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PHENOTYPIC VARIATION ACROSS THE RANGE OF THE LINED SHORE CRAB *PACHYGRAPSUS CRASSIPES* RANDALL, 1840 (DECAPODA, GRAPSIDAE)

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ABSTRACT

Two isolated clades of the lined shore crab, *Pachygrapsus crassipes*, live on opposite sides of the northern Pacific, presenting an interesting opportunity for studies of range limits and divergence. Prior to this study, *P. crassipes*' Asian range was unclear; we confirmed that it is found throughout the main Japanese Archipelago, though sporadic or absent from the Ryukyu Archipelago. We examined phenotypic variation of this species' chelae, which are conspicuously colored and larger in males, and found positive allometry for both sexes, which was stronger in males, a common feature of sexually selected ornaments and weapons. We also found that Asian and North American clades differ significantly in chela reflectance — in contrast to previous studies, which stated that these clades were phenotypically identical. We conclude that these clades are diverging phenotypically, but that these differences are not yet sufficient to warrant distinction as separate species.

RÉSUMÉ

Deux clades isolés du crabe Grapsidae *Pachygrapsus crassipes*, vivent de part et d'autre du Pacifique Nord, présentant une perspective intéressante pour les études d'amplitude des limites de répartition géographique et de divergence. Avant cette étude, la répartition en Asie de *P. crassipes* n'était pas claire ; nous confirmons ici que l'espèce est présente dans l'archipel japonais, quoique sporadique ou absente dans l'archipel des Ryukyu. Nous avons examiné la variation phénotypique des pinces de cette espèce, qui sont clairement colorées et plus grandes chez les mâles et nous avons trouvé une allométrie positive pour les deux sexes, plus forte chez les mâles, un trait commun d'ornementations et d'épines sélectionnés sexuellement. Nous avons trouvé aussi que les clades d'Asie et d'Amérique du Nord diffèrent significativement dans la réflectance des pinces — au contraire des études précédentes, qui établissaient que ces clades était phénotypiquement identiques. Nous concluons que ces clades divergent phénotypiquement, mais que ces différences ne sont pas encore suffisantes pour justifier la distinction comme espèces séparées.

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INTRODUCTION

The grapsid crab *Pachygrapsus crassipes* Randall, 1840 has a range that is both large and disjunct, occurring in two genetically distinct clades on both sides of the northern Pacific (Hiatt, 1948; Cassone & Boulding, 2006). This arrangement offers an interesting opportunity to examine the processes underlying range limitation and divergence, but the boundaries of this range, and how phenotype varies across it, have yet to be clearly established.

In North America, *P. crassipes* is an abundant member of the high intertidal community, and occurs as far north as Bamfield, British Columbia, Canada (48.8°N, Cassone & Boulding, 2006), and as far south as Isla Santa Margarita, Baja California Sur, Mexico (24.4°N, Hiatt, 1948), spanning more than 24 degrees of latitude. There are conflicting reports of *P. crassipes*' range in Asia. Early reports suggested that this species was restricted to only 3 degrees of latitude in Japan and Korea (34° and 37°N, respectively, Hiatt, 1948). More recent reports, however, greatly extend this range south to Guangdong, China (23.6°N, Dai & Yang, 1991), and Taiwan (25°N, Ng et al., 2017), and north to Hakodate, Hokkaido Prefecture, Japan (41.8°N, Komai et al., 1992). While Hiatt (1948) suggested that the restricted range in Japan he observed was due to a recent introduction of this species from North America, recent evidence suggests that these populations are genetically distinct, with an estimated time of divergence of 0.8-1.2 million years ago, and sequence divergence sufficient to warrant consideration as separate species (Cassone & Boulding, 2006). If *P. crassipes*' range is restricted within Japan, other hypotheses must be generated to explain why. In this study, we aimed firstly to clarify the extent of *P. crassipes*' range across Japan.

Variation in phenotype across the geographic range of *P. crassipes* has received little attention. While this would be the obvious first step in examining divergence, early works described Asian and North American crabs as morphologically identical (Rathbun, 1917; Hiatt, 1948), and until it was demonstrated that these are two genetically isolated clades (Cassone & Boulding, 2006), there was no reason to expect divergence.

