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NEW SPECIES OF *ILYOPLAX* (BRACHYURA: OCYPODIDAE: DOTILLINAE) FROM THE PHILIPPINES AND INDONESIA: BEHAVIORAL, MOLECULAR, AND MORPHOLOGICAL EVIDENCE

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***ABSTRACT.* –** Based on combined evidence derived from mtDNA sequence, morphology and behavior, we here describe a new species of ocypodid crab of the genus *Ilyoplax* from the Philippines and Sulawesi (Indonesia), *I. pacifica*, new species. Morphologically, *Ilyoplax pacifica* is very similar to *I. orientalis* and *I. tansuiensis*, but differs in the structure of the first male pleopod, shape of the carapace and degree of sharpness of the characteristic lobe near the outer side of the infraorbital border. Furthermore, the male waving motion in *I. pacifica* is obviously different from those of the two morphologically similarly species. The DNA sequence divergence (16S rRNA gene) between *I. pacifica* and the other two species (15-17%) is large enough in comparison to previously reported values observed between species of *Ilyoplax* (8.7-33.8%).

***KEY WORDS.* –** Dotillinae, *Ilyoplax*, new species, the Philippines, morphology, mtDNA, 16S rRNA, waving display.

INTRODUCTION

Crabs of the genus *Ilyoplax* Stimpson, 1858, currently consisting of about 25 species, are common inhabitants of intertidal mud flats from across the temperate to tropical Indo -West Pacific region. Some species of the genus have so far been reported to perform rhythmic motion of the chelipeds, which is referred to as "waving" (Tweedie, 1954; Nishihira, 1984; Kosuge et al., 1994; Wada et al., 1996; Wada & Wang, 1998). Waving is a common behavior among male ocypodid crabs, and greatly diversified at the species level. Thereby the manner of waving sometimes helps to identify species.

During our visit to the Philippines and Indonesia, we collected specimens of a species of *Ilyoplax*, which could not be identified to any known species. It closely resembled *I. orientalis* (de Man, 1888) and *I. tansuiensis* Sakai, 1939, morphologically, but the waving motion of the unidentified species was obviously different from those which have been reported for *I. orientalis* and *I. tansuiensis* (Kosuge et al., 1994; Kitaura & Wada, in press).

Molecular data are useful for understanding the relationships among cryptic or sibling species. In particular, mitochondrial DNA sequences have been effectively used in many decapod groups to discriminate between closely related species (e.g. Schubart et al., 1998, 2000; Kitaura et al., 2002; Gillkin & Schubart, 2004; Lin et al., 2004). Comparisons of morphological characters of the unidentified Philippine specimens with *I. orientalis*, and *I. tansuiensis* suggest that they represent a new species. In addition to detailed morphological studies, we examined partial DNA sequences of the 16S rRNA mitochondrial gene (864 base pairs) to affirm our suspicions that the unidentified specimens were distinct from *I. orientalis* and *I. tansuiensis*.

MATERIALS AND METHODS

***Morphological study.* –** Materials used for morphological study have been deposited at the Osaka Museum of Natural History (OMNH), and the Zoological Reference Collection (ZRC), Raffles Museum of Biodiversity Research, National University of Singapore. Carapace width is used as the standard measurement. The following comparative material was used: *Ilyoplax orientalis* and *I. tansuiensis* were examined for morphological comparisons: *Ilyoplax orientalis*, 2 males (5.2, 5.5 mm) (OMNH-Ar 7109, 7110), Thailand, Ranong, coll. K. Wada, 6 Dec.1982; *I. tansuiensis*, 1 male (5.2 mm) (OMNH-Ar 7111), 3 males (4.7, 5.0, 5.1 mm) (OMNH-Ar 7112-7114) and 1 female (5.9 mm) (OMNH-Ar 7115), Taiwan, Tanshui, coll. K. Wada, 27 Mar.1996.

