

Integrative taxonomic and genetic reassessment of Ocypode species from South Korea reveals previous misidentifications

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Abstract

Recent environmental changes have facilitated the poleward expansion of tropical ghost crabs (genus *Ocypode*) into temperate zones, where closely related species increasingly co-occur on the same sandy beaches. Their strong morphological similarity, particularly immature individuals, has hindered the consistent application of diagnostic characters and led to potential misidentifications. In particular, the taxonomic distinction between *Ocypode sinensis* and *O. cordimana* has remained uncertain despite previously described diagnostic characters. Here, we demonstrate that previously described diagnostic morphological characters are applicable to these specimens, and that their taxonomic interpretation is supported by molecular evidence from mitochondrial (*mtCO1* and *16S rRNA*) and nuclear (*28S rRNA*) loci. Phylogenetic analyses reveal that *O. sinensis* and *O. cordimana* form distinct and well-supported lineages. Morphological comparisons further identified subtle but consistent differences previously reported between the two species. Our results confirm the taxonomic validity of *O. sinensis* and clarify its diagnostic features relative to *O. cordimana*, indicating that previous records of *O. cordimana* from Korea were likely based on misidentifications. We provide a clear identification key and taxonomic reassessment of East Asian *Ocypode* species based on integrative morphological and molecular analyses. More broadly, our results highlight the importance of integrative approaches for improving the accuracy of species identification and biodiversity assessments in coastal ecosystems.

Introduction

Environmental changes, including climate change, have driven the poleward expansion of tropical and subtropical marine species (King et al. 2021; Fuchs et al. 2024), and previous studies have reported the increasing occurrence of these (sub)tropical species in temperate zones (Wong et al. 2012; Kim et al. 2025). Understanding these shifts in species distribution is crucial, as they may directly impact intertidal ecosystems by altering community structure, food webs, and interspecific interactions (Mano et al. 2008; Dutta and Phani 2023). Investigating the dynamics of range expansions requires a broader, cross-regional perspective, as pelagic larvae may disperse and establish populations beyond local boundaries (Pineda 2000; Pineda et al. 2007). Marine organisms with pelagic larval stages, such as ghost crabs, serve as effective models for studying climate-driven range expansion (Ma et al. 2018; Kim et al. 2025). In such species, increases in ocean and coastal temperatures may relax thermal constraints on survival and establishment, thereby facilitating habitat range expansions. In this context, poleward range extensions of *Ocypode cordimana* have also been reported in Australia, likely associated with warming of ocean and coastal air temperatures (Schoeman et al. 2015). Similarly, recent studies of two tropical ghost crab species, *O. ceratophthalmus* (Pallas, 1772) and *O. sinensis* (Dai & Yang, 1985), along the temperate zones represent the first records of these species in South Korea and indicating a northward range expansion (Kim et al. 2023; Kim et al. 2025).

To date, four *Ocypode* species (*O. cordimana*, *O. sinensis*, *O. stimpsoni*, and *O. ceratophthalmus*) have been recorded in the Korean Peninsula, with all species reported to co-occur on the same sandy beaches (Lee and Ko 2008; Kim and Jung 2020; Kim et al. 2023; Kim et al. 2025). Among the four *Ocypode* species, although only one previous study by Huang et al. (1998a) has conducted a direct morphological comparison between *O. cordimana* and *O. sinensis*. Molecular evidence clearly distinguished these East Asian species in studies by Wong et al. (2012), Shih et al. (2016), and Kim et al. (2023), although these studies did not include morphological assessments. However, Sakai and Türkay (2013) suggested that these two taxa are morphologically difficult to distinguish, as they exhibit highly similar morphological characteristics with variations attributable to individual differences. Moreover, although diagnostic morphological characters for *Ocypode* species have been described in previous studies, their applicability to immature individuals from newly colonized regions, such as South Korea, has not been evaluated. Overall, an integrative approaches combining molecular and morphological analysis is required to clarify the phylogenetic relationships among the morphologically confused *Ocypode* species (Shih et al. 2016), as morphological identification is particularly challenging before individuals reach full maturity (Sakai and Türkay 2013). To re-evaluate these taxonomic uncertainties, we performed integrative analyses, which is combining morphological and molecular analyses using mitochondrial (*mtCO1*, *16S rRNA*) and nuclear (*28S rRNA*) loci data using *Ocypode* specimens collected in South Korea. Accordingly, this study aims to elucidate the taxonomic relationships and morphological patterns of *Ocypode* species occurring in South Korea within a broader East Asian context.

