



Uca (Petruca), a new subgenus for the rock fiddler crab *Uca panamensis* (Stimpson, 1859) from Central America, with comments on some species of the American broad-fronted subgenera

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Abstract

Among the fiddler crabs from the Americas, *Uca panamensis* (Stimpson, 1859) (Crustacea: Decapoda: Ocypodidae) is unusual in its behavior and ecology, living in stony habitats rather than sandy or muddy substrates. This species also has several unusual morphological characters of the carapace and major and minor chelae, and had been placed in either the subgenera *Minuca* Bott, 1954, or *Leptuca* Bott, 1973. The armature at the inner corner of the orbital floor, as well as the morphology of the urocardiac ossicles of the gastric mill of *U. panamensis*, are, however, plesiomorphic characters, and are closer to the condition in species belonging the subgenera *Uca* and *Afruca*. Phylogenetic relationships, based on mitochondrial 16S rDNA and cytochrome oxidase subunit I, and nuclear 28S rDNA, supported by its unusual morphological features indicate that this species belongs to its own subgenus. A new subgenus *Uca (Petruca)* **subgen. nov.** is herein established for *U. panamensis*. In addition, the status of *Uca thayeri* Rathbun, 1900, *U. umbratila* Crane, 1941, *U. virens* Salmon & Atsaiades, 1968, and *U. longisignalis* Salmon & Atsaiades, 1968, are revised and discussed based on a reappraisal of their phylogenetic relationships.

Key words: Crustacea, Brachyura, systematics, new subgenus, *Uca panamensis*, molecular evidence, 28S rDNA, 16S rDNA, cytochrome oxidase subunit I

Introduction

Fiddler crabs are abundant in marine wetlands in tropical and subtropical zones (Crane 1975). There are currently 102 species belonging to 11 subgenera, one from West Africa, three from the Americas, and seven from the Indo-West Pacific (IWP) (Ng *et al.* 2008; Shih *et al.* 2013a; Rosenberg 2014; Shih 2015). With regard to the American subgenera, one contains all the species with narrow fronts (relative width between the bases of the eyestalks) (*Uca* Leach, 1814), whereas the other two (*Minuca* Bott, 1954, and *Leptuca* Bott, 1973) include the broad-fronted taxa (Rosenberg 2001; Beinlich & von Hagen 2006; Ng *et al.* 2008). The subgenus *Boboruca* Crane, 1975 (= *Planuca* Bott, 1973), with two species, *Uca thayeri* Rathbun, 1900, and *Uca umbratila* Crane, 1941, is currently regarded as a synonym of *Minuca* (see Ng *et al.* 2008). The morphological differences between *Minuca* and *Leptuca*, however, are not very clear, and several species have been moved between these subgenera. *Uca panamensis* (Stimpson, 1859), *U. pygmaea* Crane, 1941, and *U. subcylindrica* (Stimpson, 1859), for example, were transferred from *Minuca* to *Leptuca*; whereas *U. argillicola* Crane, 1941, was transferred from *Leptuca* to *Minuca* based on either morphology or DNA sequence (see review by Beinlich & von Hagen 2006). A recent preliminary molecular phylogeny for the broad-fronted taxa showed an unsolved genetic relationship between *Minuca* and *Leptuca*, but not all the species in these subgenera were tested (Shih *et al.* 2013b).

Among the American broad-fronted taxa, the subgeneric status of *U. panamensis* is noteworthy. Although it has long been considered to be a member of the subgenus *Minuca* mainly by the characters of the front and male

first gonopod (Bott 1954, 1973; Crane 1975), the morphological analysis of Rosenberg (2001) indicated that it belonged to the subgenus *Leptuca* instead, and this classification has been followed by most subsequent authors (see Beinlich & von Hagen 2006; Ng *et al.* 2008). Crane (1975) had, nevertheless, highlighted that *U. panamensis* was peculiar, not only morphologically, but also in its ecology and behavior. It is the only species adapted to living in cobble beaches: it does not dig deep or permanent burrows, has an atypically flat carapace for sheltering under stones, stiff setal brushes on the tips of the small chelae for scraping algae from the stones, and it swallows food particles directly (Crane 1941, 1975; Takeda & Murai 2003).

After re-examination and comparison of the characters of this species with congeners, as well as genetic support from mitochondrial 16S rRNA and cytochrome oxidase subunit I (COI) and nuclear 28S rRNA markers, a new subgenus is here proposed for *Uca panamensis* (Stimpson, 1859). This is a better reflection of its phylogenetic relationship. A neotype collected from Panamá, its type locality, is designated in this study. In addition, the uncertain subgeneric status of *Uca thayeri* and *U. umbratila* is revised, and the taxonomically uncertain *U. virens* Salmon & Atsides, 1968 and *U. longisignalis* Salmon & Atsides, 1968, is also discussed based on the molecular data obtained in this study.

Material and methods

Specimens of *Uca panamensis*, as well as species of the subgenera *Minuca* and *Leptuca*, were included for morphological examination and molecular analyses. The American subgenus *Uca*, the eastern Atlantic subgenus *Afruca*, the IWP broad-fronted subgenera *Austruca*, *Cranuca*, and *Paraleptuca*, and the narrow-fronted subgenera *Australuca*, *Gelasimus*, *Tubuca* and *Xeruca* were used as outgroups (Fig. 1, Table 1).

Material examined is deposited in the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOO); the Zoological Reference Collection of the Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore, Singapore (ZRC); and U.S. National Museum for Natural History, Smithsonian Institution, Washington D.C., USA (USNM). Other institutions include Institute of Zoology, Academia Sinica, Taipei, Taiwan (ASIZ); Muséum national d'Histoire naturelle, Paris, France (MNHN); Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan (NTOU); Queensland Museum, Brisbane, Australia (QM); Steinhardt National Collections of Natural History, Tel Aviv University, Israel (TAU); and National Taiwan Museum, Taipei, Taiwan (TMCD) (Appendix 1, Table 1).

Measurements, in millimeters (mm), are of the carapace width (CW). The abbreviation G1 is used for the male first gonopod. The characters of the gastric mill are useful for distinguishing some groups of fiddler crabs (cf. Shih 2015) and the stomachs of *U. panamensis* and other related taxa were examined and compared. The stomach was removed with forceps inserted at the suture of posterior margin between the carapace and abdomen. The description of the gastric mill mainly follows the terminology used by Yang (1986), Allardyce & Linton (2010), Brösing (2010), and Brösing & Türkay (2011). The urocardiac ossicle can be divided roughly into the anterior basal region, the stem region, and the posterior tooth plate. The median tooth is composed of several transverse tooth-like ridges or cusps, protruding from a longitudinal central ridge on the ventral side of the tooth plate as well as on the stem region for some species (Shih 2015).

Sequences of 16S, COI and 28S were obtained following the method described by Shih *et al.* (2013b) and aligned with the aid of MUSCLE function of MEGA (v. 5.2.2, Tamura *et al.* 2011), after verification with the complementary strand. Sequences of the different haplotypes were deposited in the DNA Data Bank of Japan (DDBJ) (accession numbers in Table 1), with other sequences which have been published in earlier papers of the first author (Table 1).

The sequences of 28S, 16S, and COI of *U. panamensis* were obtained from six specimens to exclude the possibility of pseudogenes (NUMT) (more than three specimens are needed as suggested by Buhay 2009). Because the COI sequences of this species are very different from the *Minuca* and *Leptuca* species of this study, different combination of primers (LCO, HCO, COH6 and COL14; see Schubart 2009) were also used to confirm the sequences obtained.

TABLE 1. Haplotypes of 16S rDNA, COI and 28S rDNA for the subgenus *Petruca* **subgen. nov.** and other related subgenera used in this study. See “Material and methods” for abbreviations of institutions. *, see “DNA analyses and discussion”.

Subgenus	Species	Locality	NCHUZOOL catalog no. (unless indicated)	DDBJ Access. no. of 16S	DDBJ Access. no. of COI	DDBJ Access. no. of 28S
<i>Petruca</i>	<i>U. panamensis</i>	(#1) Panamá: Culebra Island	USNM 1294205 (neotype, transferred from NCHUZOOL 13581)	LC087917	LC087943	LC087975
		(#2) Panamá: Culebra Island	13581	LC087918	LC087944	LC087975
		(#1)Costa Rica: San Juanillo rocky shore, Ostional	14753	LC087918	LC087945	LC087975
		(#2)Costa Rica: San Juanillo rocky shore, Ostional	ZRC	LC087917	LC087946	LC087975
		(#3)Costa Rica: San Juanillo rocky shore, Ostional	ZRC	LC087917	LC087947	LC087975
		(#4)Costa Rica: Playa San Juanillo	ZRC 2012.0126	LC087918	LC087948	LC087975
<i>Minuca</i>	<i>U. brevifrons</i>	Costa Rica: Playa San Juanillo	ZRC 2012.0126	LC087919	LC087949	LC087976
	<i>U. burgersi</i>	Bahamas: Salt Pan San Salvador	ZRC	LC087920	LC087950	LC087977
	<i>U. herradurensis</i>	Panamá: Diablo Heights mangroves	13580	AB813664	AB813680	AB813709
	<i>U. minax</i>	Virginia, USA: Chesapeake Bay	13939	LC087921	LC087951	LC087978
	“ <i>U. longisignalis</i> ”*	Texas, USA: Ingleside Cove, Corpus Christi	13938	LC087922	LC087952	LC087979
	<i>U. mordax</i>	Brazil: São Paulo	13940	LC087923	LC087953	LC087980
	<i>U. pugnax</i>	(#1)Maryland, USA: Assateague Island	13941	LC087924	LC087954	LC087981
		(#2)Maryland, USA: Assateague Island	13941	LC087925	LC087955	LC087982
	<i>U. rapax</i>	Jamaica: Trelawny	13942	LC087926	LC087956	LC087983
		British Virgin: Paraquita Bay	13943	LC087927	LC087956	LC087984
		Panamá: Bocas del Toro	13944	LC087928	LC087957	LC087984
	<i>U. victoriana</i>	Brazil: Bahia	13945	LC087929	LC087958	LC087985
	<i>U. cf. virens</i> (identified as <i>U. rapax</i>)*	(#1)Texas, USA: Ingleside Cove, Corpus Christi Bay	13584	AB813665	AB813681	AB813710
		(#2)Texas, USA: Ingleside Cove, Corpus Christi Bay	13584	LC087930	AB813681	LC087986
		Florida, USA: Money Bayou, Gulf County	13946	AB813665	AB813681	LC087984
	<i>U. vocator</i>	Brazil: Ceara	13948	LC087931	LC087959	LC087987

