36.7 mm × 32.2 mm; 39.5 mm × 34.0 mm), Cocos (Keeling) Islands: southern beach of Direction Island, CK12, photo, Cocos (Keeling) 2011 Expedition, 21.03.2011; ZRC 2019.1576, one male (36.1 mm × 31.5 mm), Cocos (Keeling) Islands: West Island, Trannies Beach, Christmas Island and Pulu Keeling Expeditions 2010–2012, 8.02.2012. ZRC 2019.1578, one male (39.6 mm × 34.8 mm), Cocos (Keeling): Alor Penyu, outside of lagoon, West Island, CK6, 12°09.511'S, 96°49.249'E, Cocos (Keeling) 2011 Expedition, 20.03.2011. ZRC 2019.1579, two females (26.2 mm × 22.6 mm; 34.5 mm × 30.3 mm), Cocos (Keeling) Islands: West Island, Trannies Beach, CK2-21, 11.02.2012. ZRC 2019.1580, one female (40.7 mm × 36.7 mm), Cocos (Keeling): North Keeling, 8.02.2012. ZRC 2019.1581, two males (24.7 mm × 21.9 mm; 33.6 mm × 29.5 mm), one female (25.9 mm × 22.6 mm), Cocos (Keeling) Islands: Beach and reef near Airport, outside of lagoon, Settlement, West Island, CK2, 12°11.343'S 96°49.714'E, 20.03.2011. ZRC 2019.1582, three males (19.0 mm × 16.5 mm; 43.6 mm × 39.4 mm; 38.8 mm × 33.8 mm), two female (40.5 mm × 35.2 mm; 41.2 mm × 36.5 mm), Cocos (Keeling): Tanjong Puji, West Island, CK1, 12°11.589'S 96°51.549'E, 19.03.2011. ZRC 2019.1583, five males (41.9 mm × 38.7 mm; 41.8 mm × 38.4 mm; 42.8 mm × 36.5 mm; 40.9 mm × 37.1 mm; 45.6 mm × 41.3 mm), two females (40.2 mm × 35.8 mm; 38.1 mm × 33.7 mm), Cocos (Keeling) Islands: North Keeling Island, west to southwest coast, intertidal area, CK2-17), 11°49.782'S 96°49.039'E, 8.02.2012. Christmas Island: QM-W55067, male (32.7 mm × 30.0 mm), Ethel Beach, night, 10° 27.805'S, 105° 42.443' E, Stn. CI-03-01, 3.01.2012. QM-W55066, two male (38.7 mm × 36.0 mm; 38.7 mm × 35.9 mm), female (25.4 mm × 22.5 mm), CI-05, Flying Fish Cove, night, 10° 25.815'S, 105° 40.180'E, Stn CI-05-2011, 20.03.2011. QM-W55065, female (31.6 mm × 27.8 mm), Ethel Beach, evening, 10° 27.805' S, 105° 42.443'E, Stn CI-38-2011, 28.03.2011. QM-W55058, male (42.2 mm × 38.3 mm), Dolly Beach, Christmas Island, Stn CI-20, 10°31.272'S, 105°40.512'E, 29.01.2010, P. Davie and P. Ng. QM-W55061, male (29.1 mm × 26.6 mm), Waterfall Beach, Christmas Island, 23.01.2010, P. Davie and P. Ng. ZRC 2010.0008, one male (42.7 mm × 38.8 mm), Dolly Beach, Christmas Island, Stn CI-20, 10°31.272'S, 105°40.512' E, 29.01.2010, P. Davie and P. Ng. ZRC 2019.1575, one male (32.6 mm × 29.9 mm), Christmas Island: road towards Christmas Is. Resort, CI3-01, night, 10°27.213'S 105°42.239'E, Christmas Island 2012 Expedition, 3 Feb. 2012; ZRC 2019.1577, one male (35.7 mm × 32.2 mm), one female (35.5 mm × 31.0 mm), Christmas Island: Greta Beach, CI3-29, evening, 10°30.127'S, 105°40.475'E, Christmas Island 2012 Expedition, 15.02.2012. WAM-C44844, male (35.6 mm × 31.5 mm) Flying Fish Cove, Christmas Island, G. Morgan, 22.02.1987.

NON-TYPE MATERIAL: Maldives: ZRC 2017.0627, 24 males, 19 females (unmeasured), Kooddoo I., Goalifu Alifu Atoll, Maldives, inside Meraure Maldives Kooddoo Resort, B. Teo, 22–25 April 2017.

Etmology

The name is in reference to the typical green colour of this species. The French word 'Celadon' has become famous as the name of a pale, jade-green pottery glaze, but it apparently has its origin from the name of the shepherd Celadon, a character in Honoré d'Urfé's French romance, *L'Astrée* (1627), who wore pale green ribbons.

Diagnosis

Carapace (Figure 4B) slightly wider than long (1.1–1.2 times), finely granular over dorsal surface. Eyestalks prolonged distally beyond cornea in a long stylus in mature adults. Supraorbital margin with inner part lateral to base of rostrum relatively flat or only weakly concave, not forming obvious concave cup; outer lateral margin oblique relatively straight or weakly concave to exorbital angle. Exorbital angles broadly triangular and weakly directed laterally in large specimens. Carapace marginally broadest at exorbital angles in larger specimens, or at about anterior third in smaller. Palm of major chela appears higher; height c. 1.1–1.2 × length (length in midline from base of gape to indent of articulation versus maximum vertical height); fingers also appear shorter, broader than *O. ceratophthalmus*; granulation on outer face of major chela prominent, coarse and more sparsely granular (Figure 6D); spination of lower margin strong, blunted and more distally pointed; alternating but more even in size than *O. ceratophthalmus*; lower margin of chela broadly evenly convex. Stridulatory crest (Figure 6H) superior half composed of c. 15–16 widely spaced chitinous tubercles; mostly broadly transverse becoming narrower ventrally. Ventral half marked by c. 20–22 much finer transverse striae, closely spaced initially, but interspaces widening ventrally to be similar to anterior part; relatively narrower anteriorly forming obvious waist at transition point; becoming broadest at about tubercles 13–17, then narrowing quickly. Minor chela ventral margin spines lower, blunter, more distally pointed than *O. ceratophthalmus* (Figure 6C,D). G1 apically narrowed, corneous tip well defined, projecting distally; subapical thumb well-developed, triangular, projecting more laterally than distally (Figure 7B,E,H).