***Behavioural study.* –** Male waving displays for *I. orientalis*, *I. tansuiensis* and *I. pacifica*, new species, were observed at following locations: *I. orientalis*: Ranong, Thailand,

9 Dec.1999; *I. tansuiensis*: Potzu-Stream, Tanshui, Taiwan, 29 May.1992; *I. pacifica*: Lucap, Alaminos Prov., Luzon Is., The Philippines, 14 Dec.2000. Observations were made only during daytime low tides, with unaided eyes and a 8 mm video camera. The general wave form and duration were determined following video frame analysis. Since waving behavior was recorded at 30 frames per second, estimates of temporal characteristics were determined by multiplying the number of frames involved by 0.033 seconds. The mean duration of each component of the display was obtained by averaging the mean values obtained from different individuals.

Molecular study. **–** In total, 13 individuals of the three species were collected for mtDNA sequencing from the following locations: *Ilyoplax orientalis*: Ranong, Thailand, 9 Dec.1999 (N = 2); *I. tansuiensis*: Tanshui, Taiwan, 27 Mar.1996 (N=4); Can Gio, Vietnam, 25 Jul.2000 (N = 3); *I. pacifica*, new species.: Lucap, Luzon Is., the Philippines, 14 Dec.2000 (N = 4). In addition, the sequence data of *Ilyoplax dentata* and *I. serrata* (see Kitaura et al., 1998; AB002123 and AB002120; nucleotide sequence database numbers) were used as outgroups for assessing genetic relationships among the above three *Ilyoplax* species. Total genomic DNA was extracted from musculature of each crab using a DNeasy Tissue Kit (QIAGEN). The target DNA segments were amplified by the polymerase chain reaction (PCR) using primers L1496i (5'-GTACATATCGCCCGTCGCTT-3') (Kitaura et al., 1998), H2492i (5'-CAGACATGTTTTTAATAAACAGGC-3') (modified from Palumbi et al., 1991), and H2716i (5'-AAGTTTTATAGGGTCTTATCGTC-3') (Kitaura et al., 1998) (PCR conditions: 30-35 cycles of 40 sec 94 ºC / 1 min 45-50ºC /1 min 72ºC denaturing/annealing/extension temperatures). Amplification products were purified with the PCR product pre-sequencing kit (USB Corporation). The purified products were sequenced directly using the ABI BigDye terminator mix in an ABI Prism 310 Genetic Analyzer. The new nucleotide sequences have been submitted to the DDBJ nucleotide-sequence databases under the accession numbers AB235164-AB235176. The obtained DNA sequences were initially aligned using CLUSTAL W (Thompson et al., 1994) with default gap penalties. Some adjustments were made by eye, and the positions that could not be aligned with certainty were excluded from the data sets. Phylogenetic relationships were analyzed by neighbor joining methods (Saitou & Nei, 1987), using PAUP* ver. 4.0b10 (Swofford, 1998). In the analysis, sequence divergence was estimated following the Tamura & Nei (1993) model, and 1000 bootstrap replicates (Felsenstein, 1985) were used to assess the confidence in the phylogenetic estimate.

TAXONOMY

Ilyoplax pacifica, new species

(Figs. 1-5)

Material examined. **–** Holotype (one pleopod originally missing): male (5.4 mm) (ZRC 2006.99), the Philippines, Luzon Is., Lucap, coll. K. Wada, 14 Dec.2000. Paratypes: 5 males (4.4, 4.8, 5.3, 5.5, 6.0 mm) (OMNH-Ar 7099-7103), data as for holotype; 2 males (4.0, 5.9 mm) (OMNH-Ar 7104, 7105), 2 females (5.1, 5.6 mm) (ZRC 2006.102-103), one ovig. female (5.6 mm) (OMNH-Ar 7106), The Philippines, Luzon Is., Lucap, coll. J. Kitaura, 14 Dec.2000; 2 males (4.8 mm) (ZRC 2006.101), (6.1 mm) (ZRC 2006.100), The Philippines, Luzon Is., Tanoborg, coll. K. Wada, 12 Dec.2000; 2 males (4.8, 6.0 mm) (OMNH-Ar 7107, 7108), Indonesia Celebes, Manado, Munthea, coll. K. Wada, 2 Sep. 2001.

Description. **–** Carapace sub-rectangular, regions poorly defined, dorsal surface smooth, or microscopically granular, with sparsely scattered very short setae on postero-lateral regions. Gastro-cardiac groove well defined, cardiac region with a low swelling on either side of mid-line; branchial regions with two short, small transverse ridges close to base of fourth ambulatory leg, each with a row of short setae. Posterior border slightly concave, with a very broad rim.