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TABLE 1 (continued)

Subgenus	Species	Locality	NCHUZOOL catalog no. (unless indicated)	DDBJ Access. no. of 16S	DDBJ Access. no. of COI	DDBJ Access. no. of 28S
<i>Leptuca</i>	<i>U. cumulanta</i>	Brazil: Rio de Janeiro	13949	LC087932	LC087960	LC087988
	<i>U. deichmanni</i>	Panamá: Culebra Island	13583	AB813660	AB813676	AB813705
	<i>U. dorotheae</i>	Costa Rica: Tempisque R.	ZRC	LC087933	LC087961	LC087989
	<i>U. leptodactyla</i>	(#1)Bahamas: Pigeon Creek, San Salvador	ZRC	LC087934	LC087962	LC087990
		(#2)Bahamas: Pigeon Creek	ZRC	LC087934	LC087962	LC087991
	<i>U. panacea</i>	Texas, USA: South Padre Island, Cameron	13950	LC087935	LC087963	LC087992
	<i>U. pugilator</i>	South Carolina, USA: Georgetown	13586	AB813662	AB813678	AB813707
		Florida, USA: Seahorse Key	ASIZ	AB813662	AB813678	LC087993
	<i>U. speciosa</i>	Florida, USA: Alligator Point	13951	LC087936	LC087964	LC087994
		Bahamas: Pigeon Creek, San Salvador	ZRC	LC087936	LC087965	LC087995
	<i>U. spinicarpa</i>	Florida, USA: Money Bayou, Gulf County	13947	LC087937	LC087966	LC087996
		Texas, USA: Boliver Island	ZRC 2009.0295	LC087937	LC087967	LC087997
	<i>U. subcylindrica</i>	(#1)Texas, USA: Kingsville	13952	LC087938	LC087968	LC087998
		(#2)Texas, USA: Kingsville	13952	LC087938	LC087968	LC087999
	<i>U. terpsichores</i>	Panamá: Culebra Island	13582	AB813661	AB813677	AB813706
	<i>U. thayeri</i>	Florida, USA: Hutchinson Island, Fort Pierce	13953	LC087939	LC087969	LC088000
		Brazil: Anchieta, Espírito Santo	13954	LC087940	LC087970	LC088001
	<i>U. umbratila</i>	(#1) Panamá: Diablo Heights mangroves	13579	AB813663	AB813679	AB813708
		(#2) Panamá: Diablo Heights mangroves	13579	LC087941	LC087971	LC088002
	<i>U. uruguayensis</i>	Argentina: Samborombón	13577	AB813659	AB813675	AB813704
<i>Paraleptuca</i>	<i>U. crassipes</i>	Ryukyus, Japan: Okinawa	13467	AB813656	AB734656	AB813700
		Moorea, Polynesia: Haapiti Cocos-Keeling	13478	AB813656	AB734656	AB813701
	<i>U. splendida</i>	Hong Kong: Tai Tam	13368	AB813655	AB734648	AB813699
		Taiwan: Cingluo, Penghu	13457	AB813653	AB734641	AB813697
		Vietnam: Nha Trang	13448	AB813654	AB734654	AB813698
<i>U. chlorophthalmus</i>	(#1)Mayotte: mangrove de Malamani	MNHN-IU-2011- 5599	AB813657	JX050999 (MDECA791 -12)	AB813702	
	(#2)Mayotte: mangrove de Malamani	MNHN-IU-2011- 5600	AB813657	JX050997 (MDECA793 -12)	AB813702	
	Tanzania: Dar es Salaam	13561	AB813657	LC087972	LC088003	

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TABLE 1 (continued)

Subgenus	Species	Locality	NCHUZOOL catalog no. (unless indicated)	DDBJ Access. no. of 16S	DDBJ Access. no. of COI	DDBJ Access. no. of 28S
<i>Cranuca</i>	<i>U. inversa</i>	Kenya: Gazi	MZUF 1024	AB813658	AB813674	AB813703
		Egypt: Sinai	TAU SLR 1475	AB813658	LC087973	LC088004
		Tanzania: Dar es Salaam	13255	AB471904	AB471917	AB813703
<i>Austruca</i>	<i>U. albimana</i>	Egypt: Nabq, Sinai	13242	AB471893	AB471906	AB813689
		Thailand: Phuket	13258	AB471894	AB491161	AB813686
	<i>U. annulipes</i>	southern Madagascar	ZRC THH04-30	AB813648	AB813669	AB813687
		Iran: Gavbandi	13245	AB471896	AB471908	AB813688
	<i>U. lactea</i>	Hong Kong	13250	AB471898	AB471912	AB813693
	<i>U. mjoebergi</i>	Australia: Bedford I., West Australia	QM-W20253	AB471900	AB471914	AB813690
		Taiwan: Dulanwan, Taitung New Caledonia: Ouano Bay	NTOU 13573	AB471901	AB471915	AB813691 AB813692
<i>Tubuca</i>	<i>U. acuta</i>	Taiwan: Kinmen	13650	LC053352	LC053369	LC053387
		Korea: Incheon	13651	LC053353	LC053370	LC053388
	<i>U. arcuata</i>	Taiwan: Penghu	13231	LC053354	LC053371	LC053389
		Malaysia: Johor	NTOU	LC053355	LC053372	LC053390
	<i>U. forcipata</i>	China: Hainan	13381	LC053356	LC053373	LC053391
	<i>U. paradussumieri</i>	Malaysia: Johor	NTOU	LC053357	LC053374	LC053392
	<i>U. urvillei</i>	Mayotte: Poroani	ZRC 1999.1107	LC053358	LC053375	LC053393
<i>Australuca</i>	<i>U. bellator</i>	Borneo: Labuan, Malaysia	13649	LC053348	LC053365	LC053383
		Australia: Lacrosse I., West Australia	QM W21038	LC053349	LC053366	LC053384
	<i>U. longidigitum</i>	Australia: Hervey Bay, Queensland	QM W19274	LC053350	LC053367	LC053385
		Indonesia: West Papua	ZRC 2000.2059	AB813668	AB813685	AB813714
<i>U. signata</i>	Australia: Hucks Landing, Queensland	QM W19211	LC053351	LC053368	LC053386	
<i>Gelasimus</i>	<i>U. tetragonon</i>	Taiwan: Kenting, Pingtung	TMCD CHCD 526	AB535405	AB535431	LC053395
		Philippines: Bohol	13667	AB535399	AB813683	AB813712
<i>Xeruca</i>	<i>U. formosensis</i>	Taiwan: estuary of Bajhang R., Chiayi	13742	LC053346	LC053363	LC053381
		Taiwan: Cingluo, Penghu	13770	LC053347	LC053364	LC053382
<i>Uca</i>	<i>U. major</i>	Bahamas: Pigeon Creek	ZRC	LC053360	LC053378	LC053397
		Brazil: Itapissuma, Pernambuco	13955	LC087942	LC087974	LC088005
<i>Afruca</i>	<i>U. stylifera</i>	Panamá: Rodman	13578	LC053361	LC053379	LC053398
		Spain: Puerto de Santa María, Cádiz	13585	AB813666	AB813682	AB813711

For a combined analysis of mitochondrial 16S, COI, and 28S markers, the phylogenetic congruence among the three dataset partitions was tested under the maximum parsimony (MP) criterion using the incongruent length difference (ILD) test (Farris *et al.* 1994) implemented in the PAUP* program (v. 4.0b10, Swofford 2003) as the partition homogeneity test. The parameters included 1000 replicates of a heuristic search with 100 random

sequence additions, TBR branch-swapping, using Steepest Descent with the MULTREES option enabled. The topologies of the three datasets were congruent ($P = 0.056$; significance level 0.01 has been suggested in Cunningham 1997) and as such, the sequences were combined.

For the combined dataset, the best-fitting models for sequence evolution of individual datasets were determined by MrModeltest (v. 2.2, Nylander 2005), selected by the Akaike information criterion (AIC). The best models obtained for the three individual datasets were all GTR + G + I, and were subsequently used for the partitioned Bayesian inference (BI) and maximum likelihood (ML) analyses. The BI analysis was performed with MrBayes (v. 3.2.3, Ronquist *et al.* 2012). The search was run with 4 chains for 10 million generations and 4 independent runs, with trees sampled every 1000 generations. The convergence of chains was determined by the effective sample size (ESS) (>200 as recommended) in Tracer (v. 1.5, Rambaut & Drummond 2009) and the first 1000 trees were discarded as the burnin (determined by the average standard deviation of split frequency values below the recommended 0.01; Ronquist *et al.* 2005). Maximum likelihood (ML) analysis was conducted both in RAxML (v. 7.2.6, Stamatakis 2006) and GARLI (v. 2.0, Zwickl 2006). In RAxML, the model GTR + G (i.e. GTRGAMMA) was used for all subsets with 100 runs, and found the best ML tree by comparing the likelihood scores. The robustness of the ML tree was evaluated by 1000 bootstrap pseudoreplicates under the model GTRGAMMA. In GARLI, 10 replicate searches (searchreps = 10) and 100 bootstraps (bootstrapreps = 100) were run and the consensus tree from GARLI output was computed using PAUP* program to assess node supports.

Systematic account

Family Ocypodidae Rafinesque, 1815

Subfamily Ocypodinae Rafinesque, 1815

Genus *Uca* Leach, 1814

Uca (*Petruca*) subgen. nov.

Minuca Bott, 1954: 160 (part); Bott 1973: 323 (part); Crane 1975: 154 (part)

Leptuca Bott, 1973: 324 (part); Beinlich & von Hagen 2006: 26 (part); Ng *et al.* 2008: 241 (part).

CelUCA Crane, 1975: 211 (part); Rosenberg 2001: 848, 852 (part).

Type species. *Gelasimus panamensis* Stimpson, 1859, by present designation.

Etymology. From the Greek *petra* for “rock or stone”, for the stony habitat (Fig. 8C) of the type species, in arbitrary combination with the genus name *Uca*. Gender feminine.