Colour (Figure 12)

Adults relatively evenly coloured over carapace and pereiopods; anterior ventral surface not noticeably darkened as in other species. Colour varies from pale olive green to darker grey–green through to almost yellowish gold; dorsal carapace may be mottled or relatively even in tone; mesogastric, cardiac and intestinal regions framed by darker green markings, but not a strong feature. Chelae typically paler but evenly coloured across outer face; upper face of carpus similar in colour. Walking legs may be mottled but without obvious banding over superior face.

Remarks

The numerous characters that separate this species from its two sibling sister species are given in Section 4.

Ocypode celadon is a western Indian Ocean form, and like *O. ceratophthalmus* appears to occur both on the continental margin of East Africa and on oceanic islands. *Ocypode urvillii* on the other hand appears to be an exclusively insular form that spreads from the islands of the eastern Indian Ocean through to the central Pacific. For example, *O. urvillii* is known from Cocos (Keeling) and Christmas Is., and on the outer cays and sandbanks of northwestern Australia (Ashmore Reef, Rowley Shoals, etc.) but there are no records from the northern Australian mainland despite numerous collections from this coast in the collections of the Queensland and Western Australian Museums. Such a distribution pattern is hard to understand but has precedence, as *O. pallidula* is similarly an insular form that is never found on the continental margins [4].

Distribution

A widespread temperate to tropical crab in the western Indian Ocean (Figure 11). Recorded localities are numerous and include the Indian Ocean coast of Africa from South Africa (from the east of Mossel Bay), KwaZulu-Natal, Mozambique, north to Somalia and the Red Sea; Saudi Arabia; Pakistan, India, the Gulf of Mannar and Palk Bay; Madagascar, Europa Island, Mauritius, la Reunion, the Seychelles, Diego Garcia (Chagos Archipelago), Aldabra, the Maldives, the Laccadives, Cocos (Keeling) Islands and Christmas Island (see Emmerson [50], for individual citations). It is possible/probable that some of the more easterly of these specific records could be of *O. ceratophthalmus* sensu stricto, but it is certain that *O. celadon* does indeed occur throughout this region and is the dominant form in much of the Indian Ocean [3].

Ecology

Emmerson [50] has provided an extensive literature review of the ecology of this species (references pertaining to the western Indian Ocean). In East Africa it is found intertidally on sandy beaches, sand flats and small cays, preferring sheltered shores with moist sand, and entering the lower reaches of estuaries, often near mangroves [51–54]. On more open exposed beaches it is displaced by *O. ryderi* Kingsley, 1880 [55]. Where these two species co-occur *O. celadon* is found just below high water neap (HWN), whereas *O. ryderi* occurs higher up between the highest water spring (HWS) and HWN, so there is some spatial separation [55].

Mature males may build a sand pyramid at the burrow entrance—termed 'copulation burrows', or 'open burrows' [43, 56–58]. Burrow structure has also been reported by Braithwaite and Talbot [59] and Chakrabarti [60] and generally appears similar to *O. ceratophthalmus sensu stricto*.

Crab numbers can be extremely high: 1500–3000 per km^{-1} beach [33, 41]; and as many as 19,000 crabs per 1800 m of beach [43].

Ocypode celadon sp. nov. is the dominant species on the Cocos (Keeling) island group; it does co-occur with both *O. ceratophthalmus* and *O. urvillii*, but those species are rare. On Christmas Island it also co-occurs with both *O. ceratophthalmus* and *O. urvillii* with all three species being abundant. Ecological separation was not specifically noted; however, at the time of our visits, we were still unclear that we were dealing with a species complex of three sympatric sister species. An intensive study of how the three species

(A) (B)

(C) (D)

(E)

Figure 12: Live photos of *Ocypode celadon* sp. nov., all taken on West Island, Cocos (Keeling) Is.: (A–C) Christmas Island and Pulu Keeling Expeditions 2010-2012; (D, E) Neville Coleman courtesy Queensland Museum.

partition their environment on Christmas Island would be fascinating.

***Ocypode urvillii* Guérin**, 1829

(Figures 5C; 6E,F; 7E,F,I; 8E,F; 9C,F,I; 13; 14)

Ocipode urvillii Guérin, 1829 [61]: Pl.1 Figure 1.

Ocypode urvillei—Guérin-Méneville, 1838 [62]:9.

Cancer francisci Curtiss, 1938 [63]:174–175; Sakai and Türkay, 2013 [2]:686.

Ocypoda brevicornis variety *longicornuta* Dana,1852 [64]:327–328; 1855 [65]: pl. 20 Figure 4a–e (see below).

Ocypoda Urvillii—Dana, 1852 [64]:328; [65], pl. 20, Figure 5a–c.

Material Examined

Types: Neotype of *Ocypode urvillii* Guerin, 1829: ZRC-2014.0250, male (40.1 mm × 37.2 mm), Tahiti, French Polynesia, B. Galil, April 2014. [Simultaneous neotype for *Ocypode francisci* Curtiss, 1938 [63]]. Neotype for *O. brevicornis* var. *longicornuta* Dana [64]: FMNH-6317, a male (37.7 mm × 36.0 mm, carapace broken dorsally), from caves near Hu'fangelupe, Tongatapu, Tonga.