Front approximately 0.26 × distance between external orbital angles. Frontal margin slightly concave from dorsal view, upper surface with median furrow. Dorsal orbital margin slightly arched, sloping backwards. External orbital angle subacutely pointed, shallow notch present just behind external orbital angle. Lateral margins behind notch sinuate, slightly divergent posteriorly. Lateral margins behind notch in females regularly convex, not sinuous. Lower orbital margin with a large projecting lobe near outer end.

Third maxilliped: merus longer than ischium; lateral and mesial margins arcuate, convergent anteriorly; anterior margin slightly concave, with plumose setae near lateral angle; outer surface smooth, with longitudinal depression adjacent to external margin. Ischium quadrangular; antero-mesial angle produced; outer surface generally smooth, but with a row of plumose setae slanting down from anterior half of ischium towards middle of external margin.

Abdomen: male telson semi-circular, with rounded tip. Sixth segment a little longer and broader than fifth, almost quadrate. Fifth segment constricted near base. Fourth and third segment divergent, third segment broadest, fourth segment slightly longer than third segment. Second segment very short, longer medially than laterally. First segment as long as second, but

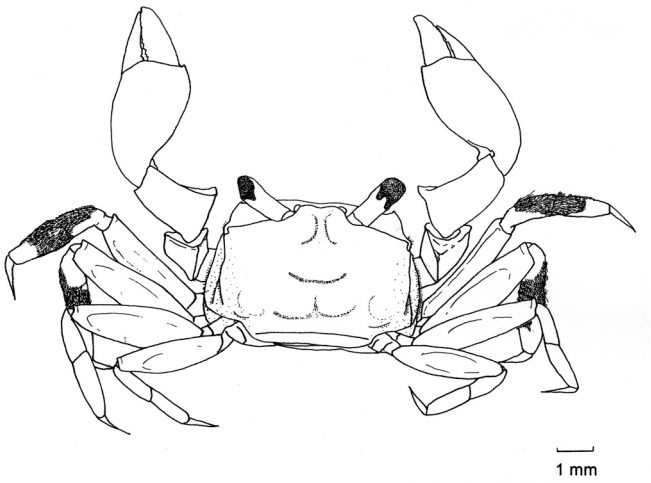

Fig. 1 *Ilyoplax pacifica*, new species, male holotype (ZRC 2006.99).

