A NEW SPECIES OF *MICTYRIS* (DECAPODA, BRACHYURA, MICTYRIDAE) FROM THE RYUKYU ISLANDS, JAPAN

BY

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ABSTRACT

The Asian soldier crab *Mictyris brevidactylus* Stimpson, 1858, was re-examined genetically and morphologically from specimens collected across its range. It was found to consist of two cryptic sister species, with crabs from the Ryukyu Islands representing a new species, *M. guinotae*. *Mictyris guinotae* is smaller at maturity than *M. brevidactylus*, has plain blue colouring without red banding on the legs, and has a differently shaped apex of its male first gonopod. The two species also differ genetically, with 16S rRNA and COI showing a mean divergence (K2P distance) of 1.08% and 4.39%, respectively, representing 2.0 and 3.5 times more divergence than present intraspecifically. Results provide further evidence that some elements of the marine fauna of the Ryukyu Islands have had a separate evolutionary history from continental Asia as well as Taiwan.

RÉSUMÉ

Le crabe soldat asiatique *Mictyris brevidactylus* Stimpson, 1858, a été réexaminé à la fois génétiquement et morphologiquement à travers son aire de répartition. Il s'avère qu'il comprend deux espèces sœurs dont les crabes des îles Ryūkyū représentent une nouvelle espèce, *M. guinotae*. *M. guinotae* est plus petit à la maturité que *M. brevidactylus*, il a une couleur bleue uniforme sans bandes rouges sur les pattes et la forme de l'extrémité du premier gonopode mâle est différente. Les deux espèces diffèrent aussi génétiquement avec le 16S rRNA et le COI montrant une divergence moyenne respective (distance K2P) de 1,08% et de 4,39%, ce qui représente 2 et 3,5 fois plus que la divergence intra spécifique. Les résultats fournissent de

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nouvelles preuves que quelques éléments de la faune marine des îles Ryükyü ont eu une histoire évolutive séparée de celle du continent asiatique, Taïwan compris.

INTRODUCTION

Soldier crabs (species of *Mictyris* Latreille, 1806) are a conspicuous inter-tidal crab on many shores throughout tropical and temperate Australia, South-east Asia and East Asia. They play an important ecological role in maintaining the proper functioning of the intertidal flats where they occur (Quinn, 1986; Dittman, 1994; Webb & Eyre, 2004) and experimental removal of one species, *M. longicarpus* Latreille, 1806, has resulted in the overgrowth of dense micro-bial mats (Webb & Eyre, 2004). *Mictyris* armies are also an important food source for shore birds (Zharikov & Skilleter, 2002, 2003, 2004; Rohweder & Lewis, 2004; Webb & Eyre, 2004).

The family Mictyridae contains a single genus *Mictyris*, with, at present, five recognized species: *M. longicarpus*; *M. platycheles* H. Milne Edwards, 1852; *M. brevidactylus* Stimpson, 1858; *M. livingstonei* McNeill, 1926; and *M. occidentalis* Unno, 2008. *Mictyris* species are remarkably similar in their appearance, and this has caused confusion about their specific status. Despite McNeill's (1926) excellent revision of the genus, there has been some longstanding confusion about the status of *M. longicarpus*. *Mictyris longicarpus* has been considered the only widespread species, with many literature records from throughout the tropical central Indo-West Pacific region (Takeda, 1978: 31). The first author is currently undertaking a modern revision of the genus, and after examining samples of *Mictyris* from throughout its known range, has concluded that *M. longicarpus* sensu stricto is confined to the eastern coast of Australia from where it was originally described. A number of new cryptic species, all with restricted, relatively narrow, geographical distributions will be described (P. J. F. Davie, in progress). Davie (2002) also pointed out that there were two undescribed species in northern and western Australia, with one of these, *M. occidentalis*, having been recently described by Unno (2008).

Takeda (1978) firmly established the separate species status of *Mictyris brevidactylus*, and this paper should be referred to for a thorough analysis of the differences between that species and *M. longicarpus*. However, as we shall demonstrate in the present paper, the Ryukyu Islands material that Takeda assumed was characteristic of *Mictyris brevidactylus* elsewhere in Taiwan, China, and the Philippines, is in fact a separate species, which is here described as new.

MATERIAL AND METHODS

The male first gonopods are referred to as G1. Measurements are given in millimetres. Carapace length (CL) was measured in the mid-line from the middle of the rostrum to the posterior margin; carapace width (CW) was measured across the widest point of the carapace. The material examined is deposited in the Queensland Museum (QM), the Muséum national d'Histoire naturelle, Paris (MNHN), the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, National University of Singapore; Ryukyus University Museum, Okinawa (RUMF); National Museum of Natural Science (NMNS), Taichung, Taiwan; Zoological Collections of the Department of Life Science (NCHUZOOL), National Chung Hsing University, Taichung, Taiwan; Coastal Ecology Laboratory, Academia Sinica, Taipei (CEL); Senckenberg Museum, Frankfurt am Main (SMF); Western Australian Museum, Perth (WAM).

Specimens of *Mictyris* for genetic analyses were collected from the Ryukyus, Taiwan, Hong Kong, and Hainan Island, China. Samples were preserved in 75-95% ethanol after collection, and deposited in several museums (as above) (table I).

Genomic DNA was isolated from the muscle tissue of legs using the DNA genomic extraction kit. A region of ∼550 base pairs (bp) at the 5′-end of the mitochondrial 16S rRNA gene was selected for amplification by a polymerase chain reaction (PCR) using the primers, 1471 (5′-CCTGTTTANCAAAAACAT-3′) and 1472 (5′-AGATAGAAACCAACCT GG-3′) (Crandall & Fitzpatrick, 1996). A portion of the COI gene was amplified by PCR using the primers, LCO1490 (5′-GGTCAACAAATCATAAAGAT ATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al., 1994). PCR conditions for the above primers included denaturation for 50 s at 94°C, annealing for 70 s at 45°C, and extension for 60 s at 72°C, followed by a final extension for 10 min. at 72°C. Sequences were obtained by automated sequencing (ABI PRISM 377 Sequencer and MegaBACE DNA Analysis System 500, Amersham, U.K.) 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 complementary strand. Sequences of the different haplotypes were deposited in the DNA Data Bank of Japan (DDBJ), and the accession numbers are given in table I. The Kimura (1980) 2-parameter distance (K2P distance) between haplotypes was calculated by the software MEGA 4 (Tamura et al., 2007). This distance measure is adopted because it has been widely used for genetic comparisons among taxa (see Lefébure et al., 2006; Costa et al., 2007; Hubert et al., 2008).