A phenotypic feature of particular interest is the coloration of the chelae. Chela coloration is used as a sexual signal by other terrestrial or semi-terrestrial crabs (Detto & Backwell, 2009; Wang & Todd, 2012). *P. crassipes* has a female-choice mating system (Bovbjerg, 1960), and chela coloration that contrasts obviously with the carapace (fig. 1), but to our knowledge, sexual selection has never been investigated in this species. Though the coloration of the carapace is well described (Randall, 1839; Kingsly, 1880; Rathbun, 1918), mentions of chela coloration are typically absent. Weymouth (1910) describes the chelae of crabs in Monterey Bay as "generally tan colored veined with red" but also comments that there is little

Fig. 1. A female *Pachygrapsus crassipes* Randall, 1840 from Bodega Bay, California, illustrates the degree to which chela coloration contrasts with the background color of the animal.

variation in chela appearance. Wicksten's (2011) description differs somewhat: "male chela bright red above, white below". While these descriptions are not inaccurate, they do not capture the variation we observe in California alone. As such, we aimed to quantify chela coloration, and to document the variation in this phenotype across the range of *P. crassipes*. Further, we tested for allometry between chela and body size, which is a common feature of sexually selected ornaments and weapons (Kodric-Brown et al., 2006). While not direct tests of sexual selection, positive allometry between chela and body size combined with divergent chela coloration between populations would raise intriguing questions about the role of sexual signaling in this species.

MATERIAL AND METHODS

We collected 234 *Pachygrapsus crassipes* with carapace length greater than 20 mm (the size at which sexual dimorphism first appears; Hiatt, 1948) from 16 sites across Japan and California in May-July, 2016 (8 sites from each region, fig. 2). We caught 2-20 (median = 16.5) crabs per site by hand in the mid to high intertidal from either natural rocky coastline or manmade rocky jetties. We photographed all crabs against an 18% neutral gray color card (Novoflex, Memmingen, Germany) in an opaque box with controlled, consistent lighting, provided by a 4000 K battery operated flexible LED light strip (LED Supply, Randolph, Vermont, U.S.A.) wrapped around the inside of the box. We captured images in Nikon Raw Format (NEF) using a Nikon D90 camera, Nikon AF-S 18-105 mm, 3.5-5.6 aperture lens, with a Kenko 12 mm lens extender. We used

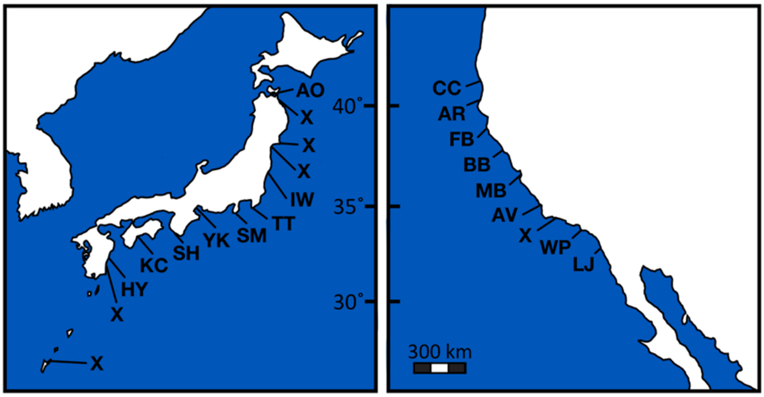

Fig. 2. Collection sites in Japan and California. X's represent sites where collection was attempted, but no *Pachygrapsus crassipes* Randall, 1840 were found. Crabs were successfully collected from eight sites in each continent. Sites in Japan, from north to south, are Aomori (GPS readings 40.903432, 140.855052), Iwaki (36.955042, 140.947412), Tateyama (34.976411, 139.768773), Shimoda (34.666271, 138.938779), Yokkaichi (34.897309, 136.639240), Shirahama (33.694456, 135.343404), Kochi (33.471835, 133.509306), and Hyuga (32.354842, 131.623053). Sites in California, from north to south, are Crescent City (41.743648, −124.197824), Arcata (40.765108, −124.220212), Fort Bragg (39.428307, −123.810364), Bodega Bay (38.334950, −123.054919), Monterey Bay (36.807185, −121.787622), Avila Beach (35.172609, −120.755846), White Point (33.717502, −118.322053), and La Jolla (32.851298, −117.273624).

the camera in manual mode with the following settings: 105 mm, shutter speed 1/250, f/20, ISO 2000. We took two images of each individual, one from above and one of the front face of the chela, with a ruler in each image for scale. We removed chelae from crabs for imaging by gently twisting while holding the crab firmly by the carapace, as *P. crassipes* abscise their chelae as a defense mechanism allowing them to escape predation (Hiatt, 1948; Warner, 1977).