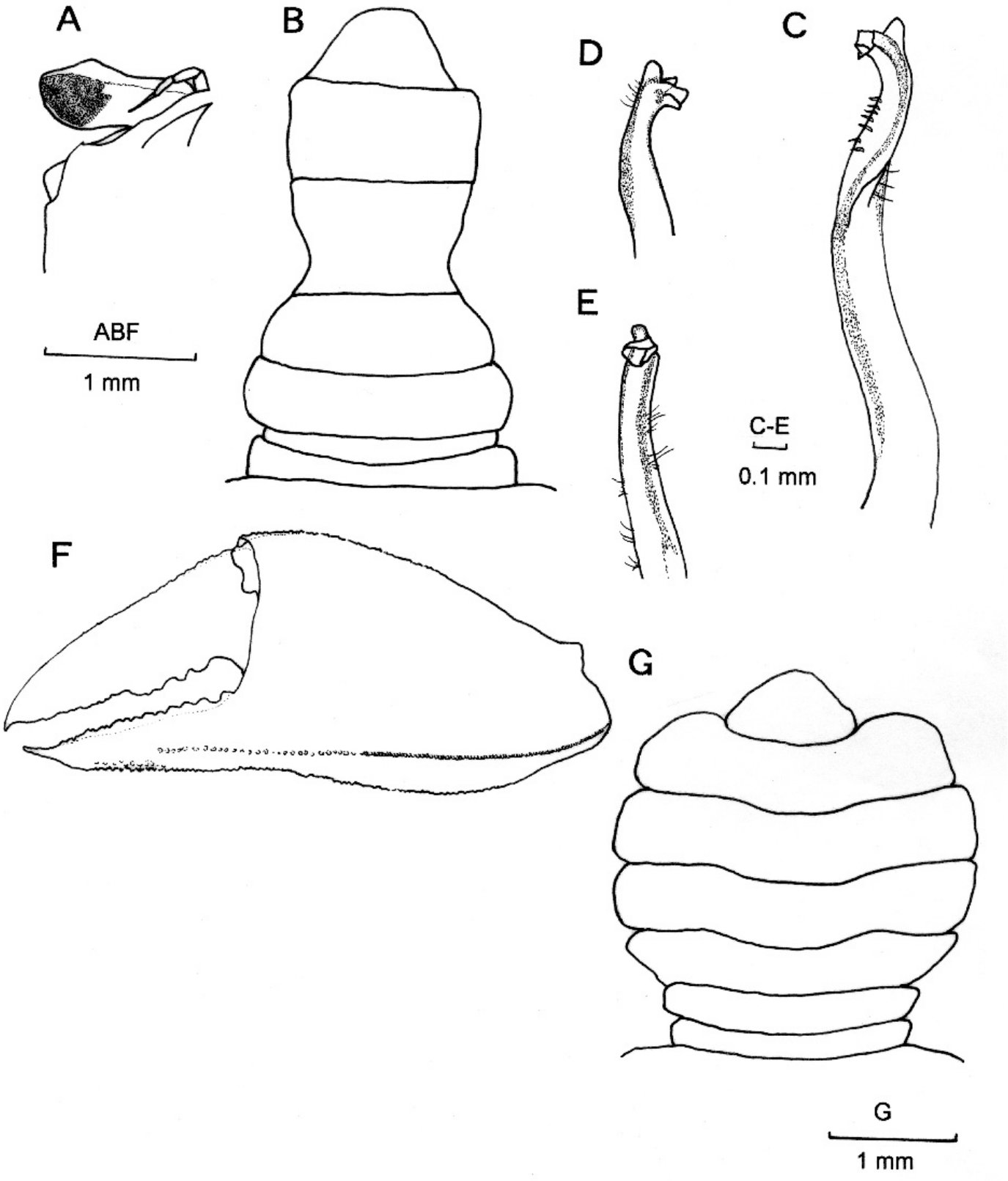

Fig. 2 *Ilyoplax pacifica*, new species: A, suborbital margin; B, male abdomen; C, male first pleopod; D, E, magnifications of apex of first pleopod; F, left chela; G, female abdomen. A, C-F, holotype male; B, paratype male (OMNH-Ar 7105); G, paratype ovig. female (OMNHAr 7106).

slightly broader. Lateral margins of abdomen fringed with short setae. Female abdomen typical for congeners.

Chelipeds: merus trihedral in cross-section, inner surface with sparse, short setae, ventral surface smooth, outer surface with a few scattered granules. Male carpus elongated (about 2 × as long as wide), widest proximally, tapering distally; in females carpus short, quadrate. Internal proximal angle of carpus with obtuse tooth, with a small tuft of short setae immediately behind tooth. Chelae elongated (length about 2.5 × height). Palm broadened distally, sharply carinate on upper margin. Outer surface of palm smooth, with granulated ridge adjacent to lower margin extending to about two-thirds of pollex. An accessory ridge of granules arises from tip of finger, extending over whole length of lower outer surface of pollex. Lower surface of pollex between these two lines finely granulated. A granulate line present near tip on inner surface of fingers, extending about mid-length of palm. Dactylus with a broad denticulated tooth on basal half of cutting margin, distal half with fine denticles. Pollex with an even row of teeth on cutting margin that range from large and rounded proximally to denticle-like distally; tips of fingers acute, slightly curved.

Walking legs: third pair longest, fifth pair shortest. Carpus and propodus of first and second pairs very thickly covered with soft simple setae. In last pair, all segments glabrous. Faintly demarcated oval tympana on each merus.

First male pleopod: Pleopod long, slightly curved, apex divided into two short lobes.

Etymology. **–** The species name, *pacifica*, is derived from their distribution area, the Pacific Ocean.