Materials and methods

Sample collection and Morphological analysis

We collected three *Ocypode* species (*O. ceratophthalmus*, *O. stimpsoni* and *O. sinensis*) from two sand beaches in South Korea: Jeju Island (33°12'39.16" N, 126°15'38.41" E) and Busan (35°15'43.26" N, 129°14'1.44" E). The specimens were preserved in 95% ethanol at -20°C. The two specimens of *O. cordimana* and *O. sinensis* were loaned from National Institute of Biological Resources (voucher number: NIBRIV0000229442 and NIBR0000907532). To compare specimens from South Korea with those from other East Asian regions, six specimens from Taiwan and Guam, including *O. sinensis*, *O. stimpsoni*, *O. cordimana*, and *O. ceratophthalmus*, were loaned from the collections of Hsi-Te Shih (National Chung Hsing University; voucher numbers: NCHUZ00L14806, NCHUZ00L15335–6, NCHUZ00L14921, NCHUZ00L14917, and NCHUZ00L14916). For morphological analysis, a total of 11 specimens of the four *Ocypode* species from South Korea were examined using a stereomicroscope (Leica 205C, Leica, Germany) and digital camera (Nikon D7000, South Korea) and were developed using Helicon Focus software v.8.3.9 (Helicon Soft, Ukraine). We compared four critical characteristics based on the previous studies by Huang et al. (1998a) and (Sakai and Türkay 2013): stridulating ridge, third maxillipeds, anterior thoracic sternum, and sixth abdominal segment (Table 3). The specimens examined for morphological analyses were as follows: *O. ceratophthalmus* (JJ41, 16.4×14.0mm) from South Korea; *O. ceratophthalmus* (NCHUZ00L15334, 36.2×31.0mm) from Taiwan; *O. ceratophthalmus* (NCHUZ00L14916, 26.9×22.4mm) from Taiwan; *O. ceratophthalmus* (CNCHUZ00L15335, 18.5×15.9mm) from Taiwan; *O. stimpsoni* (JJ59, 16.1×13.1mm) from South Korea; *O. stimpsoni* (JP20, 19×17mm) from Japan; *O. sinensis* (NIBRIV0000229442, 20.8×18.4mm) from South Korea; *O. sinensis* (NCHUZ00L14806, 19.6×17.0mm) from Taiwan; and *O. cordimana* (NCHUZ00L14917, 31.9×29.6mm) from Guam.

Table 3
Diagnostic key for *Ocypode* species inhabiting South Korea

1	Stridulating ridge present on major cheliped	2
-	Stridulating ridge absent on major cheliped	3
2	Extended eyestalks forming horns (styli) present	<i>Ocypode ceratophthalmus</i>
-	Extended eyestalks forming horns (styli) absent	<i>Ocypode stimpsoni</i>
3	Orbital margin entire, without any trace of a cleft	<i>Ocypode sinensis</i>
<i>Ocypode cordimana</i> is distinguished by an orbital margin interrupted by a distinct cleft, a character that clarifies its previous misidentification.		

Molecular analysis

Genomic DNA was extracted from the muscle tissue of the walking leg using the QIAamp Fast DNA Tissue Kit (Qiagen, Valencia, CA, USA). Partial sequences of two mitochondrial DNA (including cytochrome oxidase subunit 1, *mtCO1*, and 16S ribosomal RNA, *16S rRNA*) and a nuclear DNA (28S ribosomal RNA, *28S rRNA*) were amplified by PCR (Table 1). The reaction total volume of 20 μ L including 1 μ L of template DNA, 1 μ L of each primer (10 μ M), and 10 μ L IP pro-Taq PCR mastermix (Labopass, Korea). The PCR amplification from total nine specimens was performed by initial denaturation at 94°C for 5 min; followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 45–55°C for 30 s, and elongation at 72°C for 1 min; and final elongation at 72°C for 7 min. Annealing temperatures were 45°C for *mtCO1* using primers LCO1490 and HCO2198 (Folmer et al. 1994), 55°C for *16S rRNA* using primers 16SAR and 16SBR (Simon et al. 1994), and 54°C for *28S rRNA* using primers 28L4 and 28H4 (Ragionieri et al. 2009). Amplified products were sequenced by Applied Biosystems 3730xL DNA Analyzer (Hitachi High-Technologies Corporation, Tokyo, Japan) at Cosmogenetech Inc., Seoul, Korea. DNA sequences of other *Ocypode* species were obtained from the National Center for Biotechnology Information (NCBI) GenBank dataset (Table 1). For genetic analyses, partial sequences of *28S rRNA*, *16S rRNA*, and *mtCO1* loci from a total of 24 specimens representing the genera *Ocypode* and *Uca* were aligned in Geneious Prime v. 2023.0.1 (Kearse et al. 2012) using the MAFFT algorithm v. 7.490 (Katoh and Standley 2013). Inter- and intraspecific genetic distances were then estimated using Kimura's two-parameter model in MEGA v. 11 (Tamura et al. 2021). Phylogenetic relationships were inferred using the maximum likelihood (ML) method implemented in IQ-TREE v3.0.1 based on a concatenated alignment of *28S rRNA*, *16S rRNA*, and *mtCO1* sequences. Partitioned analyses were conducted with model selection performed using ModelFinder (MFP+MERGE), and node support was evaluated using 1,000 ultrafast bootstrap and 1,000 SH-aLRT replicates.