TABLE I

Seven haplotypes of 16S ribosomal (r)RNA and 12 haplotypes of cytochrome oxidase subunit I (COI) genes of the two species of *Mictyris* from East Asia used in this study. NCHUZOOL, the Zoological Collections of the Department of Life Science, National Chung Hsing Univ.; CEL, Coastal Ecology Laboratory, Academia Sinica; DDBJ, the DNA Data Bank of Japan

Species	Localities	Catalog no.	Haplotypes of 16S	DDBJ access. no.	Haplotypes of COI	DDBJ access. no.
M. brevidactylus Stimpson, 1858	Waziwei, Taipei County, Taiwan	CEL-MIC-TW2	Mb1	AB513630	Mb-C1	AB513638
	Waziwei, Taipei County, Taiwan	CEL-MIC-TW1	Mb2	AB513631	Mb-C2	AB513637
	Siangshan, Hsinchu City, Taiwan	CEL-MIC-TW3	Mb1	AB513630	Mb-C1	AB513638
	Siangshan, Hsinchu City, Taiwan	CEL-MIC-TW4	Mb1	AB513630	Mb-C1	AB513638
	Haomeiliao, Chiayi County, Taiwan	NCHUZOOL 13262	Mb1	AB513630	Mb-C1	AB513638
	Starfish Bay, Hong Kong	CEL-MIC-HK-1	Mb2	AB513631	Mb-C2b	AB513639
	Starfish Bay, Hong Kong	CEL-MIC-HK-2	Mb2	AB513631	Mb-C2c	AB513640
	Wenchang, Hainan, China	CEL-MIC-HN-1	Mb2	AB513631	Mb-C2d	AB513641
	Wenchang, Hainan, China	CEL-MIC-HN-2	Mb2	AB513631	Mb-C2e	AB513642
	Wenchang, Hainan, China	CEL-MIC-HN-3	Mb2	AB513631	Mb-C2f	AB513643
	Sanya, Hainan, China	NCHUZOOL 13263	Mb2	AB513631	Mb-C2f	AB513643
M. guinotae sp. nov.	Awase, Okinawa, Ryukyus, Japan	NCHUZOOL 13264	Mg1	AB513632	Mg-C1	AB513644
	southern Naha, Okinawa, Ryukyus, Japan	CEL-MIC-OK-1	Mg2	AB513633	Mg-C2	AB513645
	southern Naha, Okinawa, Ryukyus, Japan	CEL-MIC-OK-3	Mg2	AB513633	Mg-C2b	AB513639
	southern Naha, Okinawa, Ryukyus, Japan	CEL-MIC-OK-2	Mg3	AB513634	Mg-C3	AB513646
	Funaura Bay, Iriomote, Ryukyus, Japan	NCHUZOOL 13266	Mg4	AB513635	Mg-C4	AB513647
	Funaura Bay, Iriomote, Ryukyus, Japan	NCHUZOOL 13266	Mg5	AB513636	Mg-C2b	AB513648

GENETIC RESULTS

A 553 bp segment (excluding the primer regions) of the 16S rRNA from all 17 specimens was amplified and aligned; 12 positions were variable and 5 parsimoniously informative. Among the total number of sequences, 7 different haplotypes were distinguished (table I). The studied segment of 16S rRNA sequences was AT rich (71.8%) (T, 34.5%; A, 37.3%; G, 17.7%; and C, 10.5%). For the COI gene, a 658 bp segment was compared, resulting in 12 different haplotypes (table I). The studied segment of the COI sequence was also AT rich (63.0%) (T, 39.1%; A, 23.9%; G, 17.8%; and C, 19.2%). In this gene, 43 positions were variable and 28 parsimoniously informative.

The pairwise base-pair (bp) differences and nucleotide divergence with the K2P distance between those haplotypes of 16S rRNA and COI are shown in tables II and III. It is clear that there are two clades among these haplotypes. The percentage base-pair difference and nucleotide divergence between the two clades for 16S rRNA was 0.72-1.27% and 0.73-1.28%, and for COI, 3.5-4.71% and 3.62-4.94% (tables II, III), respectively. Within the first clade (with the haplotypes prefixed as "Mb"), the bp differences and nucleotide divergence of 16S rRNA was ⩽0.18% for both clades; and for COI ⩽1.37% and ⩽1.23%, respectively. For the other clade (with the haplotypes prefixed as "Mg"), the bp differences and nucleotide divergence of 16S rRNA was ⩽0.90% and ⩽0.91% respectively; and for COI ⩽0.61% for both clades (tables II, III). The mean K2P distance of 16S rRNA between the two clades is 1.08%, which is twice the mean, 0.55%, within each clade. The mean K2P distance of COI between clades is 4.39%, which is 3.5 times as high as the mean, 1.24%, within each clade.

TAXONOMY

Family MICTYRIDAE Dana, 1851

Mictyridae Dana, 1851: 247 (as Myctiridae; spelling emended to Mictyridae by Alcock, 1900: 383).

Mictyris Latreille, 1806

Mictyris Latreille, 1806: 21.

Type species. — *Mictyris longicarpus* Latreille, 1806, by monotypy. Gender masculine.

Diagnosis. — Carapace deep, globular, longer than wide; dorsal surface with cervical, cardiobranchial grooves well defined; eyes exposed, orbits obsolescent, small post-ocular spine; posterior border of carapace with short brush

TABLE II

Pairwise nucleotide percentage divergence (K2P distance) matrix (lower-left) and the base-pair (bp) differences (upper right) based on 553 bp of the 16S ribosomal (r)RNA gene between haplotypes of two species of *Mictyris* from East Asia. For abbreviations of haplotypes see table I

| | *M. brevidactylus* Stimpson, 1858 | | *M. guinotae* sp. nov. | | | | |
	Mb1	Mb2	Mg1	Mg2	Mg3	Mg4	Mg5
Mb1		1	7	4	6	6	5
Mb2	0.18		6	5	7	7	6
Mg1	1.28	1.10		3	5	5	4
Mg2	0.73	0.91	0.55		2	2	1
Mg3	1.10	1.28	0.91	0.36		4	3
Mg4	1.10	1.28	0.91	0.36	0.73		3
Mg5	0.91	1.10	0.73	0.18	0.54	0.55	