Remarks. **–** In overall appearance *I. pacifica*, new species, is most similar to *I. orientalis* and *I. tansuiensis*. However, the structure of their first male pleopods, shape of their male carapaces, and the shapes of the lobe near the outer end of the lower orbital margins of these three taxa are sufficiently different. The apex of the first male pleopod is distally divided into two short lobes in *I. pacifica*, but trilobed in the other two species, with the apex being simple in *I. tansuiensis*, but not in *I. pacifica* and *I. orientalis*. The shorter lobe of the pleopod apex is also relatively more expanded in *I. pacifica* and *I. tansuiensis* than *I. orientalis* (Fig. 3-A). The lateral margins of the carapace behind the notch are markedly sinuous in *I. pacifica* and *I. orientalis*, but is distinctively convex in *I. tansuiensis* (Fig. 3-B). The characteristic lobe near the outer end of the lower orbital margin is acute in *I. pacifica* and *I. tansuiensis* but is obtuse in *I. orientalis* (Fig. 3-C).

Habitat. **–** Obtained from soft mud flats in mid to high tide level at small inlets.

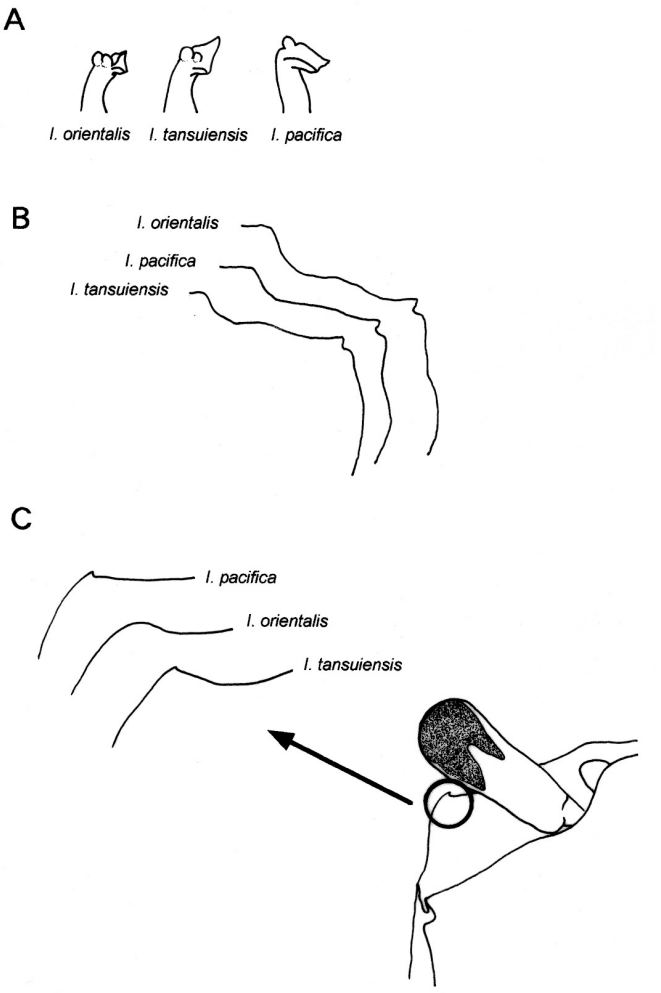

Fig. 3 Comparison of the form of the first male pleopod, shape of carapace and shape of the lobe near outer side of the infraorbital border among *I. orientalis*, *I. tansuiensis*, and *Ilyoplax pacifica*, new species. A, magnification of apex of first pleopod: *Ilyoplax pacifica*, new species, paratype male (OMNH-Ar 7105); *I. tansuiensis*, male (5.2 mm c.b.) (OMNH-Ar 7111), Tanshui, Taiwan, coll. K. Wada, (27 Mar.1996); *I. orientalis*, male (5.2 mm c.b.) (OMNH-Ar 7109), Ranong, Thailand, coll. K. Wada, (6 Dec.1982). B, side margin of male carapace: *Ilyoplax pacifica*, new species, paratype male (OMNH-Ar 7105); *I. orientalis*, male (OMNH-Ar 7109); *I. tansuiensis*, male (OMNH-Ar 7111). C, dorsal view of characteristic lobe of the infraorbital border: *Ilyoplax pacifica*, new species, paratype male (OMNH-Ar 7105); *I. orientalis*, male (OMNH- Ar 7109); *I. tansuiensis*, male (OMNH- Ar 7111).

Fig. 4 Dorsal view of living *Ilyoplax pacifica* at Lucap, Luzon Is., the Philippines, 14 Dec.2000.