Diagnosis. Carapace flat, widest distance of carapace between anterolateral angles, angles acute, produced obliquely outwards, anteriorly; anterolateral margins relatively long (Fig. 1A); boss (raised tuberculate ridge) on carapace behind dorsolateral margin (Fig. 1B); front wide, about 1/3 carapace width (Fig. 2C, D); suborbital crenulations strong, each truncate, separate, increasing in size towards antero-external angle (Figs. 1C, 2A–C); orbital floor without mound or pile, but with tubercle at inner corner adjacent to antennule (Fig. 2A–C). Male with pleonal clasping apparatus in abdominal cavity. Urocardiac ossicles of gastric mill (Fig. 5) simple, median tooth with 3 pairs of similar transverse ridges, separated by gaps, not reaching central ridge on posterior tooth plate; first pair of ridges strongest, next 2 lower, with 2 or 3 weak pairs of cusps on stem region; stem region with long, wide median part (Fig. 5A). Major pollex, dactylus with tips blunt, without or with weak tooth on cutting margins (Figs. 3A, B, 8A, B). Adult male major manus with outer surface smooth, proximal outer part disproportionately thick, with posterior extension beyond distal part of carpus (Figs. 3A, 8A); inner surface with vestigial oblique ridge, without or with low, rounded tubercles (Fig. 3B). Adult minor cheliped with manus rounded, broad almost as long; gape wide; fingers with numerous long stiff setae on tip (Figs. 3C, D, 8B). G1 (Fig. 4) with anterior flange (before genital pore) broader than posterior one (after genital pore); inner process large, broad, becoming thicker distally, bent forwards at right angles, extending beyond tip of posterior flange; thumb slender, ending below base of flange.

Remarks. One of the diagnostic characters of *Petruca* subgen. nov. is that the carapace is widest between the tips of the anterolateral angles (Fig. 1A). In this feature, it is similar to, but more pronounced than in any *Leptuca* species. The maximum carapace width in *Minuca* species is usually behind the anterolateral angles (Crane 1975).

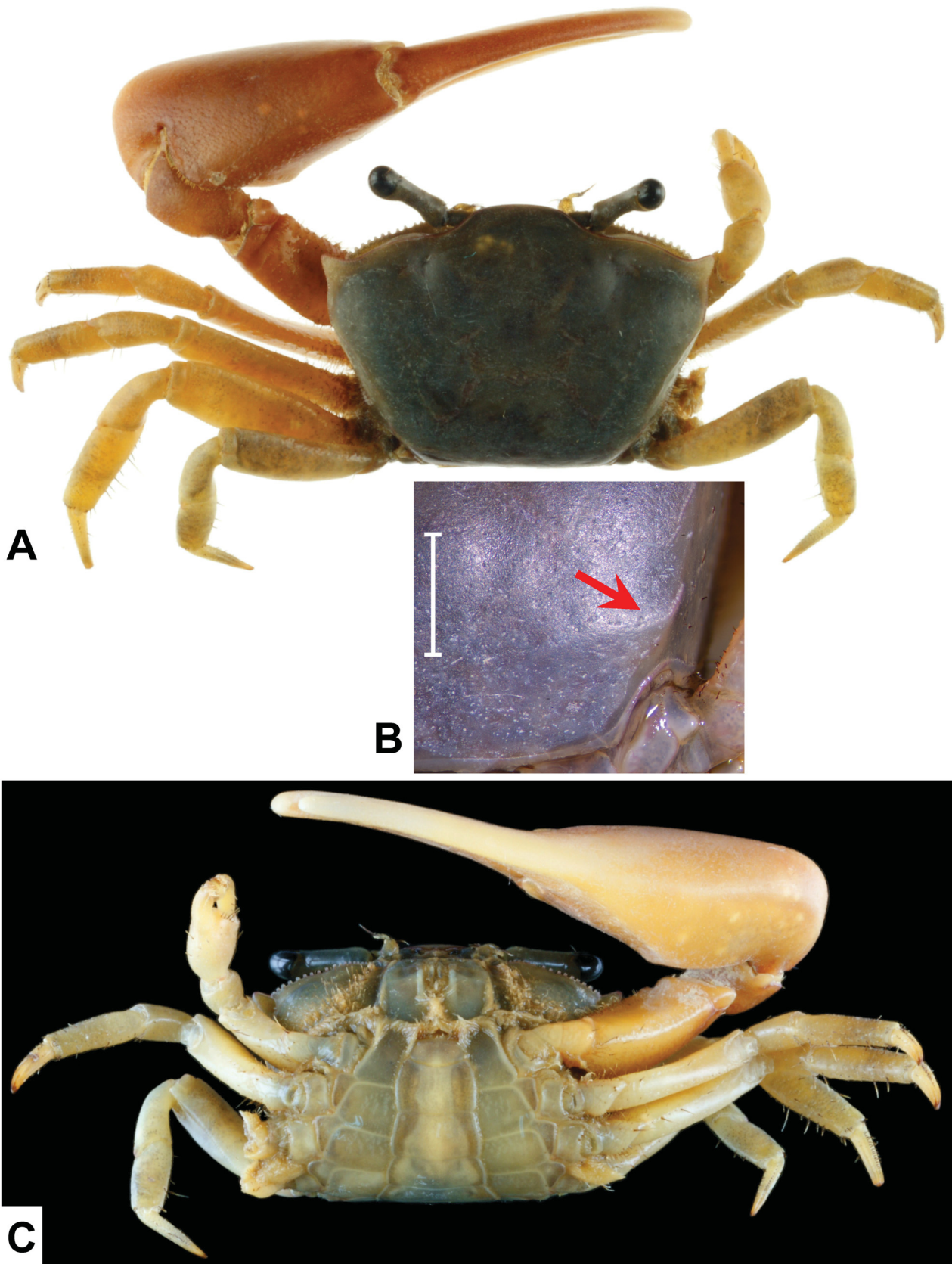


FIGURE 1. *Uca panamensis* (neotype, USNM 1294205, CW 16.8 mm). A, dorsal view; B, boss on carapace behind right dorsolateral margin (arrowed); C, ventral view. Scale, B = 2 mm.

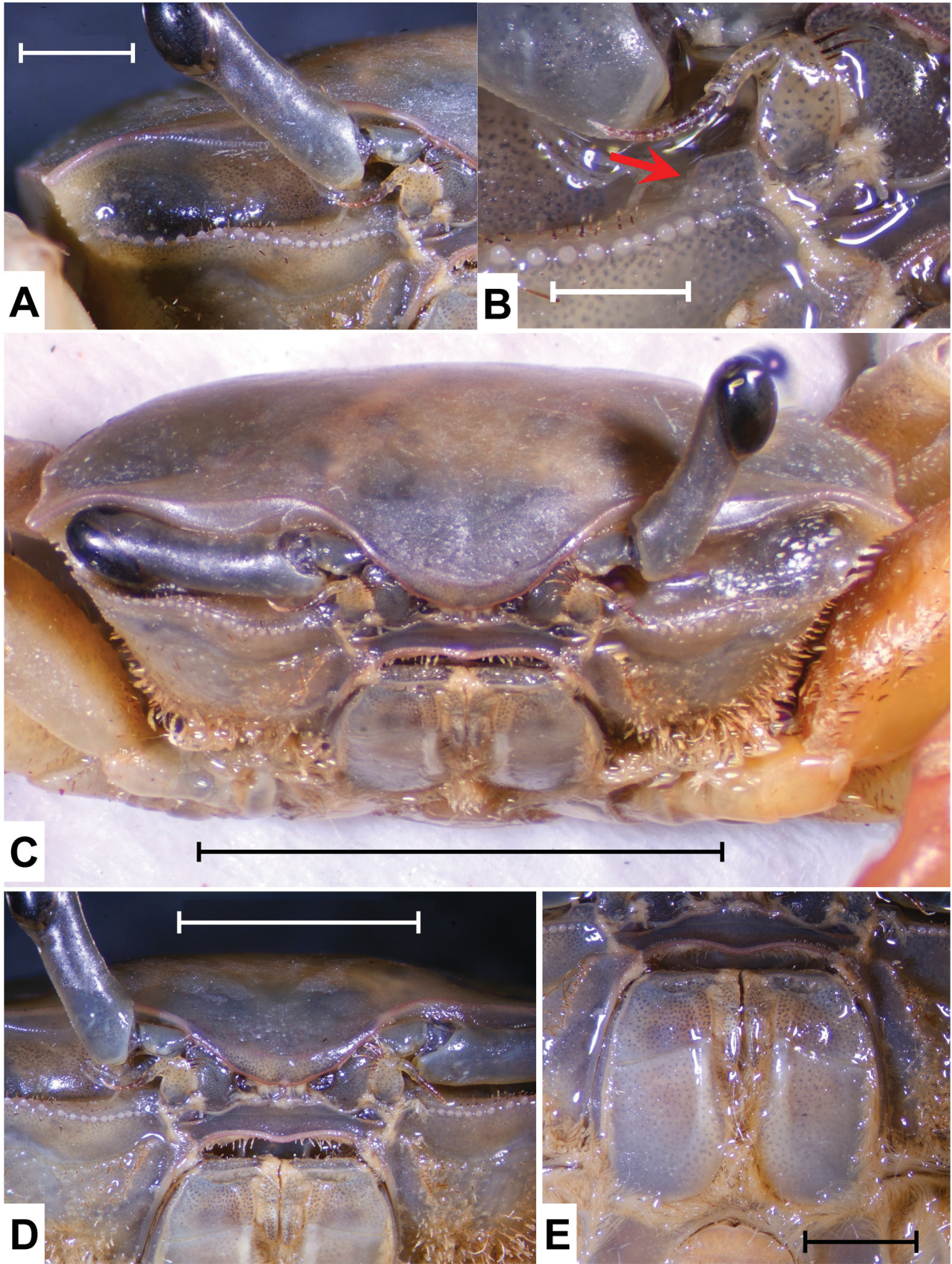


FIGURE 2. *Uca panamensis* (neotype, USNM 1294205, CW 16.8 mm). A, orbital region; B, inner side of orbital region, showing the tubercle of orbital armature (arrowed); C, frontal view; D, front; E, third maxillipeds. Scale, A, E = 2 mm; B = 1 mm; C = 10 mm; D = 5 mm.

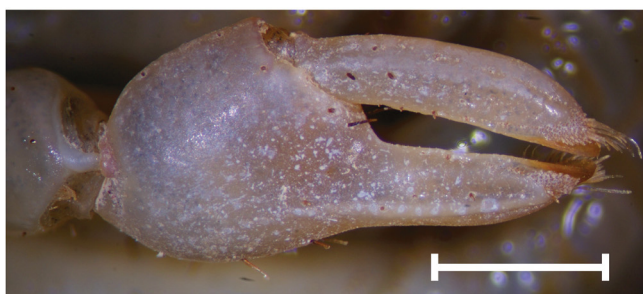


FIGURE 3. Major and minor chelipeds of *Uca panamensis* (neotype, USNM 1294205, CW 16.8 mm). A, B, outer and inner views of major cheliped; C, D, outer and inner views of minor cheliped. Scale, C, D = 2 mm.