We imported images into ImageJ to measure carapace width and propodus length (Schneider et al., 2012). We log-transformed these values to examine allometry using the reduced major axis regression software RMA (Bohonak & Van der Linde, 2004). We interpreted a slope of greater than 1 as evidence of allometry and sexual selection on chela size (Kodric-Brown et al., 2006).

We white balanced and exposure corrected chela images in Adobe Lightroom. It is not known if *P. crassipes* can see color, so we used Troscianko & Stevens' (2015) plugin for ImageJ to quantify mean percent of incident light reflected (a measure of brightness, rather than a more specific measure of color) by all pixels within the largest possible area of the propodus selected by ImageJ's circular selection tool. Averaging reflectance across the chela likely obscures specific details of pattern relevant to signaling, but still offers a basic measure of this phenotype that can be compared among geographic locations. These reflectance values were used in a mixed model ANCOVA, with continent and sex as fixed factors, site nested within continent as a random factor, and carapace width as a covariate.

RESULTS AND DISCUSSION

Range

We collected crabs from all attempted California sites except for Santa Barbara, where recent construction of seawalls at the site may have displaced crabs. In Japan, we collected individuals as far north as Aomori (40.9°N), and as far south as Hyuga (32.4°N) (fig. 2), a range nearly three times as great as Hiatt's (1948) 37° to 34°. Crabs were absent from three open coast sites in northern Honshu, as well as south of Hyuga in the city of Miyazaki, and from a southern, central, and northern location on the island of Okinawa.

The presence of *Pachygrapsus crassipes* in Aomori provides evidence that the northern range could indeed extend to Hakodate (Komai et al., 1992), 120 km north across the Tsugaru Straits. Only three individuals were encountered at this site, however, suggesting the conditions here are suboptimal for the survival of *P. crassipes*. Hakodate is one of the mildest cities on the island of Hokkaido, but still receives an average of 3.8 m of snow annually (Japan Meteorological Society), with subfreezing temperatures that likely present significant challenges for a semi-terrestrial crab. Though in North America, *P. crassipes* is found as far north as Bamfield, British Columbia, Canada (Cassone & Boulding, 2006), subfreezing temperatures there are rare (National Oceanic and Atmospheric Administration).

While there exists one record of *P. crassipes* from the Ryukyu Islands in southern Japan, specifically from Yoron Island (Muraoka, 1998), we surveyed at Cape Hedo, just 20 km from Yoron Island, as well as elsewhere across Okinawa, and found no evidence of *P. crassipes*. We conclude that while *P. crassipes* is found through most of the main Japanese Archipelago, it is sporadic or absent from the Ryukyu Islands.

Parasitism by *Sacculina* sp.

While not initially a goal of this study, we were interested to observe parasitism by the castrating rhizocephalan barnacles of the genus *Sacculina* Thompson, 1836 at three adjacent, central sites in Japan, but nowhere in North America. Rates of infection were: Shimoda (19% infected), Tateyama (44%), and Iwaki (6%). Because North American *P. crassipes* can be infected by *Sacculina carcini* Thompson, 1836 in the lab, the lack of infection in North America may be due to a lack of range overlap with the parasite, rather than immunity (Goddard et al., 2005). As such, *Sacculina* sp. may present an evolutionary pressure in Japan that does not exist in North America.