***Geographic distribution*. –** Distributed from the Philippine Islands to Sulawesi (Indonesia), not overlapping with the two allied species, *I. orientalis* and *I. tansuiensis*. *Ilyoplax orientalis* is currently known from the Malay Peninsula, Malaysia (Tweedie, 1935, 1950; Tan & Ng, 1994) while *I. tansuiensis* has been reported from Taiwan, southern China and Vietnam (Sakai, 1939; Gao & Li, 1985; Dai & Yang, 1991; Fukui et al., 1989; second author, unpublished data).

***Color while alive.* —** Dark brown on dorsal surface (Fig. 4).

WAVING DISPLAY

The manner of waving for *I. orientalis* has already been described fully by Kosuge et al. (1994). According to their study, this species performs asymmetrical waving. At the start of the waving, both chelipeds are flexed in front of the buccal region, and one chelipeds is abruptly raised, unflexed vertically, then stopped while pointing upward. Soon after the first cheliped is moved, the other is unflexed laterally, then raised. Both chelipeds are then lowered. In this study, a total of 50 waves (4 males) for *I. orientalis* were observed, and they were performed in the same way as in the reported movement. Wave duration ranged from 0.96 - 1.37 sec. (initial to final: mean ± SD = 1.15 ± 0.17 sec, initial to apex: 0.96 ± 0.17 sec, apex to final: 0.19 ± 0.04 sec; No. waves: 9; No. crabs: 2). The waving of *I. tansuiensis* was performed in the same manner as in *I. orientalis* (Fig. 5-A). Wave duration ranged from 1.00 - 1.93 sec (initial to final: mean ± SD = 1.50 ± 0.22 sec, initial to apex: 1.33 ± 0.22 sec, apex to final: 0.17 ± 0.05 sec; No. waves: 59; No. crabs: 7).