FIGURE 4. *Uca panamensis*, right G1 (neotype, USNM 1294205, CW 16.8 mm). A, dorsal view; B, dorsal view of terminal segment; C, D, ventral view of terminal segment. Scale, A = 2 mm; B, C = 0.5 mm.

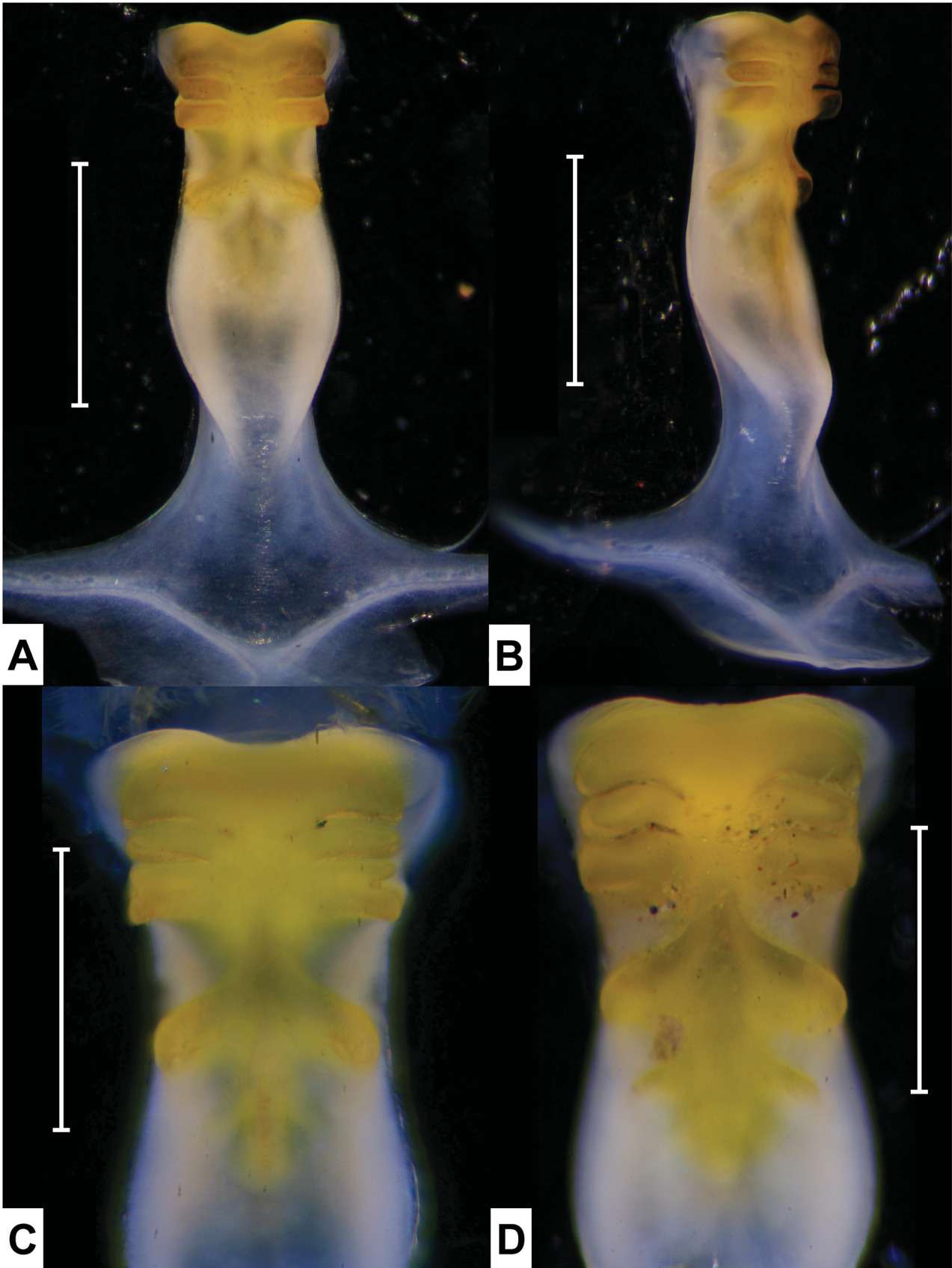


FIGURE 5. Urocardiac ossicle of *Uca panamensis*. A, B, neotype, USNM 1294205 (16.8 mm); C, ZRC (CW 12.6 mm, ♂); D, ZRC (CW 13.7 mm, ♀). A, C, D, ventral view; B, lateroventral view. Scale, A, B = 1 mm; C, D = 0.5 mm.

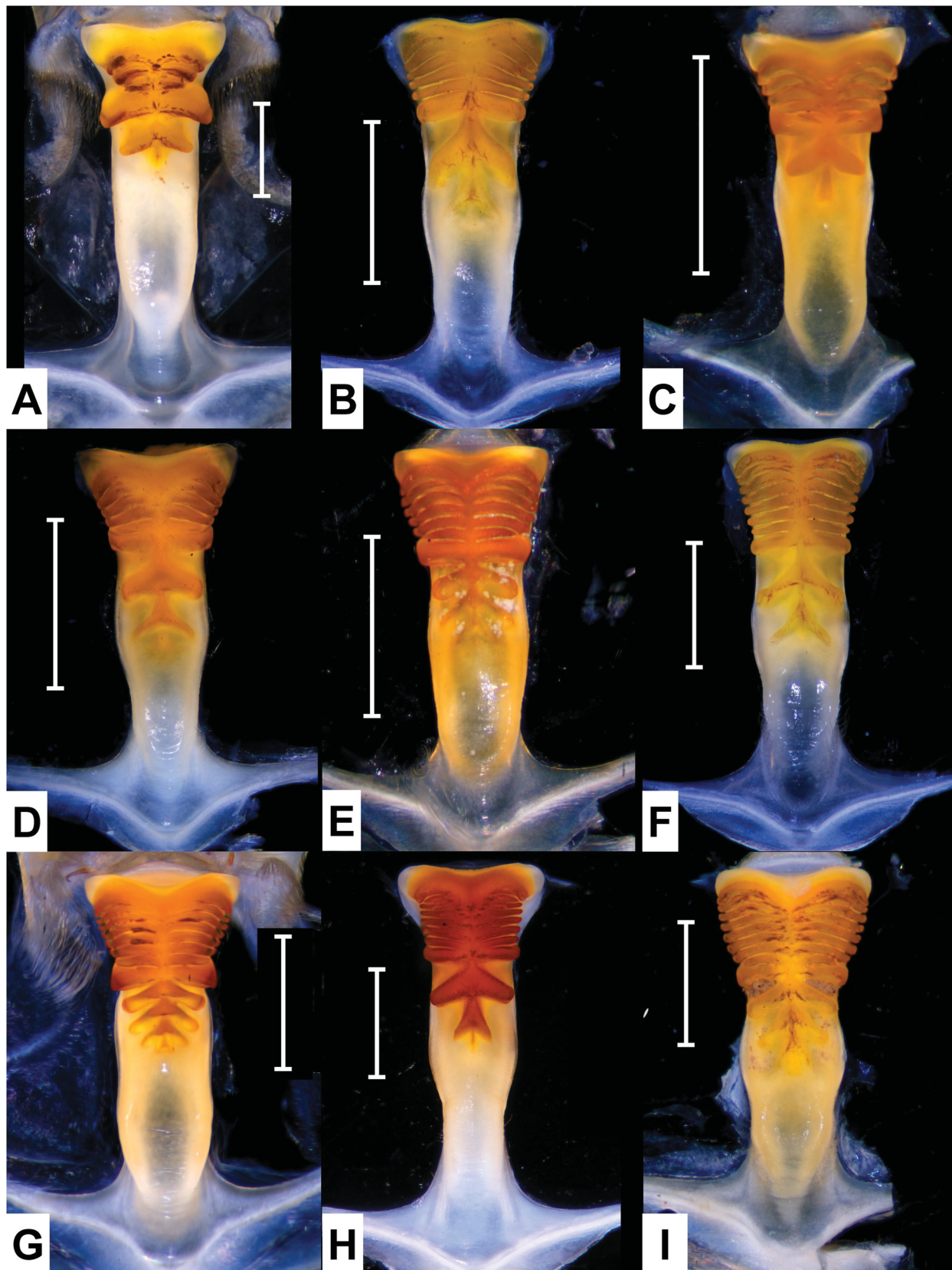


FIGURE 6. Urocardiac ossicle of the subgenus *Minuca* species. A, *Uca brevifrons* (ZRC 2012.0126, CW 22.1, ♂); B, *U. cf. virens* (NCHUZOO 13946, CW 17.0 mm, ♂); C, *U. victoriana* (NCHUZOO 13945, CW 12.2 mm, ♀); D, *U. pugnax* (NCHUZOO 13941, CW 15.2 mm, ♂); E, *U. burgersi* (NCHUZOO 13956, CW 13.0 mm); F, *U. rapax* (NCHUZOO 13942, CW 23.4 mm, ♂); G, *U. mordax* (NCHUZOO 13940, CW 18.0 mm, ♀); H, *U. minax* (NCHUZOO 13957, CW 23.2 mm, ♂); I, *U. vocator* (NCHUZOO 13948, CW 21.9 mm, ♀). Scale = 1 mm.