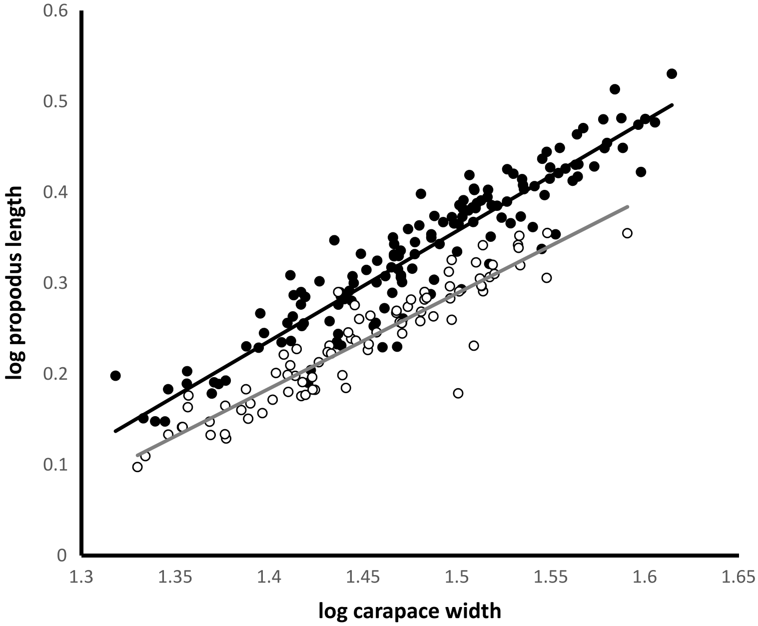

Fig. 3. Log-log plot of the relationship between propodus length and carapace width for males (black) and females (white) of *Pachygrapsus crassipes* Randall, 1840.

Allometry in chela size

Reduced major axis regression of log transformed values for carapace width and propodus length (a measure of chela size) revealed a slope significantly greater than 1, indicating positive allometry. Males ($\alpha = 1.30 \pm 0.08$, 95% confidence limits; $R^2 = 0.87$) were more strongly allometric than females ($\alpha = 1.13 \pm 0.09$; $R^2 = 0.86$) (fig. 3). This positive allometry suggests disproportionate investment in the growth of the chela; as a chela may be used as an ornament or weapon, this may reflect sexual selection on chela size, especially in males (Kodric-Brown et al., 2006). Sexual dimorphism results from divergent selective pressures on each sex, balanced by genetic constraints (i.e., each sex has the same genome). The positive allometry observed in females could be the result of genetic correlation with sexual selection on males (Fairbairn, 2007). Alternately, chelipeds serve an obvious function as weapons, and non-sexual selection can also produce allometry in these cases (Bergmann & Berk, 2012), but it is not obvious why non-sexual selection would act more strongly on males than on females. Though not a test of sexual selection, these data are consistent with the possibility that sexual selection could act on chela size in *P. crassipes*.