Additional material: Cocos (Keeling) Islands: ZRC 2019.1504, male (35.7 mm × 29.9 mm), next to boat ramp near Rumah Baru, West Island, NUS/QM Exped. Stn CK-27, evening, 24.03.2011. Christmas Island: QM-W55088, male (33.6 mm × 29.7 mm), Ethel Beach, Christmas Island, CI-38, 10°27.805' S, 105°42.443' E, 28.03.2011; QM–W55071, CI-38, male (16.5 mm × 14.1 mm), data as for previous; QM-W55069, juvenile, Greta Beach, 10°30.127'S, 105°40.475'E, NUS/QM Exped. CI-33, evening, 27.03.2011; QM–W55070, juv. female (16.7 mm × 14.3 mm), CI-33, data as for previous; QM-W55087, male (37.3 mm × 32.8 mm), CI-33, data as for previous; QM-W55059, male (39.7 mm × 35.2 mm), Ethel Beach, Christmas Island, P. Davie and P. Ng, 25.01.2010. QM-W55060, male (35.3 mm × 30.8 mm), data as for previous; QM-W55062, male (30.6 mm × 26.2 mm), data as for previous; QM-W55064, female (31.7 mm × 27.5 mm), data as for previous; QM-W55063, female (32.8 mm × 27.9 mm), data as for previous; WAM-C44844, male (35.6 mm × 31.6 mm), Flying Fish Cove, Christmas Island, 10°25'S, 106°40'E, WAM/AIMS Expedition, 22.02.1987; ZRC 2019.1521, female (32.9 mm × 28.3 mm), Ethel Beach, 10°27.805'S, 105°42.443'E, NUS/QM Exped. Stn CI-03, night, 20.03.2011; ZRC 2019.1509, two males (25.6 mm × 22.0 mm; 25.9 mm × 21.7 mm), Flying Fish Cove (intertidal), CI3-13, afternoon, 10.429863°S, 105.667135°E, 8.02.2012; ZRC 2019.1520, male (36.8 mm × 32.2 mm), Greta Beach, CI3-05, morning, 10°30.127' S, 105°40.475'E, 5.02.2012; ZRC 2019.1524, male (33.9 mm × 30.0 mm), Flying Fish Cove, 10°25.815'S, 105° 40.180'E, NUS/QM Exped. Stn CI-05, night, sandy beach, 20.03.2011; ZRC 2019.1526, male (30.7 mm × 27.5 mm), Ethel Beach, 10°27.805'S, 105°42.443'E, sandy beach, NUS/QM Exped. Stn CI-38, evening, 28.03.2011; ZRC 2019.1525, female (28.5 mm × 24.5 mm), Ethel Beach, 10°27.805'S, 105°42.443'E, sandy beach, NUS/QM Exped. Stn CI-38, evening, 28.03.2011; ZRC 2019.1527, male (32.2 mm × 28.4 mm), Greta Beach, 10°30.127'S, 105°40.475'E, NUS/QM Exped. Stn CI-40, evening, 27.03.2011. Indonesia: ZRC unreg., five males (20.6 mm × 17.4 mm; 21.7 mm × 17.6 mm; 28.2 mm × 23.6 mm; 30.7 mm × 25.9 mm; 33.7 mm × 29.2 mm), Lombok, Indonesia, fishing village near Tanjong Ringgit Temiak, coll. local fishermen, 13.02.2002. Ashmore Reef: QM-W26055, three males (31.7 mm × 28.1 mm; 28.0 mm × 24.8 mm; 30.1 mm × 26.8 mm), female (26.1 mm × 22.9 mm), Ashmore Reef, sandbank, 9.10.1998, J. Short; QM-W26056, female (29.5 mm × 25.8 mm), Ashmore Reef, 9.10.1998, J. Short. WAM-C18714, two males (37.2 mm × 33.0 mm; 40.1 mm × 34.1 mm), Ashmore Reef. Rowley Shoals: WAM-C41132, two males (39.1 mm × 34.5 mm; 39.0 mm × 34.2 mm), Mermaid Reef, Rowley Shoals; WAM-C41920, male (37.4 mm × 32.2 mm), Clerke Reef, Rowley Shoals, sand cay, 17.345940°S, 119.366521°E, no date. WAM-C14066, two males (27.1 mm × 23.5 mm; 32.9 mm × 27.7 mm), female (27.8 mm × 23.6 mm), Condillac I., 13.8155°S, 125.5428°E, west of Kimberley's, Western Australia; WAM-C14066, three males (30.0 mm × 26.0 mm–34.0 mm × 28.8 mm), three females (29.2 mm × 26.5 mm–32.0 mm × 27.4 mm), E Montalivet I., 14.0316°S, 125.2710°E, west of Kimberley's, Western Australia. Torres Straits: QM-W12347, male (43.0 mm × 39.2 mm), female (40.0 mm × 35.8 mm), Bramble Cay, eastern Torres Straits, 09°08'23"S, 143°52'54"E, coll. Charles Hadley. Coral Sea: WAM-C14066, male (45.5 mm × 41.0 mm), NE Herald Cay, Coral Sea. New Caledonia: QM-W52509, four males (38.0 mm × 33.6 mm; 37.0 mm × 33.1 mm (damaged); 41.7 mm × 38.2 mm; 42.0 mm × 37.8 mm), female (30.1 mm × 26.9 mm), beach at Mangrove du Cap, West Coast New Caledonia, 21°30'S, 165°30'E, 3.12.1993, P. Davie; QM-W52477, male (40.1 mm × 35.3 mm), Le Cap, West Coast New Caledonia, 21°30'S, 165°30'E, 12–14.12.1993, P. Davie; ZRC 2001.2280, female (30.5 mm × 27.7 mm), Noumea, New Caledonia, B. Richer de Forges, July 2001. Loyalty Islands: ZRC 2019.1505, male (39.8 mm × 35.5 mm), female (36.5 mm × 33.2 mm), Loyalty Is., Stn OU86 Kiw A3, 14.08.2010; ZRC 2019.1518, two males (13.2 mm × 11.2 mm; 25.1 mm × 21.9 mm), one juv. female (15.0 mm × 12.9 mm), five juvs., Loyalty Is., Stn OU86 Kiw A3, 14.08.2010; ZRC 2019.1519, male (32.2 mm × 27.6 mm), Loyalty Is., Stn OU94 Kiw A3, 18.08.2010. Guam: ZRC-2000.0635, two males (39.3 mm × 35.8 mm; 38.5 mm × 35.0 mm), Pago Bay, outside of University of Guam Marine Laboratory, Guam, P.K.L. Ng and C.H. Wang, 15–18.04.2000; ZRC-2001.0721, male (35.3 mm × 32.1 mm), Fai fai Beach, Guam, P.K.L. Ng, 31.07.2001. Philippines: ZRC-2009.0063, two males (19.1 mm × 15.6 mm; 26.2 mm × 22.8 mm), three females (22.4 mm × 19.4 mm; 23.0 mm × 19.6 mm; 25.9 mm × 23.1 mm), Panglao 2004: M19, 10.06.2004; ZRC-2009.0064, two females (30.2 mm × 26.3 mm; 33.6 mm × 30.1 mm), Panglao 2004, stn M7, 9.06.2004; ZRC 2019.1508, two males (29.1 mm × 25.8 mm; 32.1 mm × 27.9 mm), Balicasag I., Panglao, Bohol, Philippines, in tangle nets, coll. local fishermen, June 2003; WAM-208-73, three females (23.6 mm × 20.0 mm–28.9 mm × 24.4 mm), southern side of Taganak I., Sulu Arch., 6°5'N, 118°19'E, R.V. Pele, B.R. Wilson, 2.03.1964. WAM-210-73, male (27.6 mm × 24.1 mm), Clarendon Bay, Balabac I., Palawan, Sulu Arch., R.V. Pele, B.R. Wilson, 10.03.1964. Wallis and Fortuna: MNHN-IU-2010-6370, male (33.4 mm × 29.1 mm), Wallis et Fortuna, 2008, J. Poupin; MNHN-IU-2010-6371, male (18.7 mm × 16.0 mm), two females (15.3 mm × 13.2 mm, 17.1 mm × 14.4 mm), Wallis and Fortuna, 2008, J. Poupin. MNHN-IU-2010-6372, male (18.6 mm × 16.3 mm), female (24.2 mm × 20.8 mm), Wallis and Fortuna, 2008, J. Poupin. Kiritimati: ZRC unreg., female (39.2 mm × 35.3 mm), Kiritimati Atoll, Line Islands, R. Englund, 11.07.2001; FMNH-10873, male (41.6 mm × 35.5 mm), Kiritimati Atoll, Line Islands, shore on W side of atoll, S of point, S of main reef passage, 1.8913°S, 157.5448°E, D. Obura, 8.08.2005. Tonga: FMNH-6317, male (37.7 mm × 36.0 mm, carapace broken dorsally), caves near Hu'fangelupe, Tongatapu, Tonga, fringing sand beach, karst coastline, L. Kirkendale, 13.06.2004. French Polynesia: FMNH-23846, female (32.9 mm × 29.7 mm), outside of Cook's Bay, northeast shore, Moorea I., Society Is., French Polynesia, 17.4849°S, 149.8167°E, intertidal rocky shore with plant debris, at night, G. Paulay et al., 1.11.2009; FMNH-15714, male (22.0 mm × 18.9 mm), Opunohu Bay, northeast shore, Moorea I., Society Is., French Polynesia, intertidal, J. Poupin, 10.10.2008; MNHN-IU-2010-6374, three males (25.0 mm × 22.1 mm; 38.7 mm × 33.9 mm; 44.7 mm × 39.8 mm), two females (21.7 mm × 18.7 mm; 41.1 mm × 36.4 mm), Taiaro Atoll, Tuamotu, French Polynesia, 15°45'S, 144°40'W, 12–20.02.1994, J. Poupin. WAM-203.73, two males (41.2 mm × 36.9 mm; 43.9 mm