Table 1

List of *Ocypode* species included in the species name, voucher number for morphological analysis and GenBank accession numbers for phylogenetic analyses and genetic distance analysis

Species	Voucher number (Country)	<i>mtCO1</i>	<i>16s rRNA</i>	<i>28s rRNA</i>
<i>Austruca lactea</i>	NCHUZOOL13250 (China)	AB471912	AB471898	AB813693
<i>Ocypode ryderi</i>	-	LC150425	AM180689	LC150491
<i>Ocypode mortoni</i>	-	AB751388	ON379461	-
<i>Ocypode quadrata</i>	NCHUZOOL14920 (Brazil)	KY568729	KU313182	LC150489
<i>Ocypode cordimana</i>	-	COX1-27109155	A3259_gr02-27109146	-
<i>Ocypode cordimana</i> *	NCHUZOOL14917 (Guam)	LC150413	LC150358	LC150482
<i>Ocypode ceratophthalmus</i> *	NCHUZOOL14916 (Taiwan)	LC150410	LC150355	LC150479
<i>Ocypode ceratophthalmus</i>	ZRC 2010 0008 (Australia)	LC150411	LC150356	LC150480
<i>Ocypode ceratophthalmus</i>	ZRC 2010 0007 (Australia)	LC150412	LC150357	LC150481
<i>Ocypode ceratophthalmus</i> *	JJ41 (South Korea)	PQ289069	PX868987	PX870094
<i>Ocypode ceratophthalmus</i> *	JJ43 (South Korea)	PQ289071	PX868986	PX870095
<i>Ocypode ceratophthalmus</i> *	JJ52 (South Korea)	PQ289079	PX868984	PX870097
<i>Ocypode sinensis</i> *	JJ55 (South Korea)	OR722672	PX868983	PX870098
<i>Ocypode sinensis</i> *	NIBR0000907532 (South Korea)	OR729708	PX868982	PX870099
<i>Ocypode sinensis</i> *	BS14 (South Korea)	OR729709	PX868988	PX870093
<i>Ocypode sinensis</i>*	NIBRIV0000229442 (South Korea)	PX868976	PX868980	PX870101
<i>Ocypode sinensis</i> *	NCHUZOOL14806 (Taiwan)	LC150427	LC150372	LC150492
<i>Ocypode stimpsoni</i>	NCHUZOOL14921 (Taiwan)	LC150428	LC150373	LC150493
<i>Ocypode stimpsoni</i> *	JJ51 (South Korea)	PX868975	PX868985	PX870096
<i>Ocypode stimpsoni</i> *	JJ59 (South Korea)	PX868977	PX868981	PX870100
<i>Ocypode africana</i>	SMF 9823 (Liberia)	LC150409	LC150354	LC150478
<i>Ocypode kuhlii</i>	ZRC (Australia)	LC150415	LC150360	LC150484
<i>Ocypode nobilii</i>	NCHUZOOL14919 (Malaysia)	LC150418	LC150363	LC150487
<i>Ocypode rotundata</i>	SMF 40586 (Iran)	MF597722	MF509789	LC150490
Asterisks indicate species for which both morphological and genetic analyses were performed in this study. Specimen shown in bold was previously misidentified as <i>Ocypode cordimana</i> (NIBRIV0000229442).				

Results

Molecular assessment of *Ocypode* species

Sequence lengths obtained for *Ocypode* species were 528 bp for the mitochondrial cytochrome c oxidase subunit I (*mtCO1*), 478 bp for mitochondrial 16S rRNA (*16S rRNA*), and 565 bp for nuclear 28S rRNA (*28S rRNA*). All genetic data were deposited in GenBank at the National Center for Biotechnology Information (NCBI) (accession numbers: PX868975–PX868977, PX868980–PX868988, and PX870093–PX870101; Table 1). For phylogenetic tree, the specimen of *O. cordimana* from Taiwan was different from *O. sinensis* (NIBR0000907532) and *O. cordimana* (NIBRIV0000229442) from South Korea (Fig. 1). In the context, genetic distance analysis indicate that the ghost crab specimens collected from the Korean Peninsula, previously identified as *O. cordimana* (NIBRIV0000229442), are correctly identified as *O. sinensis* (Table 2). Based on these results, intraspecific genetic distances ranged from 0.0 to 2.84%, whereas interspecific comparisons ranged from 5.3 to 19.01% (Table 2). In particular, intraspecific genetic distances within *O. ceratophthalmus* among specimens from Korea, Taiwan, and Christmas Island ranged from 1.7 to 2.84% (Table 2). Among the three *Ocypode* species inhabiting South Korea, pairwise genetic distances between *O. sinensis* and *O. cordimana* (11.9–12.5%) were smaller than those between *O. sinensis* and *O. ceratophthalmus* (13.2–14%) and between *O. sinensis* and *O. stimpsoni* (15.1–16.1%), (Table 2). The reconstructed phylogenetic tree showed two well-supported sister groupings at the species level (Fig. 1), with specimens of *O. ceratophthalmus* clustering with *O. stimpsoni* and specimens of *O. sinensis* clustering with *O. cordimana*.