TABLE III

Pairwise nucleotide percentage divergence (K2P distance) matrix (lower-left) and the base-pair (bp) differences (upper right) based on 658 bp of the cytochrome oxidase subunit I (COI) gene between haplotypes of two species of *Mictyris* from East Asia. For abbreviations of haplotypes see table I

| | *M. brevidactylus* Stimpson, 1858 | | | | | | | *M. guinotae* sp. nov. | | | | |
	Mb-C1	Mb-C2	Mb-C2b	Mb-C2c	Mb-C2d	Mb-C2e	Mb-C2f	Mg-C1	Mg-C2	Mg-C2b	Mg-C3	Mg-C4
Mb-C1		5	6	3	3	5	5	24	26	24	23	25
Mb-C2	0.77		1	6	4	6	8	27	29	27	26	28
Mb-C2b	0.92	0.15		7	5	7	9	28	30	28	27	29
Mb-C2c	0.46	0.92	1.08		4	6	6	27	29	27	26	28
Mb-C2d	0.46	0.61	0.77	0.61		4	6	27	29	27	26	28
Mb-C2e	0.77	0.92	1.08	0.92	0.61		8	29	31	29	28	30
Mb-C2f	0.77	1.23	1.39	0.92	0.92	1.23		29	31	29	28	30
Mg-C1	3.78	4.27	4.44	4.27	4.27	4.60	4.61		4	2	3	3
Mg-C2	4.11	4.61	4.77	4.61	4.61	4.94	4.94	0.61		2	3	3
Mg-C2b	3.78	4.27	4.44	4.27	4.27	4.61	4.61	0.30	0.30		1	1
Mg-C3	3.62	4.11	4.27	4.11	4.11	4.44	4.44	0.46	0.46	0.15		2
Mg-C4	3.95	4.44	4.61	4.44	4.44	4.77	4.77	0.46	0.46	0.15	0.3	

of bristles, also present on apposed prominent edge of first abdominal somite. Interantennular septum very narrow; antennular flagellum rudimentary, folding almost vertically. Antennae small. Afferent branchial canal opening ventrally into wide cup-shaped dilatation adjacent base of third maxillipeds. Buccal cavern large, oval; completely closed by convex, expanded, foliaceous

third maxillipeds. Thoracic sternal somites 1-3 deeply recessed. Third maxilliped with long, flattened, palp articulating at antero-external angle of merus; merus smaller than large hemispherical ischium; exopod slender, largely concealed, without flagellum. Chelipeds elongated, slender, subequal; similar in both sexes. Walking legs slender. Tympana not present on meri of walking legs or on sternum. Male abdomen with all somites distinct, broad, similar to female; base entirely covering sternum. Male and female genital openings sternal.

Mictyris guinotae sp. nov. (figs. 1, 2A, 4A-F, 5)

Myctiris brevidactylus Stimpson, 1858: 99; 1907: 103, pl. 13 fig. 4 [in part, only specimens from Loo Choo Islands (= Ryukyus)].

Myctiris longicarpus — Ortmann, 1894: 748. [Not *M. longicarpus* Latreille, 1806.]

Mictyris longicarpus — Sakai, 1934: 322; 1936: 222, pl. 60 fig. 4; 1939: 645, pl. 73 fig. 5; 1976: 627, pl. 213 figs. 1-3; Takeda, 1976: 158. [Not *M. longicarpus* Latreille, 1806.]

Mictyris brevidactylus — Takeda, 1978: 32-34, fig. 1B; Miyake, 1983: 158, pl. 53 fig. 4; Wada, 1995: 412, pl. 116 fig. 9; Muraoka, 1998: 51.

Material examined. — Holotype: QM-W28919, male (13.7 × 14.8), Funaura Bay, Iriomote I., Ryukyus, Japan, coll. T. Naruse, 24 Apr. 2009. Paratypes: QM-W28920, male (14.2 × 15.6) same data as holotype; QM-W28921, 21 males (6.5 × 8.1 to 13.4 × 14.8), 18 females (5.1 × 5.7 to 11.9 × 13.6), 1 juv. (3.7 × 4.2) same data as holotype. RUMF-ZC-00914, 11 males (10.0 × 11.8 to 14.1 × 15.7), 2 females (10.1 × 11.8, 11.6 × 13.2), Yagaji I., near Okinawa I., Ryukyus, Japan, coll. T. Maenosoho, 1 May 2009. NMNS-6109-001, 13 males (10.4 × 12.0 to 14.2 × 15.6), 3 females (8.9 × 11.5 to 10.4 × 12.1), Yagaji I., near Okinawa I., Ryukyus, Japan, coll. T. Maenosoho, 1 May 2009. NCHUZOOL-13261, 8 males (10.7 × 12.5 to 14.2 × 15.7), 8 females (9.5 × 10.9 to 11.1 × 12.5), Yagaji I., near Okinawa I., Ryukyus, Japan, coll. T. Maenosoho, 1 May 2009. ZRC, 14 females (6.4 × 7.2 to 11.8 × 12.3), 23 males (5.5 × 6.5 to 13.0 × 14.6), Katabaru, Ginoza Village, Okinawa I., Ryukyus, Japan, coll. T. Nagai, 7 May 2009. MNHN, 13 females (5.8 × 6.8 to 11.8 × 12.9), 23 males (6.5 × 7.4 to 13.4 × 15.1), Katabaru, Ginoza Village, Okinawa I., Ryukyus, Japan, coll. T. Nagai, 7 May 2009. SMF-7694, 4 males (5.4 × 6.3 to 13.2 × 14.2), 2 females (4.6 × 5.7, 9.4 × 10.9), Ishigaki Is., Ryukyus, Japan.

Etymology. — Named in honour of Professor Danièle Guinot for her lifetime commitment to carcinology, for always being willing to help, and for her friendship. The species epithet is used as a noun in the genitive case.

Description. — Body subglobular, slightly longer (1.1 times) than broad, breadth about same as distance from hind margin to level of anterolateral spines. Posterior border moderately projecting, square-cut, with rounded lateral margins. Carapace relatively smooth but with sparse clusters of microscopic granules; branchial regions evenly, closely, microscopically granular. Anterolateral spines prominent, directed anteriorly dorsal, not divergent,

slightly to strongly granular, apically blunt; clearly defined ridge continuing posteriorly from anterolateral spines to edge of anterior branchials; short minutely granular ridge ventrally from anterolateral spines to form lateral edge of ill-defined lower orbital margin. Carapace regions well-defined; branchial regions moderately swollen, clearly separated from posterolateral margins above walking legs by broad sulcus; subhepatic regions visible from above, separated anteriorly by a groove running posteriorly from about level of anterolateral spine. Eyes globose with 1 or 2 short distal setae. Rostrum deflexed, distally triangular, upper surface broadly sulcate; about as long as broad. External maxillipeds as for genus.

Chelipeds (fig. 1D). Ischium with large spine directed forwards. Merus with lower outer margin with stout spine distally, 2 smaller spines and some granules posteriorly; outer surface minutely granular, with faint transverse furrowing; posterior margin becoming more defined and granular distally. Carpus smooth with faint indication of transverse furrowing; deep longitudinal sulcus running full length parallel with inner edge; inner margin with sparse setae beginning in distal half that get longer and thicker towards articulation with chela; outer margin and anterior margin without setae; brush of long setae on inner face commencing about one-third from distal end, and two-thirds towards upper inner margin. Palm broad; dorsal margin 0.22-0.23 times length of palm plus fixed finger; fingers long, slender, broadly deflexed; dactyl with broad, flat-topped elevated tooth over proximal third of cutting margin; dactyl and immovable finger otherwise unarmed; cutting margin of fixed finger with submarginal groove lined with short setae; dactyl with similar subdorsal setiferous groove.