× 38.3 mm), Haava Straits, R.V. Pele, Marquesas Exp., Stn 8, Marquesas Arch., French Polynesia, coll. B.R. Wilson, 1.10.1967; WAM-unreg., nine males (22.5 mm × 19.1 mm–40.1 mm × 35.8 mm), four females (32.9 mm × 28.1 mm–36.2 mm × 31.9 mm), R.V. Pele, Marquesas Exp. Stn 4, Marquesas Arch., French Polynesia, coll. B.R. Wilson, 29.09.1967. Hawaii: ZRC 2000.0420, male (14.3 mm × 12.8 mm), Kewalo, on sea wall, surf zone, Ala Moana area, Waikiki, Oahu, P. K. L. Ng and S. H. Tan, 22.01.2000; Clipperton Island: MNHN-IU-2010-6373, male (44.2 mm × 39.3 mm), female (40.0 mm × 36.5 mm), Clipperton Island, central East Pacific, 10°18N, 109°13W, Feb. 2005, J. Poupin.

Diagnosis

Carapace (Figure 4C) slightly wider than long (1.1–1.2 times), finely granular over dorsal surface. Eyestalks prolonged distally beyond cornea in a long stylus in mature adults. Exorbital angles broadly triangular, weakly directed laterally in large specimens. Carapace marginally broadest at exorbital angles in larger specimens, or at about anterior third in smaller. Supraorbital margin with inner part lateral to base of rostrum forming obvious concave cup (marked laterally by prominent forwardly directed angular projection); outer margin more sharply oblique before flattening out to meet exorbital angle. Palm of major chela appears higher; height c. 1.1–1.2 × length (length in midline from base of gape to indent of articulation versus maximum vertical height); fingers also appear shorter and broader than *O. ceratophthalma*; granulation on outer face of major chela mostly relatively smaller, more rounded, better separated (Figure 6F); spination of lower margin lower, more distally pointed; relatively even in size; lower margin of chela slightly concave under base of fingers; relatively straight over distal half. Stridulatory crest (Figure 6I) similar to *O. celadon*: superior half composed of c. 14–15 widely spaced, broadly transverse and chitinous tubercles, but narrowing less ventrally; ventral half marked by c. 20–22 much finer transverse striae, closely spaced initially, but interspaces widening ventrally to be similar to superior part; medial waist well defined, but wider than *O. celadon*, becoming broadest at about tubercles 12–15, then, narrowing quickly. Minor chela ventral margin spines lower, blunter and distally pointed (Figure 6E,F). G1 apically narrowed, corneous tip partially rounded but obliquely projecting distally; subapical thumb poorly developed, forming a simple broad triangular elbow (Figure 7C,F,I).

Colour (Figure 13)

Adults with dorsal carapace and pereiopods typically paler shades of reddish brown, brown and purple to grey, varying with locality; strong darker marking on lower back framing mesogastric, cardiac and intestinal regions; lower surfaces of carapace and pereiopods dark purple to dark brown or even dark blackish grey extending from orbital socket to level of thoracic somite 5, thence transitioning to pale cream posteriorly. Chelae typically pale off-white over ventral two-thirds, dark brown to purple over superior third of palm stretching from propodal articulation to mid-point of dactylar articulation, and onto upper basal third of dactyl; upper face of carpus brown to purple (this darker dorsal chela colouring is strong in Pacific populations, but not obvious in the Indian Ocean material that we observed). Walking legs with some broad darker banding over superior face.