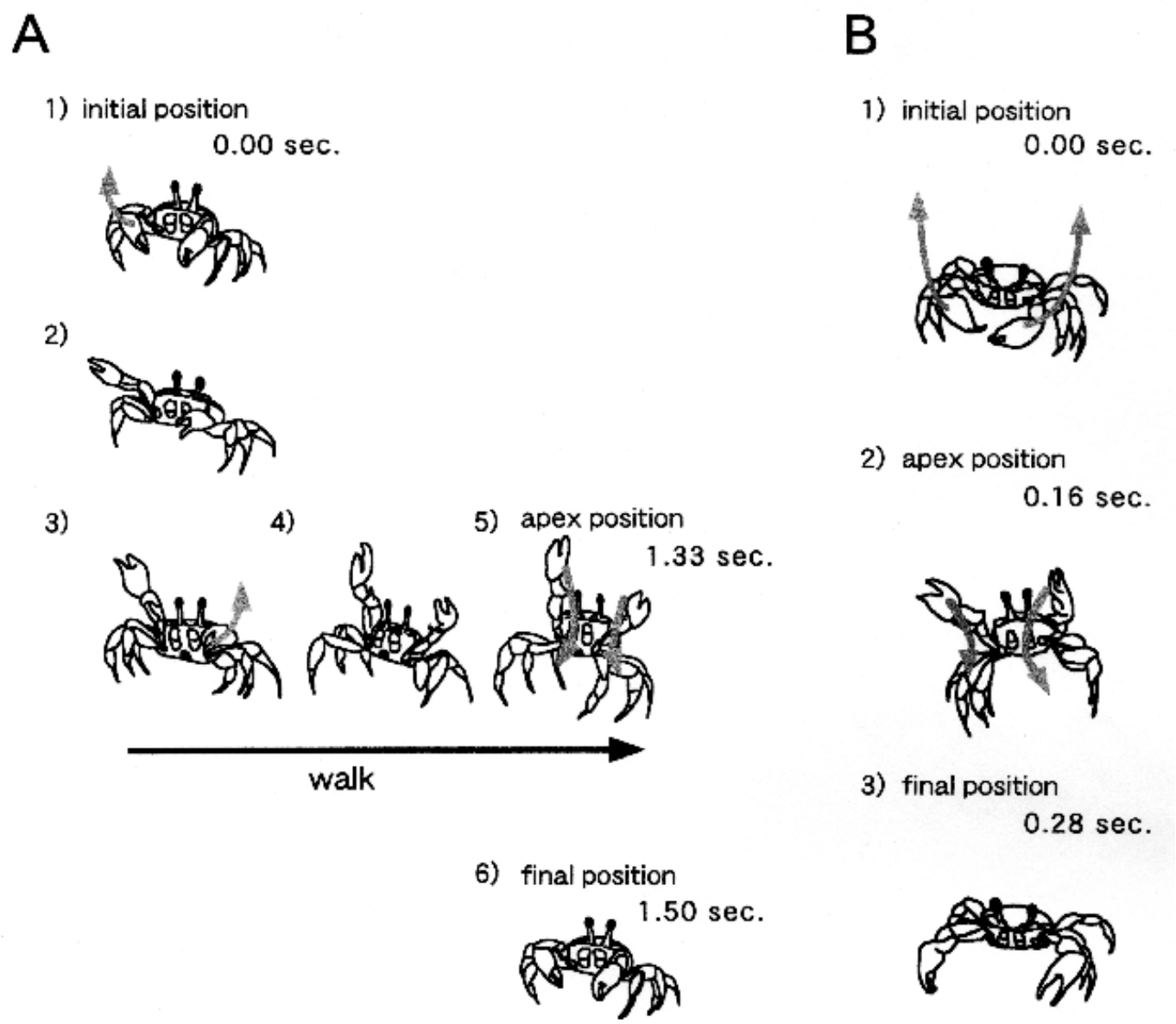

Fig. 5. A, successive postures of waving display by *Ilyoplax tansuiensis*. Values above crabs indicate time in second from the initial position (the mean value of 59 wavings, 7 males). Drawings are traced from videotapes; B, successive postures of waving display by *Ilyoplax pacifica*, new species. Values above crabs indicate time in second from the initial position (the mean value of 100 wavings, 10 males). Drawings are traced from videotapes.

The waving manner of *I. pacifica*, new species, is clearly different from that of both *I. orientalis* and *I. tansuiensis* (Fig. 5-B). At the start of the waving, both chelipeds are flexed in front of the buccal region, and both flexed chelipeds are unflexed forward, raised until the tips of chelipeds point upwards. Both chelipeds are subsequently lowered in a nearly reverse way in which they were raise. Wave duration ranged from 0.20 - 0.33 sec (initial to final: mean ± SD = 0.28 ± 0.03 sec, initial to apex: 0.16 ± 0.03 sec, apex to final: 0.11 ± 0.02 sec; air temp.: 29.5ºC; No. waves: 100; No. crabs: 10).

GENETIC RELATIONSHIPS

The total alignments of the sequenced portions of mitochondrial 16S and 12S ribosomal DNA region consisted of 894 base pairs. Of the aligned sequences, hypervariable regions that could not be aligned unambiguously were discarded from the analysis resulting in a total of 864 base pairs, which were used for phylogenetic analysis. These included 329 variable and 190 phylogenetically informative sites.

A phylogenetic analysis of partial DNA sequence of the16S rRNA mitochondrial gene revealed that the asymmetrical waving species, *I. orientalis* and *I. tansuiensis*, were more closely allied than *I. pacifica* (Fig. 6). *Ilyoplax pacifica*, new species, was more divergent, differing from the asymmetrical waving species by an evolutionary Tamura & Nei (1993) distance of 0.155 - 0.168, whereas sequence divergences between *I. orientalis* and *I. tansuiensis* was 0.07.

DISCUSSION

Morphological comparisons showed several consistent differences between the three species. These differences include the structure of the first male pleopod, suggesting some form of reproductive isolation. Furthermore, the DNA sequence divergence between *I. pacifica*, new species, and the other two species (15-17%) is large enough in comparison to previously reported values observed between *Ilyoplax* species (8.7-33.8% in Kitaura et al., 1998) to suggest that *I. pacifica* is genetically distinct from the other two species. *Ilyoplax pacifica* also had a distinctive waving style, quite different from the other two species. Considering these morphological, genetical and behavioral differences, *I. pacifica* should be regarded as a distinct species from *I. orientalis* and *I. tansuiensis*. With the description of *I. pacifica*, new species, the genus *Ilyoplax* is now represented by 26 species.