Table 2

Genetic distances (%) among species based on mitochondrial Cytochrome c oxidase subunit I partial sequences (528 bp). Bold type indicates specimens used in distance analyses. 1: *Ocypode sinensis* (OR722672, South Korea), 2: *Ocypode sinensis* (OR729708, South Korea), 3: *Ocypode sinensis* (OR729709, South Korea), 4: *Ocypode sinensis* (PX868976, South Korea), 5: *Ocypode sinensis* (LC150427, Taiwan), 6: *Ocypode cordimana* (COX1-27109155), 7: *Ocypode cordimana* (LC150413, Guam), 8: *Ocypode cordimana* (South Korea), 9: *Ocypode stimpsoni* (PX868977, South Korea), 10: *Ocypode stimpsoni* (LC150428, Taiwan), 11: *Ocypode ceratophthalmus* (PQ289069, South Korea), 12: *Ocypode ceratophthalmus* (PQ289071, South Korea), 13: *Ocypode ceratophthalmus* (PQ289079, South Korea), 14: *Ocypode ceratophthalmus* (LC150410, Taiwan), 15: *Ocypode ceratophthalmus* (LC150411, Christmas Island), 16: *Ocypode ceratophthalmus* (LC150412, Christmas Island), 17: *Ocypode mortoni* (AB751388), 18: *Ocypode quadrata* (KY5687), 19: *Ocypode quadrata* (LC150409), 20: *Ocypode kuhlii* (LC150415), 21: *Ocypode nobilii* (LC150418), 22: *Ocypode ryderi* (LC150425), 23: *Ocypode rotundata* (MF597722), and 24: *Aucajeeta*

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	0.0																						
2	0.0	0.0																					
3	0.0	0.0	0.3																				
4	0.3	0.3	0.3	0.5																			
5	0.1	0.1	0.1	0.5	11.9																		
6	11.9	11.9	11.9	11.9	11.9	0.9																	
7	12.5	12.5	12.5	12.5	12.5	0.9	17.0																
8	15.7	15.7	15.7	16.1	15.5	16.6	17.0	0.5															
9	15.3	15.3	15.3	15.7	15.1	17.0	17.4	0.5	0.1														
10	15.5	15.5	15.5	15.9	15.3	17.0	17.4	0.5	0.1	11.1													
11	14.0	14.0	14.0	14.0	13.8	16.1	16.1	10.8	11.1	11.1	0.0												
12	14.0	14.0	14.0	14.0	13.8	16.1	16.1	10.8	11.1	11.1	0.0	0.5											
13	14.0	14.0	14.0	14.0	13.8	16.1	16.1	11.1	11.5	11.5	0.5	0.5	0.7										
14	13.8	13.8	13.8	13.8	13.6	15.9	15.9	10.8	11.1	11.1	0.5	0.5	0.7	2.2									
15	13.6	13.6	13.6	13.6	13.4	16.2	16.2	11.1	11.1	11.3	1.7	1.7	2.2	2.2	2.8								
16	13.6	13.6	13.6	13.2	13.4	15.7	15.7	10.8	11.3	11.3	2.2	2.2	2.4	2.4	2.8	10.9							
17	14.5	14.5	14.5	14.2	14.3	16.2	16.6	5.4	5.4	5.3	11.3	11.3	11.1	11.1	11.9	10.9	16.1						
18	16.1	16.1	16.1	16.2	16.1	17.9	17.9	15.7	15.7	15.7	15.5	15.5	15.7	15.5	15.7	16.1	16.4	13.8					
19	13.6	13.6	13.6	13.8	13.4	18.5	18.5	12.6	12.5	12.6	12.5	12.5	12.6	12.5	12.3	13.2	13.8	13.6	19.0				
20	14.8	14.8	14.8	14.4	14.8	16.5	16.7	15.4	15.7	15.7	13.6	13.6	13.8	13.3	14.2	13.3	16.1	19.0	15.0				
21	16.6	16.6	16.6	16.6	16.6	17.2	17.8	12.8	13.0	12.8	15.7	15.7	15.7	15.7	15.3	15.9	13.0	17.2	13.4	1			
22	14.7	14.7	14.7	14.7	14.7	17.2	17.8	17.4	17.4	17.2	14.7	14.7	14.7	14.9	14.9	14.7	15.9	17.6	14.3	1			
23	14.5	14.5	14.5	14.2	14.5	15.3	15.7	12.8	13.0	13.0	12.6	12.6	13.0	12.8	12.6	11.5	13.0	18.7	14.7	1			
24	17.0	17.0	17.0	16.8	17.0	18.5	19.1	17.9	17.9	17.8	15.9	15.9	16.1	16.2	16.1	15.7	17.6	17.6	15.9	2			