Colour in *Ocypode* can vary considerably even within a species due to life stage, maturity and even ecological factors. Images we have seen of mature *O. urvillii* can vary from an overall pale cream fascies to quite dark. Such colour changes in response to background sand colour have been previously reported by Green [66] and Little [67] for this species in Hawai'i (under the name of *O. ceratophthalmus*).

Remarks

The numerous characters that separate this species from its two sibling sister species are given in Section 4.

Ocypode urvillii Guérin, 1829, was described from Tahiti, and any type specimens should have been deposited in the MNHN, Paris; however, this old collection has been thoroughly searched, and no likely specimens can be found (N. K. Ng, pers. comm.), and the types must be thus presumed lost. As there is obvious confusion concerning the identity of species in this species complex it is therefore necessary to establish a neotype, and a topotypic male (40.1 mm × 37.2 mm), from Tahiti, French Polynesia (ZRC-2014.0250), is here, thus, designated. Based primarily on Guérin's figures (1829: Pl. 1, Figure 1; reproduced here as Figure 13A,B), we are confident that there is no confusion over the identity of Guerin's species. The stridulatory ridge is in broad agreement in that it shows an evenly narrow band consisting of a similar number of evenly spaced striae, and this easily separates it from *O. ceratophthalmus* sensu stricto, although not from *O. celadon* sp. nov., but that species is only found in the Indian Ocean. Also the darker brown overall colour including on the cheliped carpus and palm, combined with the darker band along the superior margin, are also in agreement with the specimens we here recognise as *O. urvillii*.

Martin et al. [68] have discussed the dates of publication of Guerin's plates; *Ocipode* [sic] *Urvillii* was the spelling used in the caption to Plate 1 in 1829, and as such this spelling has precedence and must be followed, despite the fact that he later used the alternative spelling of *Ocypode urvillei* in his text account of the species in 1838.

Ocypoda brevicornis var. *longicornuta* Dana, 1852 [64], was described from two specimens, a male from Tongatabu in Tonga, Pacific Ocean, and a female from Singapore. Dana's type material is lost, and based on Dana's figures of the male ([65]: pl. 20 Figure 4a–e), we cannot be absolutely certain as to which species it refers. Dana seems to show more strongly spinate chelipeds and walking legs than is normal in *O. urvillii*, and closer to *O. ceratophthalmus*, but on the other hand the shape and prominence of the inner orbital angles are more typical of *O. urvillii*, as is the proportions of the somites of the male pleon. It is a further consideration that Dana also recorded a specimen of what he tentatively identified as *O. urvillii* on the same plate, however that specimen is clearly a juvenile, and as such, even more difficult to be certain of, especially as all of Dana's material of these species is lost. We have confirmed the distribution of *O. ceratophthalmus*, only as far east as Fiji, so we cannot be sure if it could co-occur in Tonga, Dana's type locality. However, we have examined a