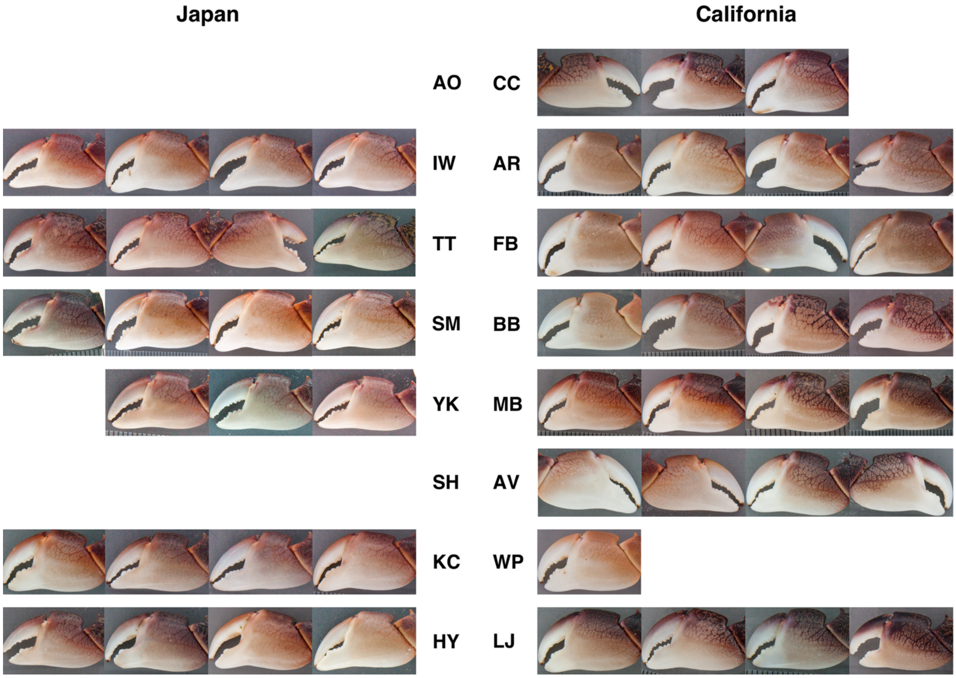

Fig. 4. Variation in chela color and pattern across the range of *Pachygrapsus crassipes* Randall, 1840. Representative chelae from each site are shown from north (top) to south (bottom) for each continent.

Phenotypic variation

Variation in coloration and pattern of the chela was observed both within and among sites (fig. 4). Generally, chelae are darker above and lighter below, and palest towards the tips of the pollex and dactylus, however, there is variation among sites in this pattern. Rather than distinct color morphs, chela brightness overall varies from light to dark. The palest chelae are orange/tan throughout, with little contrast, while the darkest approach a purplish black above, and fade to tan/gray below (fig. 5). The "veined" pattern described by Weymouth (1910) seems to be the result of the darker background being overlaid by paler pigment patches. These patches vary in size and the percentage of the background coloration they obscure, but are consistently absent from a horizontal band near the middle of the propodus, and never extend to the pollex or dactylus.

This variation is greater than has been previously described for this species. However, the variation does not follow a latitudinal cline. For example, the darkest phenotypes are found at one site in central California (Monterey Bay) and one site in southern California (La Jolla), with no obvious latitudinal pattern in either California or Japan.

Fig. 5. Comparison of dark and light chela of *Pachygrapsus crassipes* Randall, 1840. Above is a male (carapace width = 35.8 mm, mean reflectance = 33.1%) from White Point, CA. Below is a male (carapace width = 31.8 mm, mean reflectance = 15.9%) from La Jolla, CA, 160 km to the south.

Chela reflectance was significantly affected by continent and carapace width (table I). Reflectance increased as carapace width increased, and was overall higher in Japan (mean = 28.6%, stdev = 5.8%) than in California (mean = 21.8% stdev = 6.2%). There was also a significant interaction between sex and site, resulting from the fact that either males or females were the brighter sex at different sites, while at other sites, sexes did not differ. The observed difference in mean reflectance between continents is the first documentation of a phenotypic difference between the Asian and North American clades of *P. crassipes*. This is of particular interest, because coloration is an important indicator of mate quality in other crabs, most

TABLE I

Mixed model ANCOVA showing the influence of four factors (sex, continent of origin, site nested within continent, and carapace length) on percent reflectance of the chela in *Pachygrapsus crassipes* Randall, 1840

	df	SS	MS	*F*	*P*
Sex	1	247	246.7	5.57	0.0346*
Continent	1	2440	2439.7	33.28	<0.0001*
Carapace	1	2834	2833.6	129.98	<0.0001*
Site (Continent)	14	1027	73.3	3.803	<0.0001*
Sex × Continent	1	93	92.8	2.09	0.1719
Sex × Carapace	1	<0.0001	<0.0001	<0.0001	>0.9999
Continent × Carapace	1	33	33.1	1.717	0.1918
Sex × Site (Continent)	13	576	44.3	2.296	0.0080*
Site (Continent) × Carapace	14	305	21.8	1.131	0.3339
Sex × Continent × Carapace	1	1	0.6	0.04	0.8448
Sex × Site (Continent) × Carapace	12	179	15	0.775	0.6752
Residuals	173	3337	19.3		

* Statistically significant.

notably the genus *Uca* Leach, 1814 (Detto & Backwell, 2009), but also in two species of the genus *Perisesarma* De Man, 1895 (Wang & Todd, 2012).