Walking legs long, slender, somewhat flattened; minutely granular on anterior and ventral surfaces, unarmed except for small spine at anterodistal border of ischium; mostly lacking setae except for fringing setae on carpus and dactylus; dactylus of last leg recurved, apically pointed, trihedral in cross-section, with 3 prominent setal rows.

Male abdomen (fig. 1C) in form of broad flap as typical for *Mictyris* species; fringed with fine setae that become longer distally; all somites freely moveable, length of each somite similar; first somite deeply concave distally, edged with brush of short setae proximally; somites 2-5 laterally diverging, widest point near distal edge of fifth somite; sixth somite tapering, laterally rounded; telson approximately twice as wide as long, articulating slightly below margin of sixth somite, deflexed to close sternal cavity. Female abdomen similar to that of male.
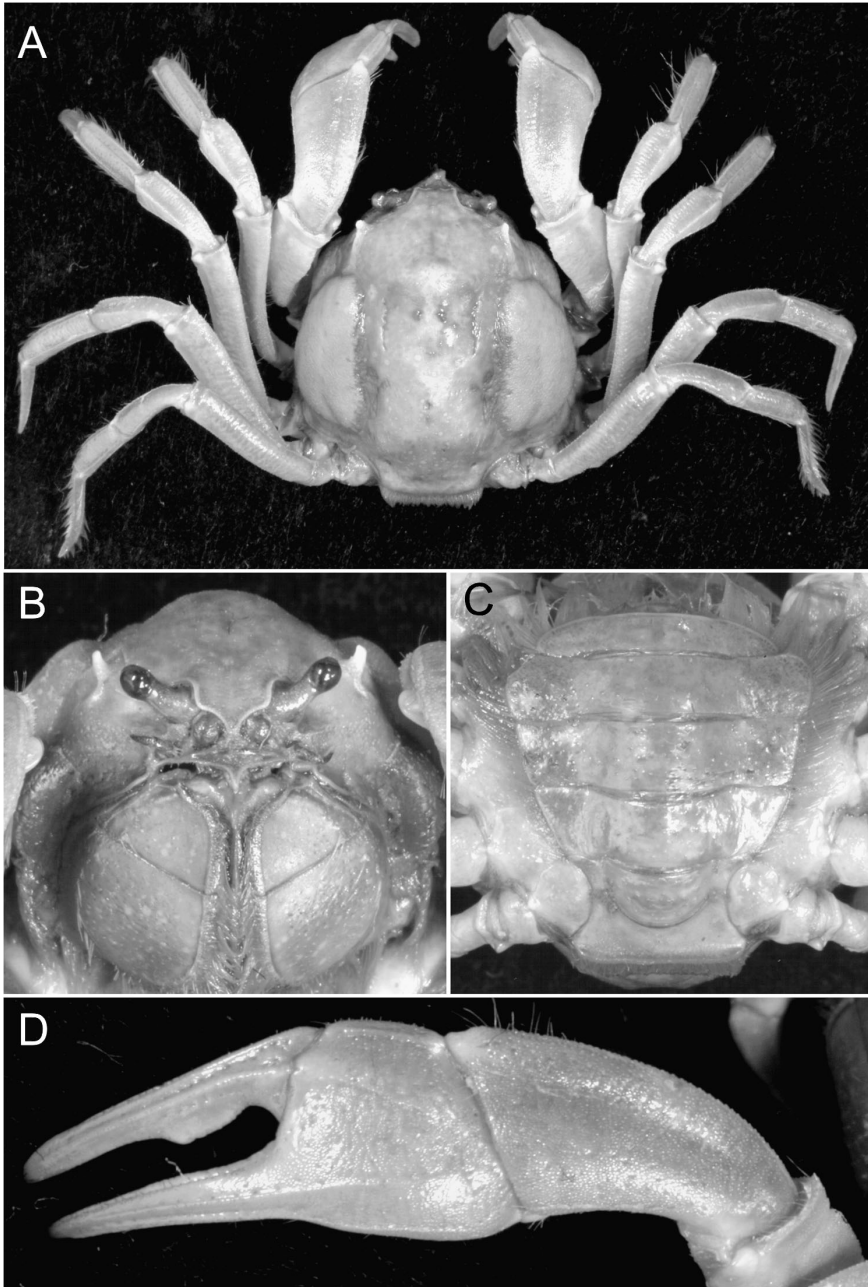
Fig. 1. *Mictyris guinotae* sp. nov. Holotype male from Funaura Bay, Iriomote Island, Ryukyu Islands (QM-W28919, CL 14.8 mm). A, dorsal view; B, mouth frame, ventral view; C, abdomen; D, cheliped.
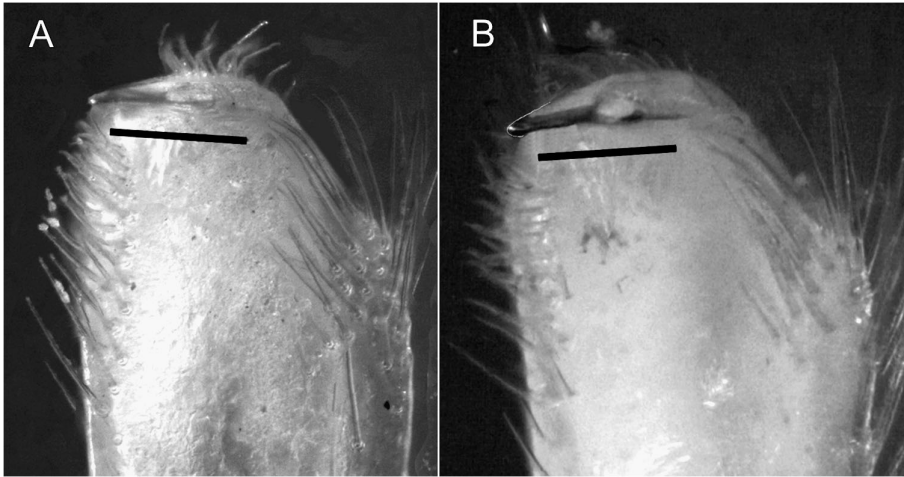
Fig. 2. Ventral view of distal portion of male G1: A, *Mictyris guinotae* sp. nov. from Amami Ohsima, Kagoshima Prefecture (QM-W28923); B, *Mictyris brevidactylus* from Taiwan (ZRC1998).

G1 (fig. 2A) slender, moderately setose, setae densest and longest distally; inner, well-developed, lateral subdistal shoulder, not produced into separate lobe; apex with conspicuous chitinous crest pointed sternolaterally and slightly upwards; opening of sperm tube clearly defined, placed medially near base of crest.