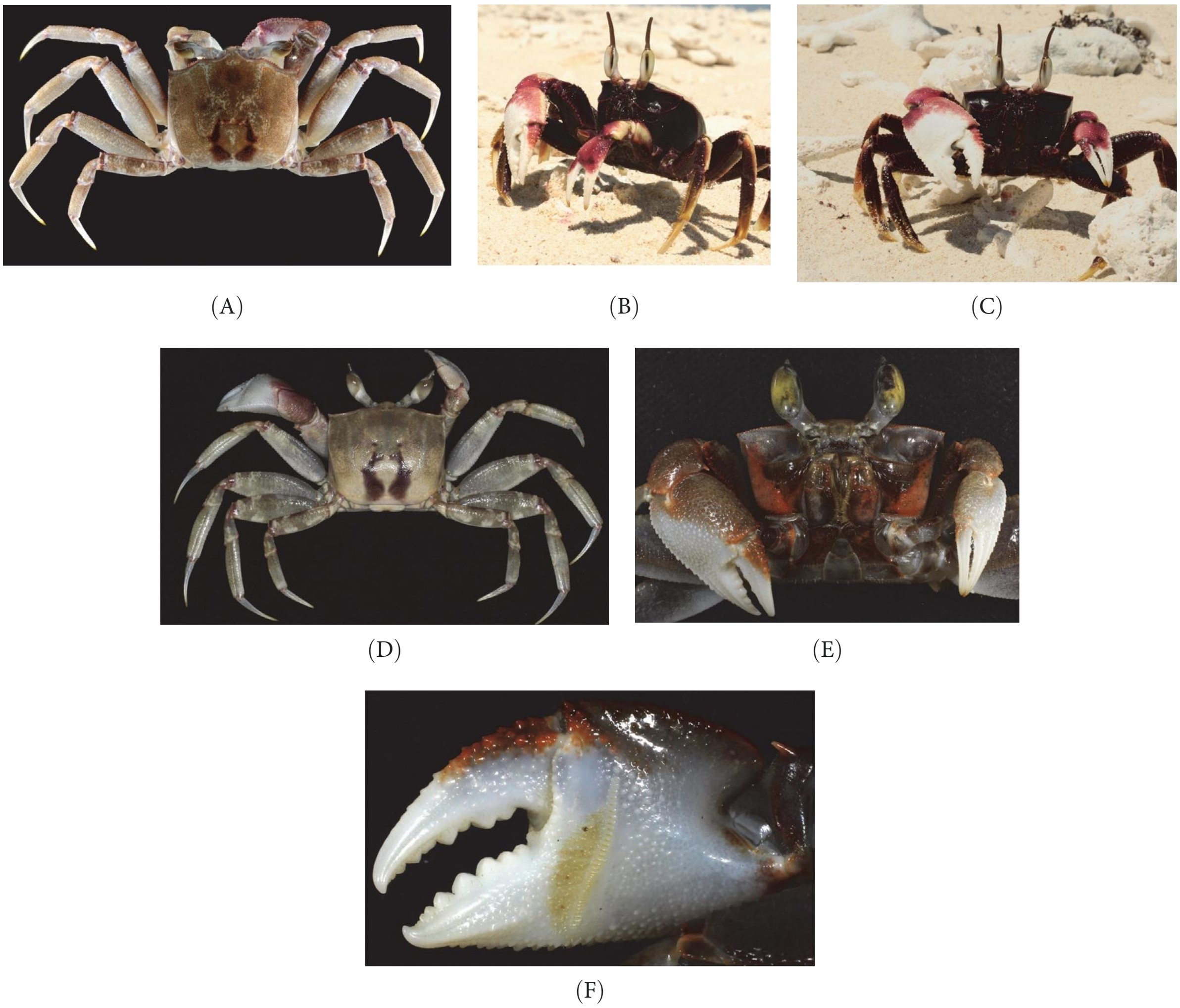

Figure 13: Live photos to show the variation in colour of *Ocypode urvillii*. (A) Moorea I, Society Islands, French Polynesia (Gustav Paulay); (B, C) New Caledonia (Joseph Poupin); (D) Nuku Hiva, Marquesas Arch., French Polynesia (Joseph Poupin); (E, F) Western Baie du Charner, Eiao, Marquesas Arch., French Polynesia (Joseph Poupin).

Figure 14: Original illustration of *Ocypode urvillii* Guérin, 1829, Plate 1, Figure 1. (A) Dorsal view; (B) inside face of major chela.

single topotypic male from Tongatabu, Tonga, and identified it morphologically and genetically as *O. urvillii*. Therefore, because of the high potential for confusion, we consider a neotype is necessary, and hereby nominate FMNH-6317, a male (37.7 mm × 36.0 mm, carapace broken dorsally), from caves near Hu'fangelupe, Tongatapu, Tonga, as the Neotype, and consequently *O. brevicornis* var. *longicornuta* Dana [64], becomes a primary synonym of *O. urvillii*.

There is little doubt that *Ocypode francisci* Curtiss, 1938 [63] is a junior synonym of *O. urvillii*, especially because it was also named from Tahiti ('the beach, near Tautira'). The issue of Curtiss' names has been extensively addressed by Evenhuis [69] and Ng et al. [70]. Curtiss did not select or deposit type specimens for his names and no figures were provided, but nevertheless enough description was given to satisfy the rules of Zoological Nomenclature, and thus, his names are valid and available. Nevertheless, while it is clear that the species belongs to *O. ceratophthalmus* sensu lato (see discussion by Ng et al, 2011:51), his description does not allow finer detailed identification. Therefore to settle the matter completely, we here elect as a neotype for *Ocypode francisci* Curtiss, 1938 [63], the same male specimen (ZRC-2014.0250, male, 40.1 mm × 37.2 mm, from Tahiti, French Polynesia) that we have used as the neotype of *Ocypode urvillii* Guérin, 1829. Thus, *Ocypode francisci* Curtiss, 1938 [63] becomes a junior objective synonym of *Ocypode urvillii* Guérin, 1829.

Distribution

Purely insular distribution from Clipperton Island in the central East Pacific, and from Hawai'i westwards through the central western Pacific and into the northeast Indian Ocean as far west as Cocos (Keeling) Islands (Figure 11; also see [3]).

Apparently the most wide-spread species belonging to *Ocypode*, and one of the very few species to have crossed the oceanic barrier into the East Pacific (see [71]), though there are no records from the southeastern Pacific islands such as Rapa Nui or Pitcairn. The only other *Ocypode* species known from the East Pacific are *Ocypode occidentalis* found from the Gulf of California to Colombia, and *O. gaudichaudii* found along the Pacific coast of the Americas from Guatemala to Chile [2].

Ecology

In Hawai'ian waters, this species has been estimated to become mature at 27–33 mm CW; females copulate between 29 and 33 mm CW, with reproduction mainly between April and August [72]. There is also evidence that they can tolerate temperatures as high as 37°C [73] commensurate with their open beach existence.

4. Discussion

4.1. Morphological Separation. The numerous characters useful to diagnose and separate the species discussed here are presented in Table 3. *Ocypode celadon* sp. nov. appears morphologically closest to *Ocypode urvillii* based on the form of the stridulatory ridge of the major chela and the G1. This seemingly close relationship is not, however, supported by the present genetic studies (Figures 1 and 2) or those of Ma et al. [3], which places *O. ceratophthalma* as closest genetically to one or the other depending on the analysis.

The major differences with *O. urvillii* are the more coarsely granular outer face of the major chela; the different shape of the outer orbit (narrower and appearing to project more laterally than *O. urvillii*, which has the outer lower margin more quadrate in appearance); the differences in the G1; and last, the strikingly different colour (see colour figures) which gives the new species its name. The fact that all three species can occur sympatrically, at least on Christmas Island, and thus far we have seen no intermediate forms, is further strong evidence that the species are all reproductively separated.

These three species help to reveal an interesting evolutionary and biogeographic separation. *Ocypode ceratophthalmus* which occurs very widely across the Indo-Pacific region, dominates almost exclusively on the sandy continental beaches east of Pakistan, though *O. celadon*, mysteriously, is the only form along the shores of continental east Africa. This can be assumed to be a result of current flows in the west Indian Ocean preventing the southwesterly spread of *O. ceratophthalmus* (see Figure 3b in Ma et al. [3]). Based on the mitochondrial 16S and COI genes, *O. ceratophthalmus* is sister to *O. celadon* sp. nov. (though cladal bootstrap support is low), however, morphologically, the two insular species, *O. celadon* and *O. urvillii*, are most similar to each other, and have almost identical stridulatory ridges on the inner face of the male chela.

While the two insular species, *Ocypode celadon* and *O. urvillii* generally predominate in the Indian and West Pacific Oceans, respectively, *O. urvillii* has invaded westwards to share some of the islands and offshore atolls of the northwestern Indian Ocean. Present records show that it is the only species present on offshore sandbanks and islands off NW Australia and is abundant on Christmas Island, however, a further 800 kms west at Cocos (Keeling), *O. urvillii* has become rare.