Because this measure of brightness averages pixels across the chela, it may or may not directly represent color or a trait used in signaling. However, it does offer a measure of a phenotypic trait that varies among sites and continents. Mean reflectance serves as a sexual signal in a cryptically-colored, colorblind mantid (Barry et al., 2015), but in many other cases, brightness contrast, rather than mean reflectance, is the signal (Prudic et al., 2007). Mean reflectance could obscure the true signal in the case of *P. crassipes* if, for example, the signal was contrast between light and dark regions of the chela, or between the background and lighter mottled patches. Mate choice experiments manipulating chela pattern would be needed to determine the nature of the sexual signal, if it exists.

When considering whether Asian and North American clades of *P. crassipes* are separate species, the recent split of *P. socius* Stimpson, 1871 and *P. transversus* (Gibbes, 1850) offers an interesting comparison. *P. crassipes* clades began diverging ∼1 mya (Cassone & Boulding, 2006), while *P. socius* and *P. transversus* likely began diverging ∼3 mya (Schubart et al., 2005). Mitochondrial 16S rRNA sequences diverge by 3.3% between *P. socius* and Caribbean *P. transversus* (cf. Cuesta & Schubart, 1998). Mean sequence divergence between *P. crassipes* clades, based on COI [cytochrome c oxidase subunit 1], is 2.5%, with a maximum sequence divergence of 3.7% (Cassone & Boulding, 2006). While COI analysis is more effective at species resolution, both are mitochondrial genes, and follow the recommended 3% species-designation threshold (Hebert et al., 2003; Wang et al., 2017). *P. crassipes* clades are just below this threshold (with some haplotypes exceeding it), while *P. socius*/*P. transversus* are just above. Additionally, adult (but not larval) morphometrics differ between *P. socius* and *P. transversus* (cf. Schubart et al., 2005), while such differences have not been examined between the two clades of *P. crassipes* since the early work of Rathbun (1917) and Hiatt (1948). Further analysis of the morphometric differences, such as those used by Schubart et al. (2005), between Asian and North American clades of *P. crassipes* deserve further attention.

Ultimately, while mean chela reflectance differs significantly between these clades, this phenotypic feature is sufficiently variable among sites within a continent that it would be difficult to determine an individual crab's continent of origin merely by chela reflectance. As such, we do not suggest that the phenotypic difference observed here be used to consider these two *P. crassipes* clades as separate species, though they are likely on a trajectory towards becoming so. It remains to be seen whether these observed phenotypic differences are adaptive in either region, or whether they help to reinforce genetic differences between clades. As a whole, the interesting patterns of variation across the range of this species complex are promising for further study of speciation in marine species with high dispersal potential.

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REFERENCES

Barry, K. L., T. W. White, D. N. Rathnayake, S. A. Fabricant & M. E. Herberstein, 2015. Sexual signals for the colour-blind: cryptic female mantids signal quality through brightness. Functional Ecology, **29**: 531-539.

BERGMANN, P. J. & C. P. BERK, 2012. The evolution of positive allometry of weaponry in horned lizards (*Phrynosoma*). Evolutionary Biology, **39**: 311-323.

BOHONAK, A. J. & K. VAN DER LINDE, 2004. RMA: software for reduced major axis regression for Java. Available online at http://www.bio.sdsu.edu/pub/andy/rma.html.

BOVBJERG, R. V., 1960. Courtship behavior of the lined shore crab, *Pachygrapsus crassipes* Randall. Pacific Science, **14**: 421-422.

CASSONE, B. J. & E. G. BOULDING, 2006. Genetic structure and phylogeography of the lined shore crab, *Pachygrapsus crassipes*, along the northeastern and western Pacific coasts. Marine Biology, **149**: 213-226.

CUESTA, J. A. & C. D. SCHUBART, 1998. Morphological and molecular differentiation between three allopatric populations of the littoral crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura: Grapsidae). Journal of Natural History, **32**: 1499-1508.

DAI, A.-I. & S.-L. YANG, 1991. Crabs of the China seas: i-xxi, 1-608. (China Ocean Press, Beijing & Springer-Verlag, Berlin, Heidelberg, New York, Tokyo; English ed.; translation from Chinese original of 1986).

DETTO, T. & P. R. Y. BACKWELL, 2009. The fiddler crab *Uca mjoebergi* uses ultraviolet cues in mate choice but not aggressive interactions. Animal Behavior, **78**: 407-411.