Morphological assessment of *Ocypode* species inhabiting South Korea

Morphological species identification of *Ocypode* specimens from South Korea comparisons were made among *O. ceratophthalmus*, *O. sinensis* (NIBR0000907532), *O. cordimana* (NIBRIV0000229442), and *O. stimpsoni*. However, morphological analyses indicate that ghost crab specimens collected from the Korean Peninsula, previously identified as *O. cordimana* (NIBRIV0000229442), are correctly identified as *O. sinensis* based on diagnostic morphological characters, including the shape of the third maxillipeds, the presence of scattered granules on the anterior thoracic sternum, and an orbital margin lacking a cleft. Based on the results of species identification, extended eyestalks forming horns (styli) were absent in all examined specimens collected from South Korea. Both *O. stimpsoni* and *O. ceratophthalmus* possessed a stridulating ridge but differed in its structure (Fig. 2). In *O. stimpsoni*, the stridulating ridge consisted exclusively of narrow striae (Fig. 2A–B), whereas in *O. ceratophthalmus* it was composed of tubercles, thick striae, and narrow striae (Fig. 2C–D). In contrast, the stridulating ridge was absent in *O. sinensis* (Fig. 2E–F). Regarding the third maxillipeds, *O. ceratophthalmus* possessed tiny tubercles on the third maxillipeds (Fig. 3A). In contrast, *O. sinensis* and *O. stimpsoni* lacked tubercles (Fig. 3C, E, and G). No consistent difference in the relative width of the merus and ischium, or in the extent of the exopod, was observed among the examined specimens (Fig. 3B, D, F, H, J, and L). The orbital margin was entire, without any trace of a cleft, in all examined specimens collected from South Korea (Fig. 3B, D, F, and H). The anterior thoracic sternum of *O. sinensis* and *O. ceratophthalmus* was directed ventrally and bore scattered granules (Fig. 3A, E, and G). The sixth abdominal segment of *O. sinensis*, *O. stimpsoni*, and *O. ceratophthalmus* was sharp (Fig. 3A, C, and E). In examined specimens of *O. sinensis* collected from South Korea, the telson did not consistently exhibit a pointed morphology and showed no clear diagnostic differences among individuals.

Morphological species identification keys of *Ocypode* crabs

Distinct interspecific differences were observed based on four main morphological characters among four *Ocypode* species, including *O. stimpsoni*, *O. ceratophthalmus*, *O. cordimana* and *O. sinensis*, collected from South Korea, Japan, Taiwan, and Guam: 1) stridulating ridge, 2) the third maxillipeds, 3) anterior thoracic sternum, 4) orbital margin, and 5) extended eyestalks forming horns (styli). Diagnostic states of these four key morphological characters for *O. stimpsoni*, *O. ceratophthalmus*, and *O. sinensis* are summarized in Table 3. Clear interspecific differences were detected in the structure and presence or absence of the stridulating ridge among the examined *Ocypode* species (Fig. 2). The stridulating ridge on the major cheliped exhibited distinct tubercle configurations in *O. stimpsoni* and *O. ceratophthalmus* (Fig. 2). In contrast, *O. sinensis* lacked a stridulating ridge entirely (Fig. 2). In the third maxillipeds, a tubercle cluster was absent in *O. stimpsoni*, whereas it was present in *O. ceratophthalmus*, *O. cordimana*, and *O. sinensis* (Figs. 3 and S1F). The anterior thoracic sternum is ventrally deflexed, and bears scattered granules in *O. sinensis* and *O. ceratophthalmus*, whereas it is laterally flattened and bears groups of granules in *O. cordimana* (Fig. 3A, I, and K). The orbital margin is entire, without any trace of a cleft, in *O. stimpsoni*, *O. ceratophthalmus*, and *O. sinensis*, but is interrupted by a distinct cleft in *O. cordimana* (Fig. 3B, D, F, H, J, and L). Extended eyestalks forming horns (styli) were observed only in *O. ceratophthalmus* (Fig. S1A–C).

Discussion

To address taxonomic uncertainty arising from morphology-based misidentification, we clarified the species composition of ghost crabs inhabiting South Korea through an integrative analysis of molecular and morphological data. Several *Ocypode* species in East Asia are morphologically similar, particularly *O. cordimana* and *O. sinensis*, making species identification based solely on morphology challenging, especially for immature specimens. Previous morphological observation by Lee and Ko (2008) provided only brief diagnoses and limited photographic documentation for the species they reported as *O. cordimana* raising doubts about the validity of previous records of *O. cordimana* from South Korea and indicating the risk of morphology-based misidentification. To resolve this taxonomic uncertainty, we obtained biological samples collected across South Korea, Japan, Taiwan, and Guam, and analyzed mitochondrial and nuclear sequence data. We also re-examined the specimen deposited by Lee and Ko (2008) at the National Institute of Biological Resources, South Korea (NIBRIV0000229442). Based on combined genetic and morphological evidence, the specimen (NIBRIV0000229442) was identified as *Ocypode sinensis* rather than *O. cordimana*.