Of all the morphological characters, colour is perhaps the least reliable. As already mentioned, colour in *Ocypode* species can vary significantly due to life stage, maturity, and ecological factors. The colour of juvenile and immature crabs of the present three species is typically a similar pale mottling and therefore not diagnostic. Adult *O. celadon* are the easiest to quickly distinguish by their distinctive olive to golden colouring. However, mature *O. ceratophthalmus* can be similar to *O. urvillii*, at least over the western part of the range of the latter species. In the West Pacific, crabs typically have obvious dark brown to purple on the upper face of the carpus, and on the superior third of the cheliped palm, stretching onto the upper basal third of the dactyl. This apparently distinctive colouring was not, however, obvious to us when collecting the Indian Ocean material for this study and is not reflected in the photos we took of a range of genetic voucher specimens. At that time, we had assumed all were *O. ceratopthalmus* not realising that a pseudo-cryptic third species was also present. Thus, on present evidence it appears that at least the Indian Ocean populations of *O. urvillii* do not show the typical colouring of the West Pacific populations. This is a subject needing further investigation.

4.2. Genetic Separation. The phylogenetic tree clearly supports three distinct clades corresponding to the three species recognised here (Figures 1 and 2), and the interspecific distances also provide further genetic support. The minimum COI interspecific K2P distance is at least 1.54% among the three species (Table 2). This is low compared to the interspecific distances recorded in fiddler crab genera in the family, for example, 4.61% among species of the *Minuca burgersi* complex [74]; 7.27% among species from Vietnam [75]; 10.75% among species from the Arabian Sea region [9];

Table 3: List of characters to separate species in the *Ocypode ceratophthalmus* species complex.

Characters	*Ocypode ceratophthalmus*	*Ocypode celadon* sp. nov.	*Ocypode urvillii*
Granulation on outer face of major chela	Mostly smaller, narrower and taller near superior margin; finer and more rounded ventrally	Prominent, coarse, more sparsely granular (Figure 6D)	Smaller, more rounded, better separated (Figure 6F)
Proportions of major chela (length in midline from base of gape to indent of articulation versus maximum vertical height)	Palm appears longer; height subequal to length	Palm appears higher; height c. 1.1–1.2 × length	Palm appears higher; height c. 1.1–1.2 × length
Fingers of major chela	Appearing longer, narrower	Appearing shorter, broader	Appearing shorter, broader
Spination of lower margin of major chela	Strong, sharp, more vertically directed downwards; more markedly alternating in size	Strong, blunter, more distally pointed; alternating but more even in size	Lower, more distally pointed; relatively even in size
Spination of minor chela	Very sharp somewhat upright, distally pointed spines; proximal half of dactyl with row of strong sub-conical spines with blunt corneous tips	Ventral margin with blunter, more distally pointed spines	Ventral margin with blunter, more distally pointed spines
Shape of lower margin of chela	Slightly concave under base of fingers; relatively straight over distal half	Evenly convex	Slightly concave under base of fingers; relatively straight over distal half
Shape of supraorbital margin	Inner part lateral to base of rostrum relatively flat to weakly concave, not forming marked concave cup; outer lateral margin oblique, relatively straight to exorbital angle	Inner part lateral to base of rostrum relatively flat to weakly concave, not forming marked concave cup; outer lateral margin relatively straight and oblique to exorbital angle	Inner part lateral to base of rostrum forming obvious concave cup (marked laterally by prominent forwardly directed angular projection); outer margin more sharply oblique before flattening out to meet exorbital angle
Stridulatory crest	Superior half composed of c. 17 widely spaced chitinous tubercles, mostly subglobular but ventral 5–6 widening into narrower transverse striae. Ventral half marked by c. 30–33 much finer broader, more closely set striae, that maintain same interspacing over entire length; slightly narrower anteriorly but without obviously defined waist at transition point; relatively even in width over most of its length (Figure 6G)	Superior half composed of c. 15–16 widely spaced chitinous tubercles; mostly broadly transverse becoming narrower ventrally. Ventral half marked by c. 20–22 much finer transverse striae, closely spaced initially but interspaces widening ventrally to be similar to superior part; relatively narrower anteriorly forming obvious waist at transition point; becoming broadest at about tubercles 13–17, then narrowing quickly (Figure 6H)	Similar to *O. celadon*: superior half composed of c. 14–15 widely spaced, broadly transverse, chitinous tubercles, but narrowing less ventrally. Ventral half marked by c. 20–22 much finer transverse striae, closely spaced initially but interspaces widening ventrally to be similar to superior part; medial waist well defined, but wider than *O. celadon*, becoming broadest at about tubercles 12–15, then narrowing quickly (Figure 6I)
G1	Apically broadly rounded, corneous tip directed laterally, not projecting; subapical thumb strongly developed, hooked, projecting distally (Figure 7A,D,G)	Apically narrowed, corneous tip well defined, projecting distally; subapical thumb well-developed, triangular, projecting more laterally than distally (Figure 7B,E,H)	Apically narrowed, corneous tip partially rounded but obliquely projecting distally; subapical thumb poorly developed, forming a simple broad triangular elbow (Figure 7C,F,I)
Colour	Adults with dorsal carapace and pereiopods pale sandy cream, but with strong maroon/brown marking on lower back framing mesogastric, cardiac and intestinal regions; lower surfaces of carapace and pereiopods dark maroon to reddish brown from orbital socket to level of thoracic somite 6, thence transitioning to pale cream posteriorly. Chelae typically white; without marked indication of darker colour over superior margin of palm or base of dactyl; upper face of carpus pale creamy white. Walking legs without obvious banding over superior face. (Figure 10A–F)	Adults relatively evenly coloured over carapace and pereiopods; anterior ventral surface not noticeably darkened as in other species. Colour varies from pale olive green to darker grey green through to almost yellowish gold; dorsal carapace may be mottled or relatively even in tone; mesogastric, cardiac and intestinal regions framed by darker green marking, but not a strong feature. Chelae typically paler but evenly coloured across outer face; upper face of carpus similar in colour. Walking legs may be mottled but without obvious banding over superior face. (Figure 12A–E)	Adults with dorsal carapace and pereiopods typically paler shades of reddish brown, brown, purple to grey, varying with locality; strong darker marking on lower back framing mesogastric, cardiac and intestinal regions; lower surfaces of carapace and pereiopods dark purple to dark brown or even dark blackish grey extending from orbital socket to level of thoracic somite 5, thence transitioning to pale cream posteriorly. Chelae typically pale off-white over ventral two-thirds, dark brown to purple over superior third of palm stretching from propodal articulation to mid-point of dactylar articulation, and onto upper basal third of dactyl; upper face of carpus brown to purple. Walking legs with some broad darker banding over superior face. (Figure 13A–F)