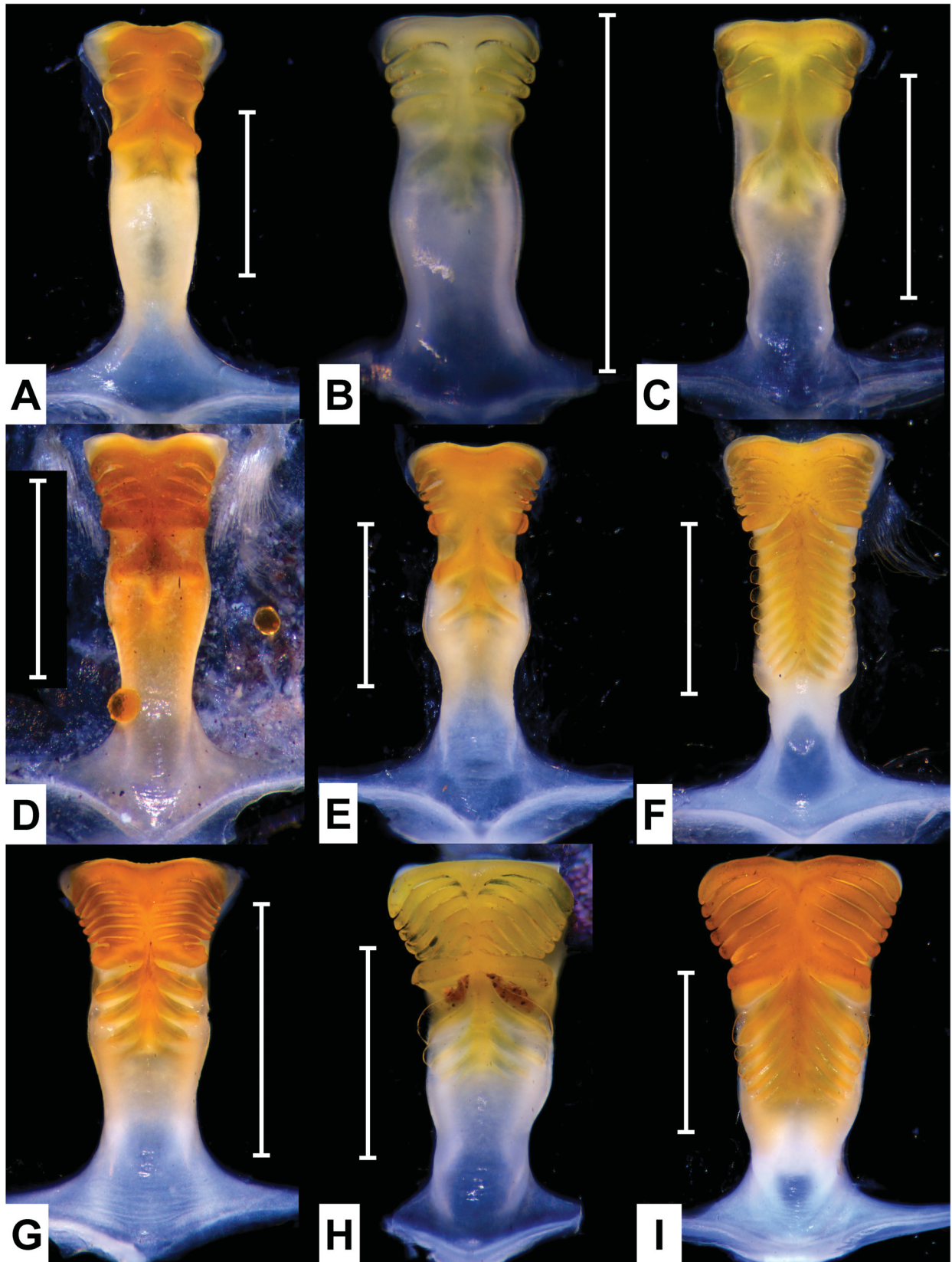


FIGURE 7. Urocardiac ossicle of the subgenus *Leptuca* species. A, *Uca subcylindrica* (NCHUZOOOL 13952, CW 15.2 mm, ♂); B, *U. terpsichores* (NCHUZOOOL 13582, CW 9.9 mm, ♂); C, *U. uruguayensis* (NCHUZOOOL 13577, CW 14.1 mm, ♂); D, *U. spinicarpa* (NCHUZOOOL 13947, CW 13.3 mm, ♀); E, *U. panacea* (NCHUZOOOL 13950, CW 14.8 mm, ♂); F, *U. pugilator* (NCHUZOOOL 13586, CW 15.9 mm, ♂); G, *U. speciosa* (NCHUZOOOL 13951, CW 12.6 mm, ♂); H, *U. umbratila* (NCHUZOOOL 13579, CW 16.2 mm, ♂); I, *U. thayeri* (NCHUZOOOL 13953, CW 19.0 mm, ♂). Scale = 1 mm.

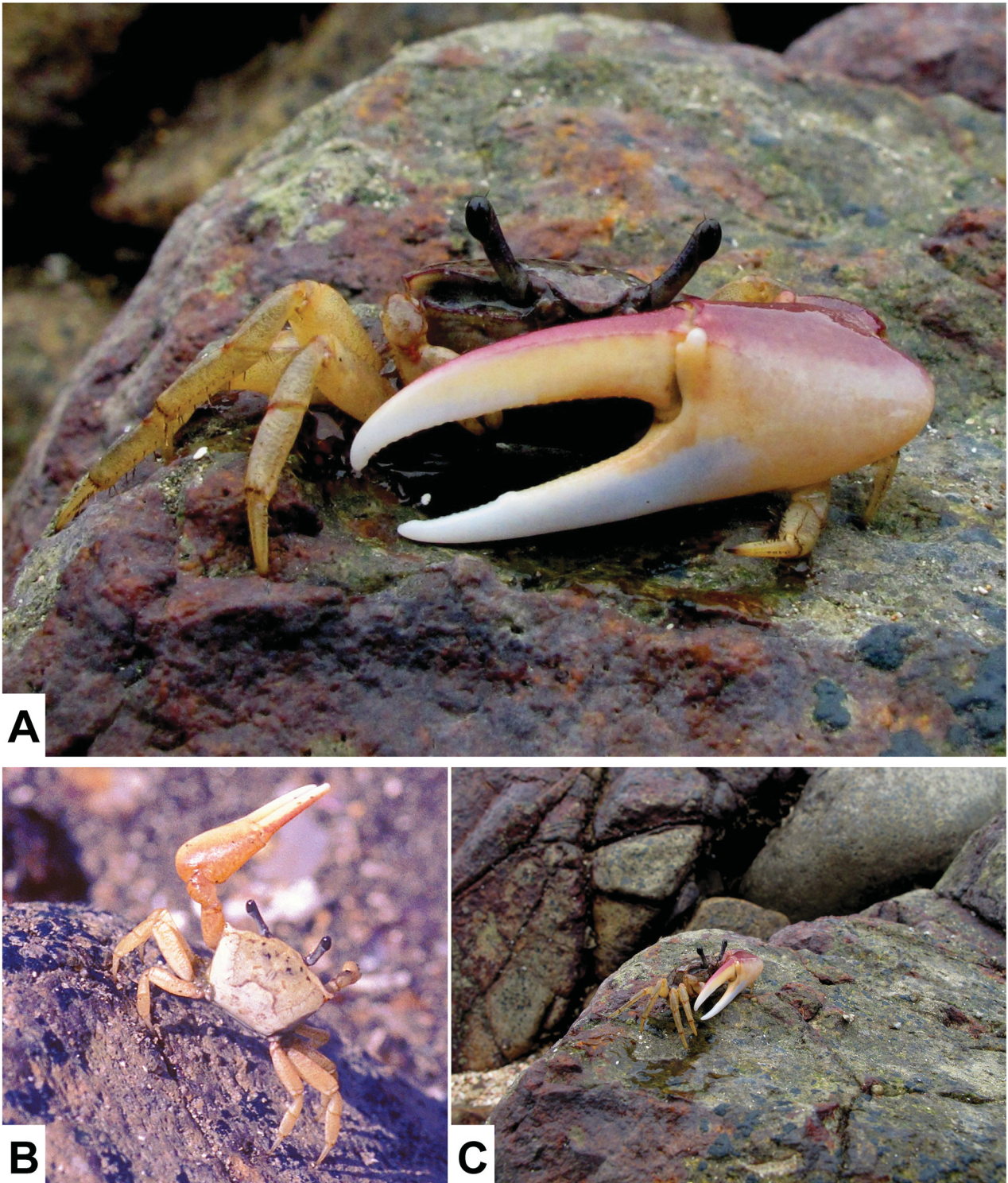


FIGURE 8. *Uca panamensis* ♂ (A, B) and its habitat (C). Photographs taken in Panamá. B, courtesy of P. Backwell.

Beinlich & von Hagen (2006) suggested that the function of the orbital armature at the inner corner of the orbital floor is to secure the eyestalk in its depressed position. This character of *U. panamensis* (Fig. 2B; Beinlich & von Hagen 2006: fig. 7j) is considered to be ancestral because it is only present in the subgenera *Uca* (Crane 1975: figs. 26E, 31D, 32J–K; Beinlich & von Hagen 2006: fig. 7d) and *Afruca* (Crane 1975: fig. 27D–F; Beinlich & von Hagen 2006: fig. 7i), and is also seen in *Ocypode* (Ocypodidae: Ocypodinae; Orchard 2012: 232–251; Wong *et al.* 2012: fig. 6b) and *Heloecius* (Heloeciidae; Beinlich & von Hagen 2006: fig. 7c). Other fiddler crabs do not have this character, or have instead evolved other structures that may secure the eyestalks (such as broadening of

the margins of the orbits, and one or more rows of tubercles, partly on raised “mounds” behind the lower orbital border) (see Beinlich & von Hagen 2006). The supposedly more plesiomorphic orbital characters of *U. panamensis* supports our hypothesis that *Petruca* **subgen. nov.** separated earlier from the other two American broad-fronted subgenera, *Minuca* and *Leptuca* (Fig. 9, see below).

The posterior extension of the major manus (Fig. 1A, C) is a unique character of the new subgenus, as previously noted by Crane (1975). The posteriorly extended rounded protuberance prevents a full lateral extension of the manus and Crane (1975: 158) suggested that males strike the ground with this part of their claw when they court producing a seismic signal. Subsequent observations (J. Christy & U. Schober unpublished), however, revealed that the claw is held well above the substrate during the entire wave. Crane also seldom saw courtship waving. Indeed, courtship waving by this species on a cobble beach near the Pacific entrance of the Panamá Canal occurs during a relatively short interval of approximately an hour beginning late in the tidal cycle well after low tide and after the crabs have fed, and on only a few days each semi-lunar breeding cycle. Males, which typically are very dark in colour at this location, lighten on the carapace to a khaki or cream colour when they court (Fig. 8B), typically from the highest point on a stone, one male per perch. Males that court from elevated positions may be seen more easily by prospective mates but also by their predators including great-tailed grackles [*Quiscalus mexicanus* (Gmelin, 1788)] and the furtive but quick grapsid crab *Geograpsus lividus* (H. Milne Edwards, 1837). When disturbed, courting males drop from their perch landing at the seam between the stone and the sand or shell hash matrix where the openings to their burrows are located.