The genetic distance and phylogenetic analyses based on mitochondrial and nuclear genes showed that the *O. sinensis* from South Korea (NIBR0000907532 and NIBRIV0000229442) clustered together with *O. sinensis* from Taiwan and are separated from *O. cordimana* from Guam. Our morphological results, based on diagnostic characters described by Huang et al. (1998b), including the absence of tubercles on the third maxilliped, a laterally flattened anterior thoracic sternum, and the absence of a gap within the orbital margin, further indicate that the specimens are consistent with previously described diagnostic features of *Ocypode sinensis*. According to previous phylogenetic studies, *O. sinensis* and *O. cordimana* have consistently supported the phylogenetic distinction (Shih et al. 2016, Wong et al. 2012) and are inferred to have diverged approximately 20.41 million years ago based on fossil-calibrated analyses (Kim et al. 2023). Taken together, our results revise the previous findings of Lee and Ko (2008) regarding *Ocypode* species diversity in South Korea and demonstrate how misidentification can influence records of species distributions, particularly when species identification is based solely on either morphological or molecular evidence.

Consistent with these studies, species revisions and recognition of new or unrecorded taxa in the region increasingly benefit from integrative approaches combining morphological and genetic evidence (Wong et al. 2011; Wong et al. 2012; Jang et al. 2020; Song et al. 2023), particularly when dealing with immature specimens (Guerreiro et al. 2025). In particular, we could not detect differentiation in several additional key characters (telson, tip height of the immovable finger, male abdominal proportions, and third maxillipeds) previously proposed as diagnostic between *O. cordimana* and *O. sinensis* described by Huang et al. (1998b). This limitation is likely due to our limited sample size and suboptimal specimen preservation. In the genus *Ocypode*, reliance on morphology alone may lead to misidentification because diagnostic characters may be absent or poorly developed during early ontogenetic stages (Sakai and Türkay 2013). For example, in the genus *Ocypode*, immature specimens of *O. ceratophthalmus* lack extended eyestalks forming horns (styli), which constitute a key diagnostic morphological character (Takada and Wada 2011; Sakai and Türkay 2013; Watanabe et al. 2018; Kim et al. 2025). These limitations further illustrate the difficulty of relying solely on morphology for species identification using immature specimens.

According to Haley (1973), based on specimens from Hawaii, the eyestalk horns of *O. ceratophthalmus* appear when carapace width reaches approximately 27 mm in males and 31 mm in females. This observation is further supported by a specimen (NCHUZ00L14916, 26.9×22.4mm, 26 Mar. 1998) from Taiwan, which exhibited incompletely developed eyestalk horns (Fig. S1). However, previous studies have reported even smaller-sized specimens lacking extended eyestalk horns (styli) from higher latitudes (Yodo et al. 2006; Takada and Wada 2011; Kim et al. 2025), such as South Korea and Japan, compared to Taiwan. This suggests that patterns of ontogenetic development and the timing of reproductive maturation and settlement may vary geographically, further increasing the risk of misidentification when specimens are collected near the limits of their known distributions. The occurrence of immature individuals at higher latitudes has sometimes been interpreted as evidence of northward range expansions of tropical ghost crab species. In particular, previous studies have shown that the dispersal capacity of larval-stage organisms facilitates their range expansion across adjacent temperate regions, indicating that such species are particularly responsive to climate-driven changes in ocean temperature and circulation (Pineda 2000; Pineda et al. 2007). Consistent with this pattern, recent studies have documented an increasing occurrence of several tropical marine species along the coasts of South Korea, including the spiny lobster (*Panulirus homarus*), bivalves (*Pillucina pisidium*), and blue-lined octopus (*Hapalochlaena fasciata*) (Hettiarachchi et al. 2022; Kajino et al. 2024; Shin et al. 2024). Takada and Wada (2011) reported a specimen of a previously unrecorded ghost crab species inhabiting Japan (37°22'22" N, 138°31'48" E), suggesting that tropical ghost crab species may occasionally settle on sandy beaches at higher latitudes than previously documented. Similar high-latitude occurrences of tropical ghost crabs have been discussed by Kim et al. (2025). In this context, the frequent occurrence of immature specimens underscores the need for integrative approaches combining morphological and genetic evidence to ensure accurate species diagnosis, as reliance on morphology alone can lead to systematic errors in species identification.

Declarations

Competing of interests

The authors declare no competing financial interests or personal relationships.

Ethical approval

No animal testing was performed during this study. All specimens used were obtained from existing collections and no live animals were involved.

Sampling and field studies

The study does not contain sampling material or data from field studies.

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Data availability

The sequence data are deposited in NCBI GenBank under the accession number: PX868975–PX868977, PX868980–PX868988, and PX870093–PX870101.