13.7% among species of the *Austruca variegata* complex [76], but it is similar to the small minimum interspecific distances shown by some pseudocryptic species within grapsoid taxa, for example, 1.38% among most species of *Parasesarma bidens* complex [77]; 1.23% between *Tuerkayana rotundum* (Quoy & Gaimard, 1824) and *T. latens* Ng & Shih, 2023 [78], and 1.54% between *Pseudohelice subquadrata* (Dana, 1851) and *P. annamalai* Prema, Hsu, Shih & Ravichandran, 2022 [79]. Therefore, we consider that the distances of $\geq$1.54 among the *O. ceratophthalmus* complex can be accepted as supporting three morphological distinct species.

Mazumder et al. [80] calculated the K2P divergence values of COI across 16 morphospecies of *Ocypode* based on their own and published data. They found that intraspecific divergence varied from 0 to 0.189 (with a mean value of 0.020 ± 0.047), while interspecific divergence between different species ranged from 0.042 to 0.280, with a mean of 0.180 ± 0.019. Although they reported very high intraspecific divergence for '*O. ceratophthalmus*', they still treated it as a single species despite the presence of three clades in their trees ([80]: Figures 2–4). They also listed a number of erroneous country localities in their data. After checking the localities given in the original literature we here confirm that their three clades align with the distributions of the three species described in our study.

4.3. Biogeography. The distributions of the three species recognised here are shown in Figure 11. Our results are in broad agreement with Ma et al. [3] who undertook an important study on the biogeography of *O. ceratophthalmus* s. lato using the COI and NaK genetic markers. Ma et al. (2018:2661) also observed three well supported clades exhibiting defined geographical patterns. Their central clade had the widest distribution, from West and South India to most of the Indo-West Pacific; their west clade was confined to only four sites in the western Indian Ocean (including Maldives); and their east clade was present in over a dozen sites in the West Pacific (CP). Madagascar appears to be an overlap zone for the central and west clades because of a single haplotype record of the otherwise centrally distributed *O. ceratophthalmus* (an outlier that needs to be confirmed). The east and central clades overlapped in many parts of the Indo-Australian region and South Pacific islands, with only Guam and French Polynesia possessing only East clade haplotypes. Ma et al. [3] indicated that the genetic structure observed fitted what has been called the Centre of Accumulation hypothesis [81]. They suggested that the pattern of surface currents in the two oceans helps explain the current distribution of the three clades, with the more isolated West clade likely to be a pseudocryptic taxon, evolving because of possible oceanographic barriers in the Western Indian Ocean. Ma et al. [3] suggested there was also a unique genotype in the northern shores of Papua New Guinea which is divergent from the prevailing Central clade present there. This was found as part of their analysis using the nuclear sodium–potassium ATPase α-subunit (NaK) gene as a molecular marker, but interestingly the COI gene did not differentiate this population as different from their Central clade (*O. ceratophthalmus*). They noted more samples will be needed to verify this.

Our present genetic and morphological results agree with most aspects of Ma et al.'s [3] study; there are three distinct clades that more or less correspond with their central, west and east clades. We are confident all three clades should be recognised as separate species and can be distinguished by colour as well as morphological features. Our samples are concentrated on Christmas and Cocos (Keeling) Islands, and while some of them overlap with those used by Ma et al. [3], most do not. We find all three species on Christmas and Cocos (Keeling) Islands, while the more westward Cocos (Keeling) Islands mostly has what Ma et al. [3] calls the West Clade (our *O. celadon*). As we go eastwards to Christmas Island, we get fewer elements of the West Clade, and more of their Central and East clades (*O. ceratophthalmus* s. str. and *O. urvillii*, respectively). Our western Indian Ocean samples are all *O. celadon*. In insular Southeast Asia, we have only found the Central clade (*O. ceratophthalmus* s. str.). In the Ryukyus, we have both *O. ceratophthalmus* s. str. and *O. urvillii*. Our understanding of the distribution of the three species, based on our material and data, indicates that while currents and oceanographic conditions are certainly important to explain their distributions, there is also a distinction between insular versus continental habitats. Oceanic island systems, with their small size, small or absent continental shelves as well as more saline and less sediment laden waters provide habitat preferred by species like *O. celadon* and *O. urvillii*, with the former dominant in the western Indian Ocean, while the latter spans from the eastern Indian Ocean to French Polynesia. Continental systems (including continental shelf islands) are generally larger in size, and the influence of rivers and swamps results in distinctly less saline waters with a higher sediment load, and is the habitat preferred by *O. ceratophthalmus* s. str.. But preference is not exclusion, so the species can occur together, possibly due to the dispersive effects of currents. In the more medially situated Christmas and Cocos (Keeling) Island systems, all three species live together. In most other areas, two species overlap, and at the extremities of their distribution, one species dominates. It is noteworthy that the less saline waters of the Sahul Shelf (where most of Southeast Asia sits), the main species present is *O. ceratophthalmus* s. str.. As for Ma et al. [3] hint that the populations in northern New Guinea may be also different, we cannot speculate as we have had no access to specimens from that area. However, a preliminary analysis of their COI haplotypes (564 bp; MH722449, MH722450, MH722452, MH722453, MH722455, MH722448, MH722454 and MH722451) indicates that they clearly belong to the clade of *O. ceratophthalmus* s. str. (data not shown).

Christmas Island has had a long history of crab research (see [82]), but even so, our work has revealed a hitherto unrealised diversity of *Ocypode* species, with six species sharing just one small, enclosed beach: the three present species, *Ocypode cordimana* Latreille 1818, *Ocypode kuhlii* De Haan 1835 and *Ocypode sinensis* Dai, Song and Yang, 1985. An amazing story of ecological partitioning.

Data Availability Statement

The genetic sequence data that support this study are available in the DNA Data Bank of Japan (DDBJ) at https://www.ddbj.nig.ac.jp/ddbj/index-e.html.

Conflicts of Interest

The authors declare no conflicts of interest.

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