FAIRBAIRN, D. J., 2007. Introduction: the enigma of sexual size dimorphism. In: D. J. FAIRBAIRN, W. U. BLANCKENHORN & T. SZÉKELY (eds.), Sex, size and gender roles. Evolutionary studies of sexual size dimorphism: 1-10. (Oxford University Press, Oxford).

GODDARD, J. H. R., M. E. TORCHIN, A. M. KURIS & K. D. LAFFERTY, 2005. Host specificity of *Sacculina carcini*, a potential biological control agent of the introduced European green crab *Carcinus maenas* in California. Biological Invasions, **7**: 895-912.

HEBERT, P. D. N., A. CYWINSKA, S. L. BALL & J. R. DEWAARD, 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society, (B) **270**: 313-321.

HIATT, R. W., 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pacific Science, **2**: 134-213.

KINGSLY, J. S., 1880. Carcinological notes, no. IV. Synopsis of the Grapsidae. Proceedings of the Academy of Natural Sciences of Philadelphia, **32**: 187-224.

KODRIC-BROWN, A., R. M. SIBLY & J. H. BROWN, 2006. The allometry of ornaments and weapons. Proceedings of the National Academy of Sciences, **103**: 8733-8738.

KOMAI, T., S. MARUYAMA & K. KONISHI, 1992. A list of decapod crustaceans from Hokkaido, northern Japan. Researches on Crustacea, **21**: 189-205.

MURAOKA, K., 1998. Catalogue of the brachyuran and anomuran crabs donated by Prof. Dr. Tune Sakai to the Kanagawa Prefectural Museum. Catalogue of the Collection in the Kanagawa Prefectural Museum of Natural History, **11**: 5-67, pls. 1-16.

NG, P. K. L., H. T. SHIH, P. H. HO & C. H. WANG, 2017. An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). Journal of the National Taiwan Museum, **70**: 101.

PRUDIC, K. L., A. K. SKEMP & D. R. PAPAJ, 2007. Aposematic coloration, luminance contrast, and the benefits of conspicuousness. Behavioral Ecology, **18**: 41-46.

RANDALL, J. W., 1840. Catalogue of the Crustacea brought by Thomas Nuttall and J. K. Townsend, from the west coast of North America and the Sandwich Islands, with descriptions of such species as are apparently new, among which are included several species of different localities, previously existing in the collection of the Academy. Journal of the Academy of Natural Sciences of Philadelphia, **8**: 127.

RATHBUN, M. J., 1918. The grapsoid crabs of America. Bulletin of the United States National Museum, **97**: 1-461.

SCHNEIDER, C. A., W. S. RASBAND & K. W. ELICEIR, 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods, **9**: 671-675.

SCHUBART, C. D., J. A. CUESTA & D. L. FELDER, 2005. Phylogeography of *Pachygrapsus transversus* (Gibbes, 1850): the effect of the American continent and the Atlantic Ocean as gene flow barriers and recognition of *Pachygrapsus socius* Stimpson, 1871 as a valid species. Nauplius, **13**: 99-113.

TROSCIANKO, J. & M. STEVENS, 2015. Image calibration and analysis toolbox — a free software suite for objectively measuring reflectance, colour and pattern. Methods in Ecology and Evolution, **6**: 1320-1331.

WANG, W. Y. & P. A. TODD, 2012. Evidence for carotenoid pigments in the facial bands of two mangrove crab species from Singapore. Nature in Singapore, **5**: 159-164.

WANG, Z. L., X. Q. YANG, T. Z. WANG & X. YU, 2017. Assessing the effectiveness of mitochondrial COI and 16S rRNA genes for DNA barcoding of farmland spiders in China. Mitochondrial DNA, (A). DOI:10.1080/24701394.2017.1350949.

WARNER, G. F., 1977. The biology of crabs: 1-202. (Elek Science, London).

WEYMOUTH, F. W., 1910. Synopsis of the true crabs (Brachyura) of Monterey Bay, California: 1-140. (Stanford University, Palo Alto, CA).

WICKSTEN, M. K., 2011. Decapod Crustacea of the Californian and Oregonian zoogeographic provinces: 1-420. (University of California, San Diego, La Jolla, CA).

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