Author Contribution Statement

Dain Kim: Conceptualization, Methodology, Investigation, Resources, Formal analysis, Data curation, Visualization, Writing – original draft, Writing – review & editing, and Funding acquisition. **Sang-Kyu Lee:** Conceptualization, Methodology (Photos), Investigation, Resources, and Writing – review & editing. **Sook-Jin Jang:** Conceptualization, Methodology, Investigation, Resources, and Writing – review & editing. **Taewon Kim:** Resources, Writing – review & editing, Funding acquisition, Supervision, and Project administration.

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Figures

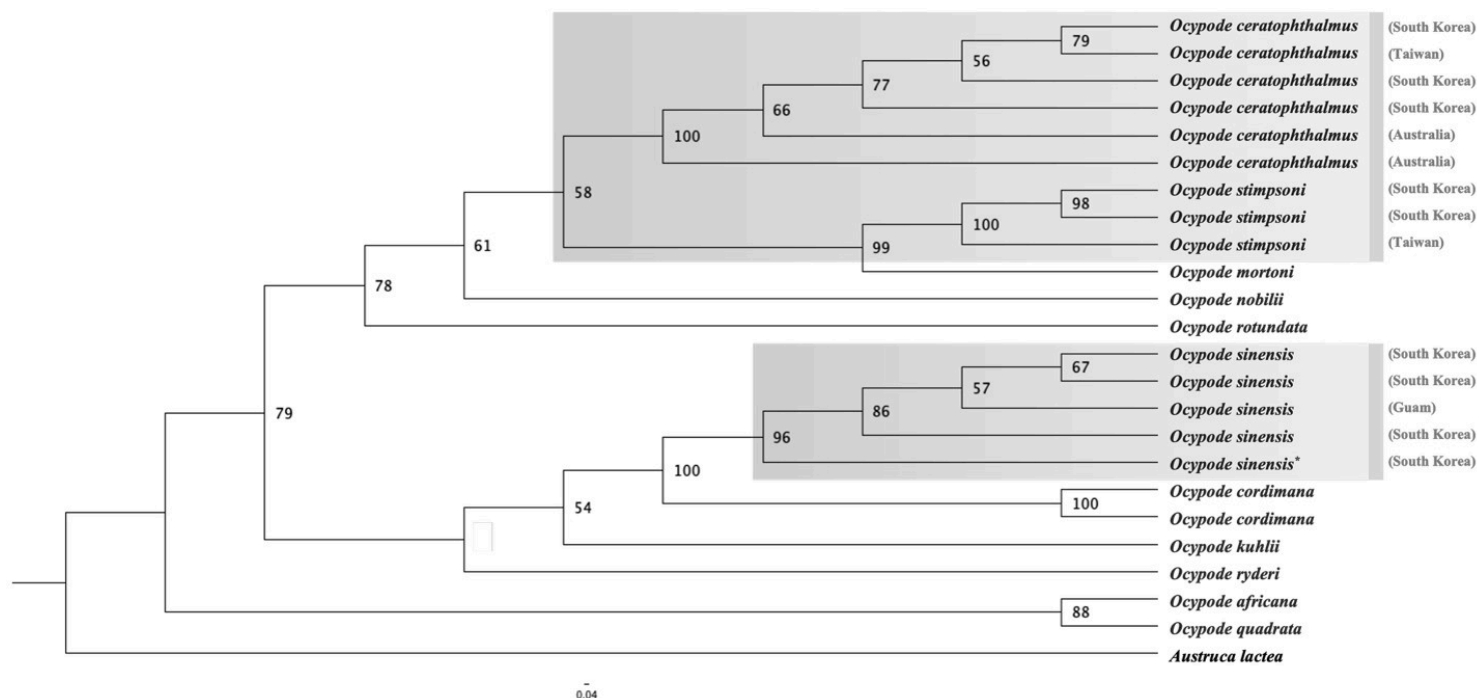


Figure 1

Phylogenetic tree of *Ocypode* crabs based on three genes (*mtCO1*, *16S rRNA*, and *28S rRNA*). Numbers at nodes indicate SH-aLRT support values followed by ultrafast bootstrap percentages. Only node support values $\geq 60\%$ are shown. Scale bar indicates substitutions per site. An asterisk indicates a specimen previously misidentified as *Ocypode cordimana* (NIBRIV0000229442). Colored labels denote species confirmed as occurring in South Korea based on this study, while the phylogenetic analyses also include conspecific individuals from other geographic regions.