Colour. — *Mictyris guinotae* typically has pale and dark colour forms, though individuals can range from pale blue to a darker blue-grey to a dark ink-blue; occasional individuals may even be pale pinkish-fawn (see fig. 4A-F). The smallest ones tend to be the darkest, lightening as they grow and mature. The pale blue individuals are usually large, sexually mature males, and are more common in summer (T. Naruse, pers. comm.), which is perhaps related to mating. Walking legs similarly coloured to carapace but typically paler; never with red banding.

Remarks. — *Mictyris guinotae* sp. nov. is very similar morphologically to *M. brevidactylus* Stimpson, 1858. However, mature adults of both species can be easily separated by differences in colour pattern, with only *M. brevidactylus* exhibiting the broad red bands at the base of the walking legs.

There are also small but consistent morphological differences in the shape of the tip of the G1, and this is crucial for identifying preserved samples from which the colour has been lost. Even so, the differences in the G1 apex, while consistent, are not dramatic. In *M. guinotae* the chitinous apical crest is pointed sternolaterally and slightly upwards, whereas in *M. brevidactylus* it is a little

more deflexed and pointed slightly downwards. This difference is emphasized by the placement of the black bars parallel with the apical crests in fig. 2A and B.

The shape of the G1 is proving consistently useful in separating known and putative new species of *Mictyris* (cf. P. J. F. Davie, work in progress), and it was through careful examination of the G1 that subtle but consistent differences between the Ryukyus and Hong Kong "*Mictyris brevidactylus*" were first noticed. While this, combined with the obvious colour differences, may have been enough to describe the new species, it was felt that genetic studies would be a useful test of the hypothesis since DNA differences would reinforce the value of the G1 as a useful diagnostic character among species. The present result is particularly useful in validating morphology as the differences between *M. guinotae* and *M. brevidactylus* are perhaps the most subtle of any of the future new species that will be recognized.

It also appears that individuals of *M. guinotae* are smaller than those of *M. brevidactylus*. There is commonly a disparity of size classes according to the amount of time since larval settlement events, and armies of smaller individuals commonly occur in *Mictyris*. Nevertheless, of more than 300 specimens examined from a number of localities, the largest *M. guinotae* individuals attained only 15.7 mm CL, and crabs of this size were rare. Sakai (1976) gave measurements of only 11 mm CL. On the other hand, we examined a number of specimens of *M. brevidactylus* that reached 17-18.9 mm CL, Stimpson (1858) himself gave a size of 17.3 mm (0.683 inches) CL, and Dai & Yang (1991: 453) recorded specimens up to 17.8 mm CL for that species. Pictures of marching armies (fig. 5B) generally seem to show smaller crabs than those of *M. brevidactylus* commonly seen around Hong Kong and on other continental beaches.

Ecology. — Sandy-mud intertidal flats, including estuaries; forming droving "armies" at low tide (Yamaguchi, 1976). Takeda & Murai (2004) discussed microhabitat use, and surface and subsurface feeding through burrow structure alteration. Fig. 5 shows a typical surface view of burrows in a sandy-mud flat in Ohura Bay, Okinawa, and a "marching troop" (dark colour form) at the same locality.

Reproduction and larval development. — Takeda (2005) reported on the sexual differences in the behaviour of *M. guinotae* during the breeding season. Nakasone & Akamine (1981) documented the reproductive cycle and early growth, and Fukuda (1990) described the early larval and postlarval morphology (under the name *Mictyris brevidactylus*), and made comparisons with the Australian *M. longicarpus* (see Fielder et al., 1984).

Geographical distribution. — Only known from the Ryukyu Islands, southern Japan, north to Tanega I. and south to Iriomote I. More precise localities include: Okinawa (Stimpson, 1907), Amami-Oshima and Okinawa (Sakai, 1976), Tanega I. (Takeda, 1976), Ishigaki I. (Miyake, 1983), Okinoerabu I. and Yoron I. (Muraoka, 1998).

Mictyris brevidactylus Stimpson, 1858 (figs. 2B, 3, 4G, H)

Myctiris brevidactylus Stimpson, 1858: 99; 1907: 103, pl. 13 fig. 4 (specimens from Hong Kong and China only).

Mictyris brevidactylus — Huang, Yu & Takeda, 1992: 155, fig. 18, pl. 2F; Kosuge et al., 1997: 180, 182; Ng et al., 2001: 39.

Not *Mictyris longicarpus* var. *brevidactylus* — McNeill, 1926: 116-119, text-fig. 2, pl. 9 figs. 3, 4 [undescribed species from the Philippines; P. J. F. Davie, in prep.].

Myctiris longicarpus — White, 1847: 34 (specimen from China only); Miers, 1884: 248 (specimens from South China Sea only); Ortmann, 1894: 748 (specimens from Hong Kong only); Parisi, 1918: 100 (specimen from Formosa [=Taiwan] only); Balss, 1922: 144 (specimens from Annam [Vietnam] only). [Not *M. longicarpus* Latreille, 1806.]

Mictyris longicarpus — Dai, Yang, Song & Chen, 1986: 415; Dai & Yang, 1991: 452, fig. 229B, pl. 58(1). [Not *M. longicarpus* Latreille, 1806.]