The significance of the smooth inner and outer surfaces of the major chela (Fig. 3B) is unknown. This feature is also present in species inhabiting sandy or muddy habitats, e.g., *U. (Cranuca) inversa* (Hoffmann, 1874), *U. (Austruca) sindensis* (Alcock, 1900), *U. (Minuca) argillicola* Crane, 1941, *U. (M.) zaca* Crane, 1941, *U. (Leptuca) latimanus* (Rathbun, 1894), *U. (L.) panacea* Novak & Salmon, 1974, *U. (L.) pugilator* (Bosc, 1802), *U. (L.) subcylindrica* (Stimpson, 1859), and *U. (L.) tenuipedis* Crane, 1941 (see also Rosenberg 2001). Christy & Wada (2015) noted that the claws of male *U. pugilator* often slip when males fight and that the relatively dry sand can be difficult for a challenger to grip. They suggested a smooth claw may allow males in their role as challengers to persist in a fight at the entrance to a burrow without being thrown by the defender, which has the positional advantage and is able to grip the burrow shaft. Similarly, a defending male *U. panamensis* in a burrow under stones may have a decided positional advantage over challengers attempting to grip sand or shell hash. Too little is known about possible positional asymmetries during combat in the other species to know whether selection for proficiency in combat when males are challengers may explain why they too have smooth claws.

The brush of long stiff setae on the finger’s tips of minor cheliped (Fig. 3C, D) is a very unusual character not present in other fiddler crab taxa; and is apparently an adaptation for scraping algae from the hard rock surface (Crane 1941, 1975; Takeda & Murai 2003).

The urocardiac ossicles of gastric mill in *Petruca* **subgen. nov.** are of the simple form, i.e., with fewer transverse ridges of median teeth, especially those on the posterior tooth plate (Fig. 5; Shih 2015). Another character is the swollen median part of the stem region of the gastric mill in this subgenus (Fig. 5A), which is present in the subgenera *Xeruca*, *Afruca*, and *Uca* (Shih 2015: fig. 8A, B; Franklin Barnwell, personal communication), but not yet observed in *Minuca* (Fig. 6) and *Leptuca* (except in *U. panacea*, Fig. 7). Although the median part of the stem region of *U. panacea* is swollen, it is not wider than the median teeth in *Petruca* **subgen. nov.**, and the median teeth on the posterior tooth plate also are more complex in structure (with 5 transverse ridges) (Fig. 7E).

The urocardiac ossicles of *Minuca* show a more consistent pattern than those of *Leptuca* (Figs. 6, 7). In *U. burgersi*, *U. minax*, *U. mordax*, *U. pugnax*, *U. rapax*, *U. victoriana*, *U. cf. virens*, and *U. vocator* of *Minuca* (Fig. 6), there are 6–9 transverse ridges on the median teeth of the posterior tooth plate and 2–4 weak pairs of cusps on the stem region; except for *U. brevifrons*, which has only four ridges on the posterior tooth plate and a pair of cusps on the stem region. Species of *Leptuca* show a more diverse pattern of the urocardiac ossicles (Fig. 7), with 3–8 transverse ridges on the posterior tooth plate and 1–10 pairs of cusps on the stem region, e.g., 3 and 2 (= three ridges on posterior tooth plate and two pairs of cusps on stem region, hereinafter the same) of *U. subcylindrica*; 4 and 1 of *U. terpsichores*; 4 and 2 of *U. uruguayensis*; 5 and 1 of *U. spinicarpa*; 5 and 2 of *U. panacea*; 7 and 10 of *U. pugilator*; 8 and 3 of *U. speciosa*; 8 and 4 of *U. umbratila*; and 8 and 6 of *U. thayeri*.

Crane (1975) treated *U. panamensis* as a member of *Minuca*, in part because of the similarity of their G1 structures, especially with *U. vocator*, *U. ecuadoriensis*, and *U. pygmaea* (Crane 1975: fig. 66). The G1 of *U.*

panamensis is still unusual, with the large inner process bent at right angles to cover the flanges (Fig. 4B), a character not seen in any *Minuca* or *Leptuca* species (see Crane 1975: figs. 66–71).

Uca (Petruca) panamensis (Stimpson, 1859)

(Figs. 1–5, 8)

Gelasimus panamensis Stimpson, 1859: 63; Smith 1870: 139, pl. 4(5); Kingsley 1880: 150, fig. 10(24); Cano 1889: 235.

Uca panamensis — Nobili 1901: 49; Rathbun 1918: 412, pl. 149; Crane 1941: 204, test-fig. 4X; Garth 1948: 60; Takeda & Murai 2003: 179, fig. 1.

Uca (Minuca) panamensis — Bott 1954: 162, fig. 4, pl. 15(4); Crane 1975: 158, pl. 22A–D, figs. 46H, 66G; Prael & Guhl 1979: 147, figs. 1–2.

Uca (Leptuca) panamensis — Rosenberg 2001: 848, 852; Beinlich & von Hagen 2006: 22, 26, fig. 7j; Ng *et al.* 2008: 241.

Material examined. Neotype for *Gelasimus panamensis*, 1 ♂ (16.8 mm), USNM 1294205 (transferred from NCHUZOO 13581), Culebra Island, Panamá, coll. J. Christy, 2008; 1 ♂ (13.0 mm), NCHUZOO 13581, same data as neotype; 1 ♂ (12.6 mm), ZRC 2012.0126, Playa San Juanillo, Costa Rica, coll. Z. Jaafar, 25–27 July 2011; 4 ♂♂ (11.1–15.1 mm), 2 ♀♀ (11.7, 13.7 mm), ZRC, 1 ♂ (16.4 mm), 1 ♀ (16.8 mm), NCHUZOO 14753, San Juanillo rocky shore, Ostional, Costa Rica, coll. Z. Jaafar, 26–29 July, 2011.

Comparative material. See Appendix 1.

Remarks. *Gelasimus panamensis* was described by Stimpson (1859) from three specimens, all apparently immature, from an undisclosed site in Panamá. No figures were provided. In any case, the types are no longer extant. Like most of his material, they were almost certainly lost in the great Chicago Fire (see Evans 1967; Deiss & Manning 1981; Manning 1993; Vasile *et al.* 2005; Manning & Reed 2006). Although the species has been well treated by many authors, notably Crane (1975), since a new subgenus is established here for the species, the designation of a neotype for *Gelasimus panamensis* Stimpson, 1859, is important for longer term taxonomic stability. This is especially important given that there is now active research on *Uca*. To this effect, we here select an adult male with CW of 16.8 mm collected from Panamá as the neotype of the species. It is a recently collected specimen (USNM 1294205) that also has genetic data.

DNA analyses and discussion. A 589 bp segment of the 16S, 658 bp segment of COI and 689 bp segment of 28S, from 55 species of fiddler crabs, were amplified and aligned (Table 1). The phylogenetic tree of the combined markers was reconstructed from the BI analysis, with the support values from two methods of ML analyses (Fig. 9). To estimate the divergence time, the substitution rate of 1.17% /10⁶ year for the combined 16S and COI of marine sesarmids (cf. Schubart *et al.* 1998; Ragionieri *et al.* 2009) was applied to the p-distance between clades.

The relationships of the IWP subgenera (Fig. 9) generally agree with Shih *et al.* (2013b) and Shih (2015) and are not repeated here. The American broad-fronted species form a highly-supported main clade by three methods, with three distinct clades corresponding to three subgenera with high support at least by the BI method.

The subgenus *Petruca* **subgen. nov.** diverged earlier than the others at about 14 million years ago (mya) (p-distance of the combined 16S and COI = 16.45%). Both *Minuca* and *Leptuca* are monophyletic, are closely related and diverged at 9 mya (p-distance = 10.63%).

The six specimens of *U. panamensis* from the Pacific coasts of Costa Rica and Panamá form a highly supported clade supporting the establishment of *Petruca* **subgen. nov.** Its intraspecific K2P divergence COI is average 1.73% (0.33–2.81%), which is lower than *U. splendida* (1.86%; cf. Shih *et al.* 2012), but higher than other reported fiddler crabs. For example, the largest intraspecific divergences are 1.23% in *U. jocelynae* (recalculated from Shih *et al.* 2010); 0.98% in *U. annulipes* (Shih *et al.* 2009); about 0.83% in *U. pugnax* (cf. Sanford *et al.* 2006); 0.46% in *U. sindensis* (recalculated from Shih *et al.* 2015); about 0.32% in *U. maracoani* (cf. Wieman *et al.* 2014); and about 0.13% in *U. annulipes* (= *U. aff. annulipes*, see Shih *et al.* 2013b) from East Africa (Silva *et al.* 2010). The high genetic variability within a species may be explained by past historical or present barriers (e.g., ocean currents and salinity) affecting their larval dispersal (see López-Duarte *et al.* 2011; Shih *et al.* 2015).

Within the *Minuca* clade, *U. brevifrons* diverged earliest at 8 mya (p-distance = 9.27%), and is sister to the remaining species of this subgenus. The habitat of *U. brevifrons* is unusual. This species lives on the muddy banks of freshwater and brackish streams, sometimes even in wet forest several meters from the nearest stream (Crane 1941, 1975). Perhaps the simpler form of urocardiac ossicles of gastric mill present in this species (Fig. 6A) is an

ancestral character. Crane (1975) treated *U. brevifrons* and *U. minax* as the same “superspecies [*minax*]” but their close relationship is not supported genetically.

The taxonomy of *Uca virens* Salmon & Atsides, 1968, and *U. longisignalis* Salmon & Atsides, 1968, has been debated since the publication of the description of the two species (Salmon & Atsides 1968). By comparing the holotypes of the above two species, von Hagen (1980) confirmed them as synonyms of *U. rapax* and *U. minax*, respectively.

The synonymization of *U. virens* as *U. rapax* has been followed by later studies (e.g. Barnwell & Thurman 1984; Beinlich & von Hagen 2006). Although there are several studies still using the name of “*Uca virens*” (Rosenberg 2001; Swanson *et al.* 2013; Pérez-Mozqueda *et al.* 2014; del Castillo *et al.* 2015), the identification of the species in these studies will need to be reconfirmed (C. Thurman, pers. comm.).

Based on the allozyme study of hemolymph amylases (Barnwell & Thurman 1984) and esterase-1 and -2 (Salmon & Kettler 1987), it is apparent that there are two “forms” of *U. rapax*, corresponding to the distribution of *U. virens* and *U. rapax*. In our study based on 16S, COI and 28S markers (Fig. 9), there is a clade sister to *U. rapax* with similar morphology. Before additional studies are done to confirm whether it is actually *U. virens*, we use the name “*U. cf. virens*” for convenience. The two species diverged at 2 mya (p-distance = 2.32%), although Salmon & Kettler (1987) estimated the divergence time is 20–50 thousand years based on the allozyme data.