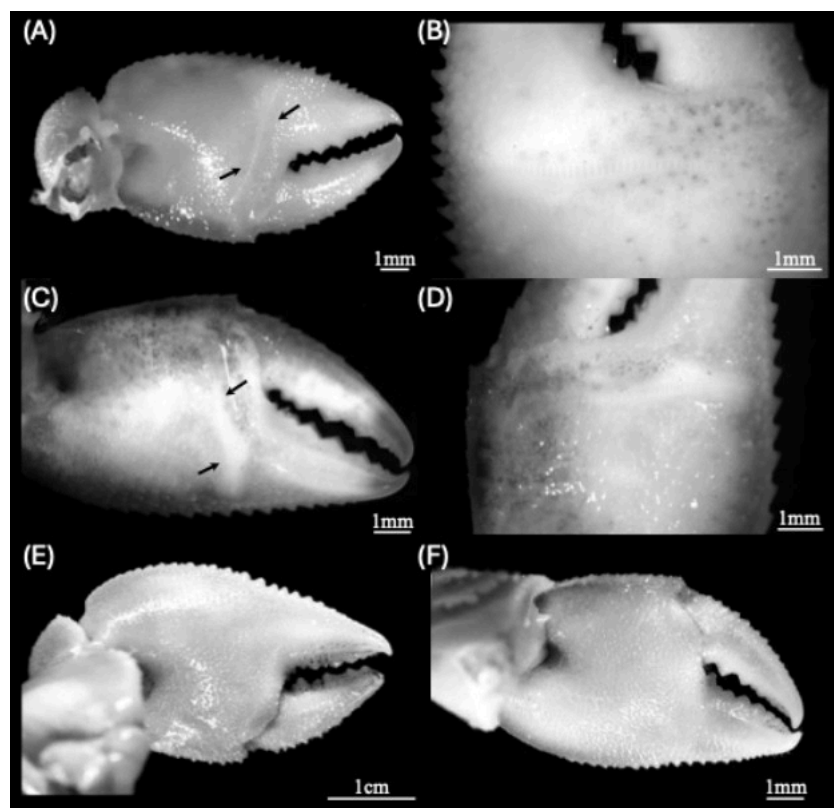


Figure 2

Morphological data of stridulating ridge among three *Ocypode* species in South Korea. (A) and (B), *Ocypode stimpsoni* (JJ59, South Korea); (C) and (D) *Ocypode ceratophthalmus* (JJ41, South Korea); (E) *Ocypode sinensis* (NIBRIV0000229442, South Korea); and (F) *Ocypode sinensis* (NIBR0000907532, South Korea).

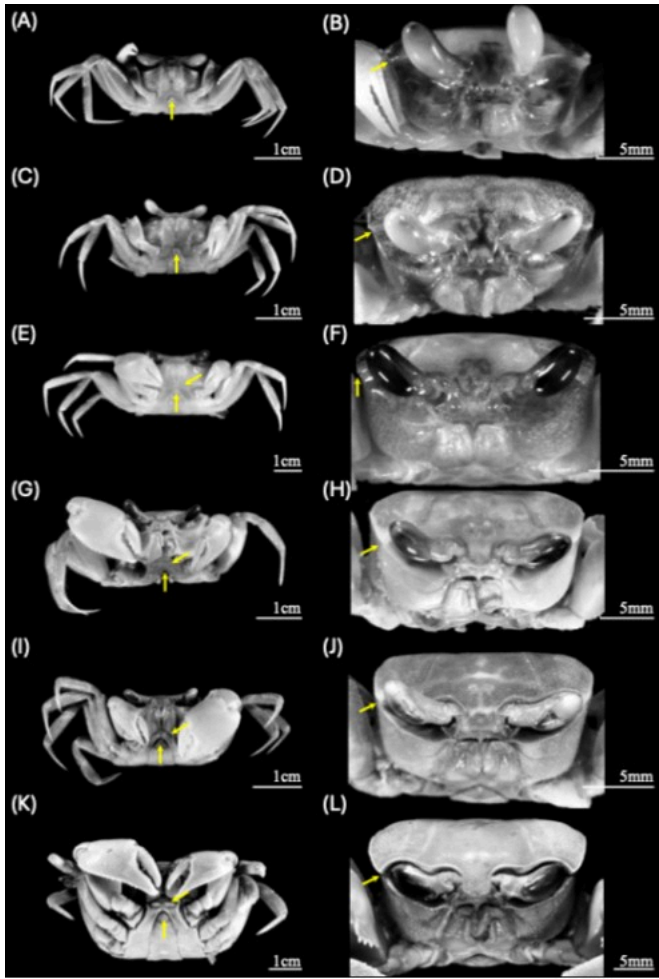


Figure 3

Morphological data of third maxilipeds, anterior thoracic sternum, and sixth abdominal segment among four *Ocypode* species. (A) and (B) *Ocypode ceratophthalmus* (JJ41, South Korea); (C) and (D) *Ocypode stimpsoni* (JJ59, South Korea); (E) and (F) *Ocypode sinensis* (NIBR0000907532, South Korea); (G) and (H) *Ocypode sinensis* (NIBRIV0000229442, South Korea); (I) and (J) *Ocypode sinensis* (NCHUZ00L14806, Taiwan); and (K) and (L) *Ocypode cordimana* (NCHUZ00L14917, Guam).

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