Material examined. — Neotype: WAM-237-80, male (CL 18.9, CW 17.1), Tong Fuk, Lantau, Hong Kong, coll. L. Bones, 29.iv.1980. Other material: WAM-239-80, 2 females (8.6 × 9.9, 8.1 × 9.6), male (12.2 × 14.3), Starfish Bay, Hong Kong, 21.iv.1980, coll. R. W. George. QM-W21355, 6 males (9.8 × 11.8 to 13.6 × 16.4), 3 females (9.2 × 11.3 to 11.3 × 12.3), sand flat, in pools, Three Fathom Cove, Hong Kong, 22°25′N 114°16′E, 20.iv.1989, P. Davie. QM-W27378, 2 males (8.7 × 10.1, 6.5 × 7.5), Starfish Bay, Hong Kong, 22°43′N 114°23′E, 12.iv.1989, coll. P. Davie. QM-W27379, 4 males (8.0 × 10.0 to 10.7 × 11.8), Hong Kong, 15.iv.1989, coll. P. Davie. QM-W27380, 2 females (8.1 × 10.1, 7.25 × 9.1), Starfish Bay, Wu Kwai Sha, Hong Kong, 22°43′N 114°23′E, 13.iv.1989, coll. R. Choi. ZRC-1999.1485, 2 males (8.4 × 9.4 to 9.4 × 10.7), 15 km from Halong City, Gulf of Tonkin, northern Vietnam, muddy sand, intertidal, 29.x.1999, coll. P. S. Tan. QM-W21919, 3 males (13.8 × 15.8, 13.9 × 15.5, 14.2 × 15.6), western Taiwan, 1996. QM W28888, 3 females (10.4 × 11.9, 11.0 × 11.7, 11.0 × 12.2), ovig. female (9.4 × 10.7), Anping, Tainan, Taiwan, 22°59′N 120°09′E, 26.iii.1998. QM-W28889, 6 males (12.1 × 13.6 to 13.6 × 15.2), Haomeiliao, Chiayi, Taiwan, 23°28′N 120°26′E, 06.ii.1996. ZRC-1995.619 (TMCD-2293), 2 males (15.6 × 17.5, 16.5 × 17.4), Yunlin County, Taiwan, 18.x.1987, coll. C. H. Wong. ZRC-1998.499 (CHC D388), 10 females (5.8 × 7.5 to 12.7 x 14.2), 11 males (8.0 × 10.0 to 15 × 16.4), Santiaolun, Yunlin County, Taiwan, 24.v.1994, coll. H. C. Lim. ZRC-1999.0705, 6 males (6.3 × 7.4 to 9.1 × 10.8), 7 females (7.0 × 8.0 to 8.7 × 10.0), Danshuei mangroves, Taipei County, Taiwan, 30.v.1999, coll. P. K. L. Ng. SMF-8786, male, near Mailiao, Yunlin County, western Taiwan, 27°47.02′N 120°10.80′E, silt/clay, fine sand, 29.viii.1977. SMF-8787, 5 males, 5 females, near Mailiao, Yunlin County, western Taiwan, 23°47.25′N 120°10.95′E, fine sand, silt/clay, 29.viii.1977. SMF-8788, female (7.7 × 9.1), stn 5, near Mailiao, west coast of Taiwan, 23°47.55′N 120°11.5′E, silt/clay, fine sand, 02.viii.1977. SMF-8789, 1 female (7.2 × 8.2), near Mailiao, Yunlin County, western Taiwan, 23°47.9′N 120°11.1′E, fine and medium grained
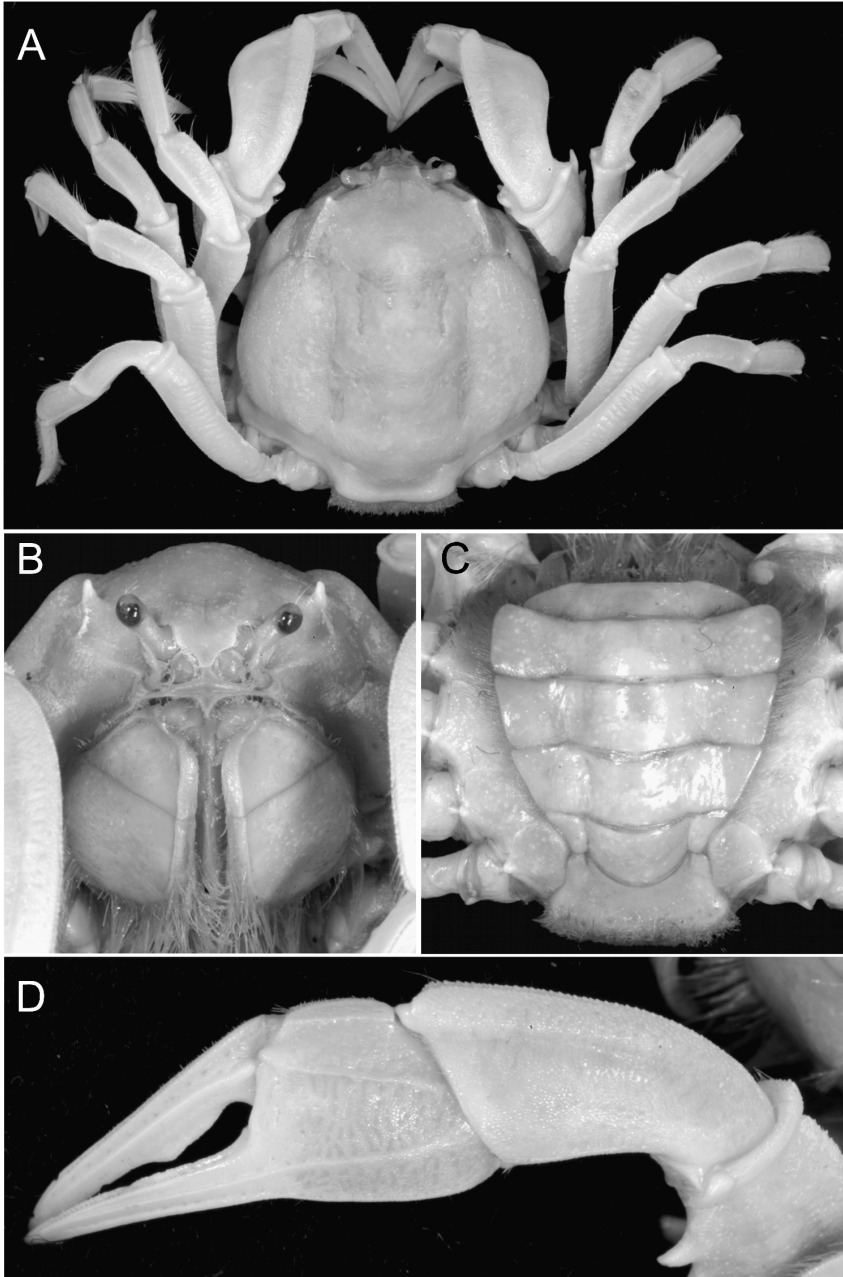
Fig. 3. *Mictyris brevidactylus* Stimpson, 1858. Neotype male (CL 18.9 mm), Tong Fuk, Lantau, Hong Kong (WAM-237-80). A, dorsal view; B, mouth frame, ventral view; C, abdomen; D, cheliped.

sand, 3.viii.1977. SMF-8790, 11 males (10.7 × 12.2 to 15.1 × 17.0), Taiwan, 1977. SMF-10675, 2 males (9.5 × 10.8, 9.5 × 9.6), female (9.0 × 9.9), east coast Taiwan, 1977.

Diagnosis. — See description of *M. guinotae* sp. nov. from which it is almost morphologically indistinguishable; apex of G1 (fig. 2B) has conspicuous chitinous crest that is more deflexed than *M. guinotae* sp. nov. and pointed slightly downwards.

Colour. — Adult males have a characteristic pale blue carapace, with wide bright red bands at the base of the walking legs, and pale creamy-yellow legs and claws (fig. 4G, H). Juveniles and immature crabs can be more plainly, evenly, and darkly coloured without the banding on the legs.

Remarks. — A nomenclatural complication has been caused by the fact that Stimpson's types of *M. brevidactylus* were lost when the Chicago Academy of Sciences was destroyed by fire in 1871 (fide Rathbun in Stimpson, 1907: 4). Because species differences in *Mictyris* can be subtle and confusing, it is necessary to establish a neotype for *M. brevidactylus* to stabilize the name. As Stimpson (1858) listed specimens from Hong Kong, China Sea, and "Loo Choo Islands" [= Ryukyus] which have two species among them, it is necessary to decide which species should bear Stimpson's name. Because Stimpson (1858) made extensive collections from Hong Kong, and because the Chinese and Taiwanese species is larger in size, more conspicuous, and more colourful than that from the Ryukyus, we believe that this was probably the species that Stimpson would have been most familiar with, and the one that would have most caught his attention. We have thus selected a specimen from Hong Kong (WAM-237-80) as the neotype of *M. brevidactylus* (fig. 3), and the soldier crab from the Ryukyus must have the new name, *M. guinotae*.