While previous studies considered the morphological characters of *U. virens* were within the range of *U. rapax* (Hagen 1980; Barnwell & Thurman 1984), their gastric mill structures show differences in the posterior tooth plate of urocardiac ossicles, with 8 ridges in *U. rapax* (Fig. 6F) and 6 ridges in *U. virens* (Fig. 6B). More studies of morphological characters, especially the gastric mills, are necessary to clarify the identity of *U. virens*.

Another confused species is *U. longisignalis*, which has been synonymized as *U. minax* by von Hagen (1980). Thurman (1982) considered it is a valid species because there are substantial morphological differences between the two species, a decision that has been followed by other studies thereafter. Genetically, Felder & Saton (1994) showed that the allozyme evidence did not support the hypothesis that *U. longisignalis* is different from *U. minax*. Landstorfer *et al.* (2008) and Warwick *et al.* (2009) also reported the failure to separate the two species by mitochondrial COI or nuclear internal transcribed spacer (ITS-1) markers. We included in our study specimens of the two species with typical characters of each taxon (mainly based on with or without pubescence ventrally; cf. Barnwell & Thurman 1984), but the molecular data only shows one clade (Fig. 9), therefore agreeing with earlier genetic studies. Further studies, with more complete sampling, will be necessary to clarify the taxonomy of the *U. minax* complex.

The close relationship of *U. burgersi* and *U. mordax* suggested by Salmon & Kettler (1987) is highly supported (Fig. 9). Within the *Leptuca* clade, *U. panacea*, and *U. pugilator* are closely related, with the divergence time at 2.8 mya (p-distance = 3.24%), which supports the original hypothesis that both species have diverged recently (Novak & Salmon 1974; Barnwell & Thurman 1984).

The supposed close relationship of *U. speciosa* and *U. spinicarpa* (Crane 1975; Barnwell & Thurman 1984) is not supported in this study (Fig. 9). Our study, however, agrees well with the allozyme studies (Salmon *et al.* 1979; Salmon & Kettler 1987) that the genetic distance of two species is large. *Uca speciosa* is distinct from other species genetically, although it forms a main clade, with *U. dorotheae*, *U. deichmanni*, and *U. cumulanta*. *Uca spinicarpa* is, however, closely related to the species pair, *U. thayeri* and *U. umbratila* (see below).

Crane’s (1975) subgenus *Boboruca* (= *Planuca* Bott, 1973), established for *U. thayeri* and *U. umbratila*, was synonymized with *Minuca* by Albrecht & von Hagen (1981), based on combined allozyme and morphological characters, and this has been followed by all later authors (e.g., von Hagen 1987; Salmon & Zucker 1988; Rosenberg 2001; Beinlich & von Hagen 2006; Ng *et al.* 2008). In this study, *U. thayeri* and *U. umbratila* came out clearly inside the *Leptuca* clade (Fig. 9). In the studies of Levinton *et al.* (1996) and Sturmbauer *et al.* (1996) using the 16S marker, the position of *U. umbratila* is within a “derived American clade” composed of a mixture of the subgenera *Minuca* and *Leptuca*. *Uca umbratila* is nevertheless located within *Minuca* in Landstorfer & Schubart’s (2010) study, although their sequences of COI (FN430708) and 28S (FN430719) agree well with *U. umbratila* in our study. The different conclusions are probably caused by the inclusion of 16S marker, as well as the number of species used in ingroups and outgroups. Hampton *et al.* (2014) have pointed out the unsolved relationship of *Boboruca* from the above studies. Our study gives genetic support for including *U. thayeri* and *U. umbratila* in the subgenus *Leptuca* (Fig. 9), although their morphology is closer to *Minuca*.

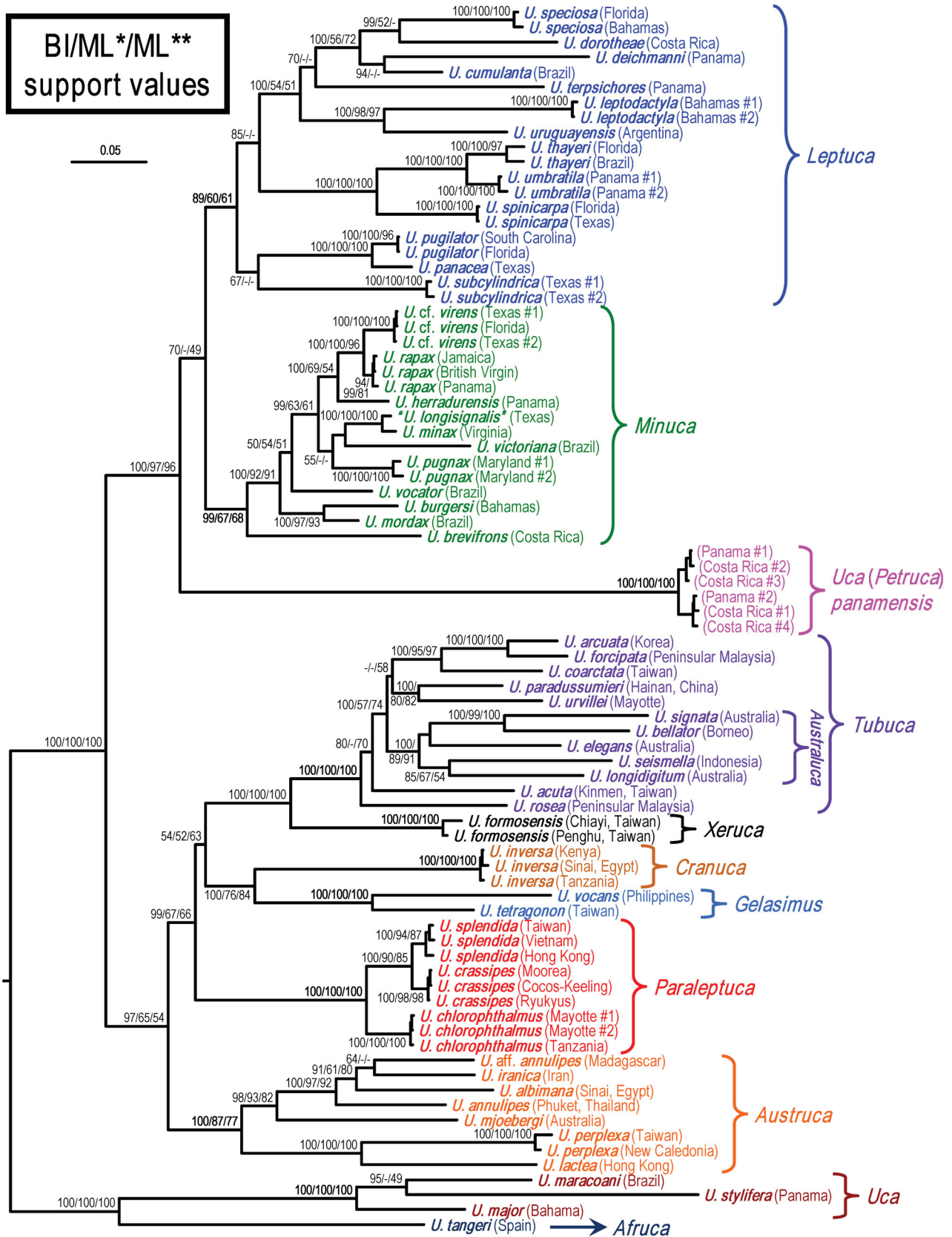


FIGURE 9. A Bayesian inference (BI) tree of *Petruca* subgen. nov. and other related subgenera, based on the combined 16S rDNA, cytochrome oxidase subunit I genes (COI) and 28S rDNA. See Table 1 for details of the specimens. Probability values at the nodes represent support values for BI, as well as two methods of maximum likelihood (ML), with ML* from RAxML and ML** from GARLI.

One of the main characters placing these two species in *Minuca* is the presence of two posterolateral striae on each side of carapace (cf. Beinlich & von Hagen 2006; Bezerra 2012). This character, however, can be variable. While there are two striae on each side of the carapace in *U. thayeri*, *U. umbratila* only has one stria (cf. Crane 1941: text-fig. 7). This has not been discussed before. The available data also implies the morphological similarity between the two species and *Minuca* is convergent.

The present study shows that *U. thayeri*, *U. umbratila*, and *U. spinicarpa* form a highly supported clade which may be the result of allopatric speciation. Whereas *U. thayeri* and *U. umbratila* diverged at 3.7 mya (p-distance = 4.34%), a well-known species pair separated after the closure of the Isthmus of Panamá around 3.1 million years ago (reviewed by Schubart *et al.* 1998; Lessios 2008), *U. spinicarpa* is endemic to the Gulf of Mexico in a more northern distribution, and it diverged from the other two species at 6.3 mya (p-distance = 7.38%). *Uca subcylindrica* is endemic along the border between Texas and northern Mexico in the Gulf of Mexico, and has been considered as an anomalous form, with unusually rounded body, striking form of G1 and hypersaline lagoonal habitat, without close alliance to other species (Crane 1975; Barnwell & Thurman 1984; Thurman 1987). Crane (1975) placed it in *Minuca*, but noted with reservation that it was close to *Leptuca*. Because some characters of *U. subcylindrica* are shared with several members of *Leptuca*, Barnwell & Thurman (1984) considered it was not suitable to retain in the homogeneous *Minuca* and transferred it to *Leptuca*. Their action is supported by our study, as *U. subcylindrica* forms a distinct clade from other species of this subgenus (Fig. 9). The simpler form of urocardiac ossicles of the gastric mill (Fig. 7A) may also be a reflection of the early split of this species from others.

Uca panamensis was placed in *Minuca* mainly by the characters of the front of the carapace and male first gonopod (Bott 1954, 1973; Crane 1975). Based on a morphological analysis, Rosenberg (2001) placed it in *Leptuca* along with *U. terpsichores*, *U. deichmanni*, *U. leptodactyla*, and *U. dorotheae*. The many unusual features of *U. panamensis* (e.g., flatter carapace, stiff setal brushes on the tips of the small chelae, the posterior extension of major manus, preference for rocky habitats etc.) suggest this classification is incorrect. The present use of new morphological characters (*viz.* the orbital armature at the inner corner of orbital floor, simple form of urocardiac ossicles of gastric mill, large and bent inner process of the G1) as well as molecular evidence using mitochondrial and nuclear markers (Fig. 9), support the hypothesis that *U. panamensis* belongs to its own subgenus (*Petruca subgen. nov.*), and diverged from other American *Minuca* and *Leptuca* at about 14 mya.

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APPENDIX 1. Comparative material examined.