In some ocypodid crabs, the importance of non-morphological characters, such as waving displays, for systematics have been well recognized (e.g. Salmon & Atsaides, 1968; Salmon et al., 1979; Salmon & Kettler, 1987; Wada & Sakai, 1989; Davie & Kosuge, 1995). The waving motion of *I. pacifica* is obviously different from those of the other two species, and thereby *I. pacifica* can be easily distinguished from allied species by observing its waving manner in a field without detailed morphological examination under the stereoscope. This study has also indicated that the information of waving display is very important for systematics, equivalent to morphological characteristics, and sometimes gives us an opportunity to discover new species.

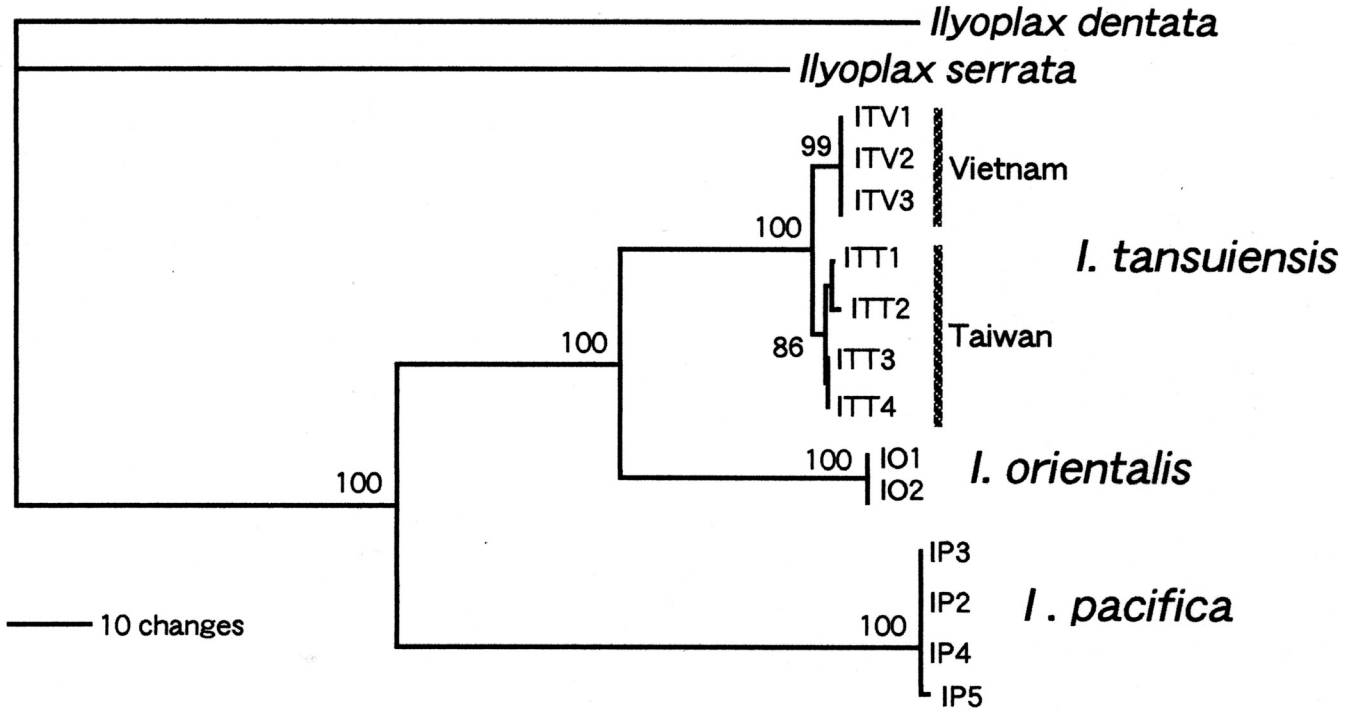

Fig. 6. Neighbor-joining tree for three morphologically similar species of *Ilyoplax* based on 864 base pairs of mtDNA coding for the 16S rRNA, with *Ilyoplax dentata* and *Ilyoplax serrata* as outgroups. Numbers are bootstrap values obtained after replicates.

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