Differences between *M. brevidactylus* and *M. guinotae* sp. nov. are provided under the account of the latter species. In having broad red bands at the base of the walking legs, *M. brevidactylus* is similar to *M. longicarpus* from eastern Australia, and some earlier authors have considered it merely a subspecific variant of that species. *M. longicarpus* however has a much narrower band

Fig. 4. Live colour patterns. A-F, *Mictyris guinotae* sp. nov.: A, dark form male, from Ohura Bay, Okinawa I. (CW 15 mm); B, unusual pale colour form from Awase, Okinawa I.; C, intermediate darker form from Funaura Bay, Iriomote I. (paratype, QM-W28920, CW 14.2 mm); D, blue form from Ohura Bay (CW 20 mm); E, F, pale blue adult male from Funaura Bay, Iriomote I., Ryukyus (holotype, QM-W28919, CW 13.7 mm); G, H, *Mictyris brevidactylus* Stimpson, 1858 from Haomeiliao, Chiayi, Taiwan: G, dorsal view; H, frontal view; note characteristic pale blue carapace of adult males, with wide bright red bands at base of walking legs, and pale creamy-yellow legs and claws.
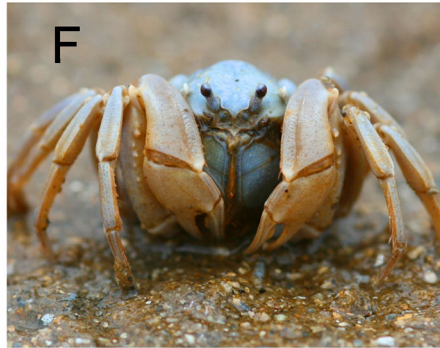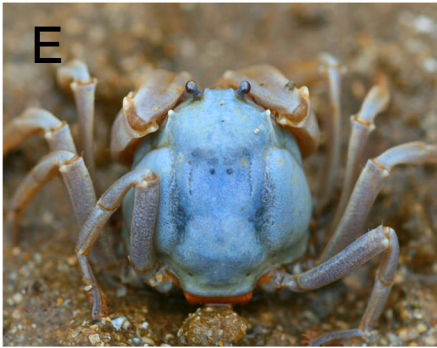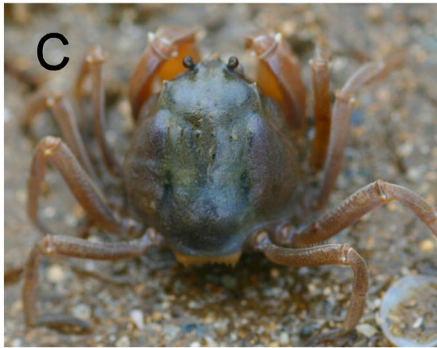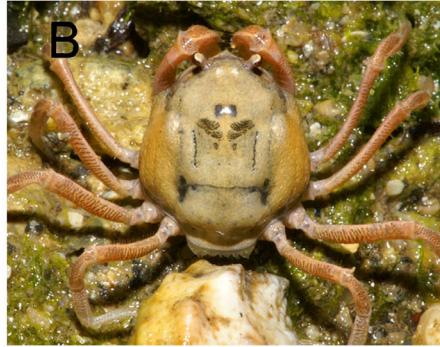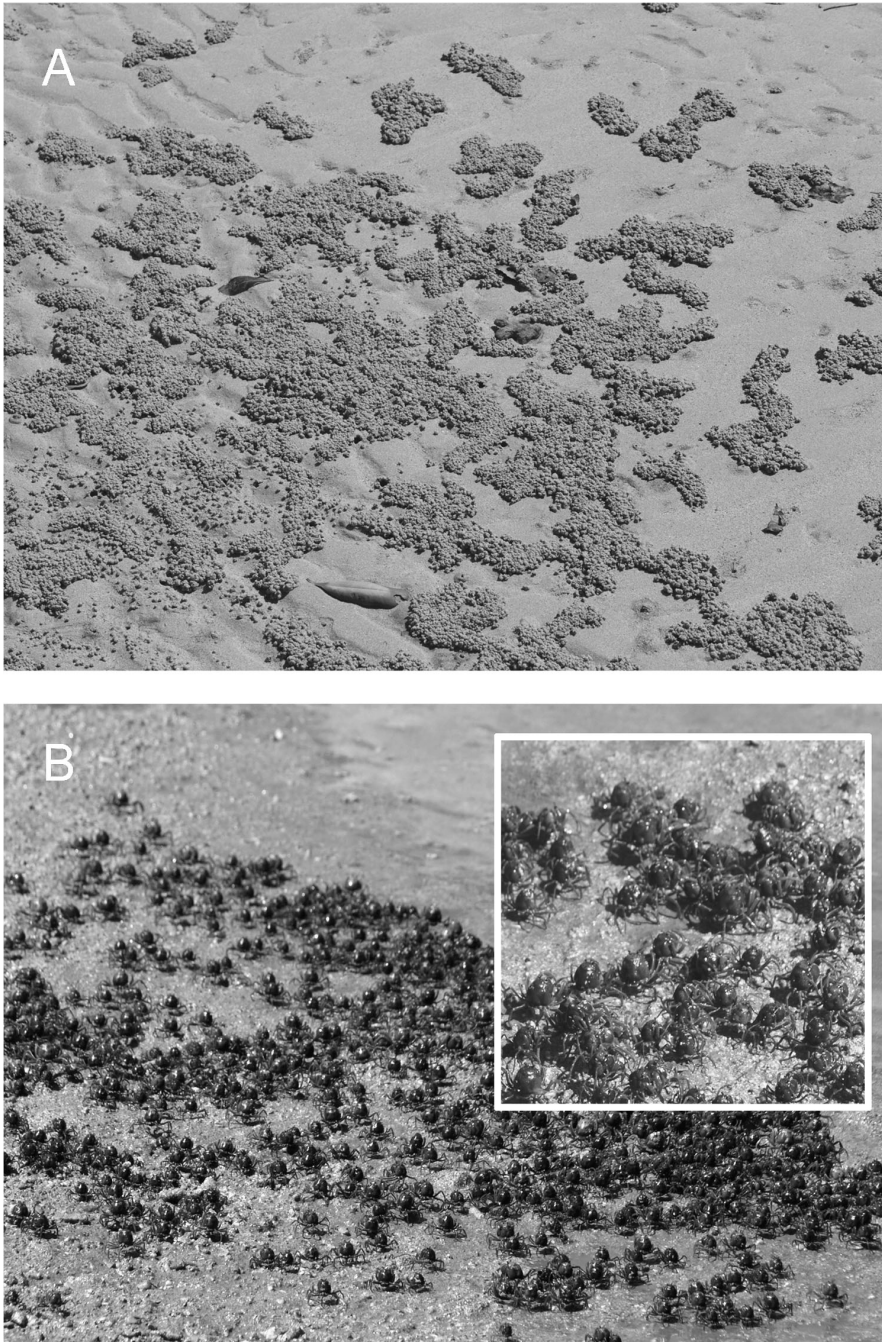
Fig. 5. A, typical feeding burrows of *Mictyris guinotae* sp. nov.; B, a marching troop (dark colour form). Both photographs taken on the sandy-mud flat of Ohura Bay, Okinawa.

at the base of the legs, and also another similar band over the meral-carpal articulation on each leg and on the cheliped (also see Takeda, 1978, for other morphological differences). Some *Mictyris* species, such as *M. livingstonei* and a number of the new species to be described, are naturally drab and inconspicuous in colour, but where a *Mictyris* species is brightly coloured, the colour and pattern appear to be useful diagnostic features.

Ecology. — Typically found at mid- to low tidal level on cleaner, sandy, sheltered, intertidal flats, where they form droving "armies" on the surface at low tide (Morton & Morton, 1983). Surface "armies" typically emerge in warm and sunny conditions, and mostly consist of adult or sub-adult males. Characteristic feeding pellets are deposited on the substrate, especially near the water's edge. When marching, the troop seems to wander with no purposeful direction. Females and juveniles tend to feed by tunnelling just below the surface forming raised meandering trails of pellets. Predators include shore birds and crabs of the family Matutidae, notably *Ashtoret lunaris* (Forskål, 1775) in Hong Kong (see Morton & Morton, 1983: 178), and *Matuta victor* (Fabricius, 1781) in Taiwan. Other predatory shore crabs such as species of *Ocypode*, *Helice*, and *Helicana* may also opportunistically prey on *Mictyris* (cf. Ho, 1995; H.-T. Shih, pers. obs.). See also Shih (1995) for a discussion of population densities and annual activity, and Shih et al. (1997) on the role of the hepatopancreas in young female crabs.

Geographical distribution. — Taiwan: Danshuei (Sakai, 1939), Danshuei River, Lugang, Wengang, and Cigu (Huang et al., 1992), Fukui et al. (1989), and present records. China: Hong Kong (Stimpson, 1858; Ortmann, 1894), Guangxi, Guangdong, including Hainan Island and Fujian (Dai & Yang, 1991). North Vietnam (Balss, 1922; Kosuge et al., 1997; present record).

DISCUSSION

This work has combined morphological and DNA approaches to understand a relatively subtle speciation event, and in so doing, provides further evidence to understand regional biogeography.

Different groups of crustaceans show different and varying degrees of divergence between species (see Lefébure et al., 2006; Costa et al., 2007) obviously reflecting the length of time since separate lineages have diverged. There is no simple rule that can be applied to DNA results that will necessarily guarantee that two putative species are reproductively isolated and thus biological

species, however, comparisons with other taxa provide a rule-of-thumb approach, and a discontinuity in genetic variation between intra- and interspecific populations must also be expected. In the present study, *Mictyris brevidactylus* and *M. guinotae* have mean divergences (K2P distance) of 1.08% for 16S rRNA and 4.39% for COI (tables II and III), and these values, while low, are much larger (2.0 and 3.5 times respectively) than the intraspecific values. Thus the evidence from both genes supports the hypothesis that speciation has occurred. Similar results have also been recently reported for intertidal varunid crabs in the *Helice/Chasmagnathus* complex from East Asia (Shih & Suzuki, 2008). In that case minimum divergence between species of the *Helice latimera* Parisi, 1918 clade and *H. tridens* (De Haan, 1835) is 1.3% for 16S rRNA and 4.7% for COI (re-calculated from Shih & Suzuki, 2008).

Biogeographically, *M. guinotae* appears limited to the Ryukyus, while *M. brevidactylus* is more widely distributed from Taiwan and along the coast of China to Hainan Island and northern Vietnam. This distribution pattern closely mirrors that of another pair of intertidal crab sister-species, *Tmethypocoelis ceratophora* (Koelbel, 1897) and *T. choreutes* Davie & Kosuge, 1995 (Dotillidae), that are also separated by the strait between Taiwan and the Yaeyama Islands (which include Ishigaki and Iriomote Islands) (Davie & Kosuge, 1995). Naruse & Ng (2008) have also found the same distribution pattern for two sesarmid species, *Chiromantes haematocheir* (De Haan, 1833) and *C. ryukyuanum* Naruse & Ng, 2008. Similarly, *Scopimera ryukyuensis* Wong, Chan & Shih, 2010 has been described as endemic to the Ryukyu Islands, while its sister species *Scopimera intermedia* Balss, 1934 is found in Taiwan and mainland Asia south to Singapore and northern Indonesia. A further similar case concerns the mitten crab *Eriocheir japonica* (De Haan, 1835), with crabs from Okinawa proving to be genetically distinct from Taiwanese and Chinese populations, so also suggesting that there is a barrier to gene flow between the Ryukyus and waters to the south (Xu et al., 2009). This conjecture is strengthened by the floral composition of the mangrove communities between the two regions. Although Iriomote I. and north-eastern Taiwan are very close, the mangroves in Iromote I. are dominated by *Rhizophora* and *Bruguiera*, which are never found in NE and E Taiwan and are replaced by *Kandelia* in western Taiwan (Hosokawa et al., 1977). *Rhizophora*, *Bruguiera*, and *Kandelia* all produce dropper propagules that are dispersed by currents, so evidently the currents between the two areas are not intermixing. Contrary to this, an intertidal barnacle, *Tetraclita kuroshioensis* Chan, Tsang & Chu, 2007, that is common to mainland Japan and the Ryukyus, does also occur in

northern Taiwan, though absent from the coast of mainland China (Chan et al., 2007a, b).

While there may be no universally consistent biogeographic pattern, nevertheless the Ryukyus appear to be much more influenced by the main Kuroshio Current in contrast to the continental coastline, which is impacted mainly by the South China Sea Current and westerly flowing Kuroshio Branch Current (Jan et al., 2002). Perhaps also the deep-water strait between Taiwan and the Yaeyama Islands plays an important role in the local circulation patterns of the region, and becomes an effective barrier for species that may have rapid larval development and/or abbreviated life cycles. In this respect, it would be particularly interesting to test the importance of the strait as a dispersal barrier by undertaking genetic studies on species pairs in groups such as benthic peracarids that brood their young and thus have much more limited dispersal capability.

ACKNOWLEDGEMENTS

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