Uca acuta: 1 ♂ (18.8 mm), NCHUZOOOL 13650, estuary of Wujiang R., Kinmen, Taiwan, coll. J.-H. Lee, 21 May 2005. *Uca albimana*: 1 ♂ (15.2 mm), NCHUZOOOL 13242, Nabq, Sinai, Egypt, coll. S. Barbaresi *et al.*, 14 Oct. 2004. *Uca annulipes*: 1 ♀ (12.3 mm), NCHUZOOOL 13258, Phuket, Thailand, coll. H.-T. Shih, 5 Apr. 1995. *Uca* aff. *annulipes*: 1 ♂ (9.7 mm), ZRC, southern Madagascar, coll. H.H. Tan, 29 Jan.–2 Feb. 2004. *Uca arcuata*: 1 ♀ (25.2 mm), NCHUZOOOL 13651, Ganghwa I., Incheon, South Korea, coll. K. Kim, July 2005. *Uca bellator*: 1 ♂ (16.2 mm), NCHUZOOOL 13649, Labuan, Malaysia, coll. H.-T. Shih, 24 July 2010. *Uca brevifrons*: 1 ♂ (22.1 mm), ZRC 2012.0126, Playa San Juanillo, Costa Rica, coll. Z. Jaafar, 25–27 July 2011. *Uca burgersi*: 1 ♂ (13.8 mm), 1 ♀ (11.8 mm), ZRC, Salt Pan San Salvador, Bahamas, coll. S. Lim & A. Yong, 4 Feb. 2011; 1 ♀ (13.0 mm), NCHUZOOOL 13956, Rio de Janeiro, Brazil, coll. C. Thurman *et al.*, 29 Aug. 2009. *Uca chlorophthalmus*: 1 ♂ (18.6 mm), MNHN-IU-2011-5599, 1 ♂ (19.2 mm), MNHN-IU-2011-5600, mangrove de Malamani, Mayotte, 8 Oct. 2008; 1 ♂ (18.9 mm), NCHUZOOOL 13561, Dar es Salaam, Tanzania, coll. S. Cannicci, 1 Sep. 2006. *Uca coarctata*: 1 ♀ (21.0 mm), NCHUZOOOL 13231, Citou, Penghu, Taiwan, coll. H.-T. Shih & Y.-H. Wang, 19 May 2007. *Uca crassipes*: 1 ♂ (damaged), NCHUZOOOL 13467, Okinawa, Ryukyus, Japan, Feb. 2002; 1 ♂ (17.2 mm), NCHUZOOOL 13457, Taiwan: Cingluo, Penghu, coll. H.-T. Shih, 18 Aug. 2009; 1 ♂ (14.8 mm), NCHUZOOOL 13478, Haapiti, Moorea, Polynesia, coll. J. Poupin, Dec. 2006; 1 ♂ (13.6 mm), ZRC, Cocos-Keeling Islands, coll. P.K.L. Ng, 20–24, Mar. 2011. *Uca cumulanta*: 1 ♂ (10.7 mm), NCHUZOOOL 13949, Rio de Janeiro, Brazil, coll. C. Thurman *et al.*, 29 Aug. 2009. *Uca deichmanni*: 1 ♂ (10.4 mm), NCHUZOOOL 13583, Culebra Island, Panamá, coll. J. Christy, 2008. *Uca dorotheae*: 1 ♂ (6.4 mm), ZRC, Tempisque R., Costa Rica, coll. Z. Jaafar, 22 July 2011. *Uca elegans*: 1 ♂ (19.5 mm), QM W21038, Lacrosse I., West Australia, Australia, coll. J. Short, 20 Nov. 1995. *Uca forcipata*: 1 ♂ (30.9 mm), NTOU, Johor, Malaysia, coll. P.-H. Ho, 19 July 2001. *Uca formosensis*: 1 ♀ (22.8 mm), NCHUZOOOL 13742, estuary of Bajhang R., Chiayi, Taiwan, coll. H.-T. Shih, 30 Mar. 1996; 1 ♂ (27.2 mm), NCHUZOOOL 13770, Cingluo, Penghu, Taiwan, coll. H.-T. Shih, 14 Aug. 1996. *Uca herradurensis*: 1 ♂ (16.9 mm), NCHUZOOOL 13580, Diablo Heights mangroves, Panamá, coll. J. Christy, 2008. *Uca inversa*: 1 ♂ (18.2 mm), NCHUZOOOL 13255, Dar es Salaam, Tanzania, 20 Sep. 2006; MZUF 1024 (specimen not examined, only for DNA study), Gazi, Kenya; 1 ♂ (17.4 mm), TAU SLR 1475, Sinai, Egypt, 19 May 1968. *Uca iranica*: 1 ♂ (14.4 mm), NCHUZOOOL 13245, Gavbandi, Iran, coll. E. Kamrani, July 2008. *Uca lactea*: 1 ♂ (12.0 mm), NCHUZOOOL 13250, Hong Kong, coll. B.K.K. Chan, July 2004. *Uca leptodactyla*: 2 ♂♂ (10.2–10.5 mm), ZRC, Pigeon Creek, Bahamas, coll. A. Yong, 30–31 Jan. 2011; 1 ♂ (8.5 mm), ZRC, Pigeon Creek, San Salvador, Bahamas, coll. S. Lim & A. Yong, Feb. 2011. *Uca longidigitum*: 1 ♂ (16.1 mm), QM W19274, Hervey Bay, Queensland, Australia, coll. P. Davie *et al.*, 25 Oct. 1993. *Uca major*: 1 ♀ (16.8 mm), ZRC, Pigeon Creek, Bahamas, coll. A. Curran *et al.*, Feb. 2011. *Uca maracoani*: 1 ♀ (23.3 mm), NCHUZOOOL 13955, Itapissuma, Pernambuco, Brazil, C. Thurman *et al.*, 9 June, 2009. *Uca minax*: 1 ♂ (21.5 mm), NCHUZOOOL 13938 (identified as “*U. longisignalis*”), Ingleside Cove, Corpus Christi, Texas, coll. C. Thurman, July 2000; 1 ♂ (28.6 mm), NCHUZOOOL 13939, Chesapeake Bay, Virginia, USA, coll. B.K.K. Chan, June 2005. *Uca mjoebergi*: 1 ♂ (9.9 mm), QM-W20253, Bedford I., West Australia, Australia, coll. J. Short, 19 Nov. 1994. *Uca mordax*: 1 ♀ (18.0 mm), NCHUZOOOL 13940, Rio Itapanhau, São Paulo, Brazil, coll. C. Thurman & S. Faria, 22 Oct. 2009. *Uca panacea*: 2 ♂♂ (13.3–14.8 mm), NCHUZOOOL 13950, South Padre Island, Cameron, Texas, USA, coll. C. Thurman, 6 Sep. 2000. *Uca paradussumieri*: 1 ♂ (33.7 mm), NCHUZOOOL 13381, Dongzhai, Hainan, China, coll. H.-T. Shih & J.-H. Lee, 23 June 2004. *Uca perplexa*: 1 ♂ (17.2 mm), NTOU, Dulanwan, Taitung, Taiwan, coll. P.-H. Ho, 7 pr. 2001; 1 ♂ (10.5 mm), NCHUZOOOL 13573, Ouano Bay, New Caledonia, coll. B. Richer de Forge, 30 Nov. 2008. *Uca pugilator*: 1 ♂ (15.9 mm), 1 ♀ (15.0 mm), NCHUZOOOL 13586, Georgetown, South Carolina, USA, coll. R. Brodie, Sep. 2004; 1 ♂ (21.2 mm) ASIZ, Seahorse Key, Florida, USA, coll. H.-C. Liu, 20 Nov. 2005. *Uca pugnax*: 1 ♂ (15.2 mm), 1 ♀ (11.7 mm), NCHUZOOOL 13941, Assateague Island, Maryland, USA, coll. C. Thurman, 30 May 2000. *Uca rapax*: 1 ♂ (23.4 mm), NCHUZOOOL 13942, Trelawny, Jamaica, coll. C. D. Schubart, 22 Mar. 2003; 1 ♂ (16.5 mm), NCHUZOOOL 13943, Paraquita Bay, British Virgin, coll. A. Deacon, 6 Aug. 2002; 1 ♂ (19.9 mm), NCHUZOOOL 13944, Bocas del Toro, Panamá, coll. S. De Grave, 9 Aug. 2005. *Uca rosea*: 1 ♂ (26.3 mm), NTOU, Johor, Malaysia, coll. P.-H. Ho, 19 July 2001. *Uca seismella*: ZRC 2000.2059 (specimen not examined, only for DNA study), West Papua, Indonesia. *Uca signata*: 1 ♂ (17.5 mm), QM W19211, Hucks Landing, Queensland, Australia, coll. P. Davie *et al.*, 28 Oct. 1993. *Uca speciosa*: 1 ♂ (12.6 mm), 1 ♀ (11.4 mm), NCHUZOOOL 13951, Alligator Point, Florida, coll. C. Thurman, 14 Mar. 2001; 1 ♂ (13.2 mm), ZRC, Pigeon Creek, San Salvador, Bahamas, coll. A. Yong *et al.*, 4 Feb. 2011. *Uca splendida*: 1 ♂ (14.4 mm), NCHUZOOOL 13368, Tai Tam, Hong Kong, coll. Y.-C. Fang, 27 July 2006; 1 ♂ (15.5 mm), NCHUZOOOL 13448, Nha Trang, Vietnam, coll. I.H. Chen & K.J.H. Wong, 24 Nov. 2010. *Uca spinicarpa*: 1 ♀ (13.3 mm), NCHUZOOOL 13947, Money Bayou, Gulf County, Florida, USA, coll. C. Thurman, 14 Mar. 2001; 1 ♂ (18.6 mm), ZRC 2009.0295, Boliver Island, Texas, USA, coll. J.C.Y. Lai, 11 June 2008. *Uca stylifera*: 1 ♂ (21.9 mm), NCHUZOOOL 13578, Rodman, Panamá, coll. J. Christy, 2008. *Uca subcylindrica*: 2 ♂♂ (13.7–15.2 mm), 1 ♀ (11.2 mm), NCHUZOOOL 13952, Kingsville, Texas, USA, coll. C. Thurman, July 2000. *Uca tangeri*: 1 ♀ (31.3 mm), NCHUZOOOL 13585, Puerto de Santa María, Cádiz, Spain, coll. P. Fernández, 23 May 2007. *Uca tersichores*: 2 ♂♂ (~9.4 mm, damaged; 9.9 mm), NCHUZOOOL 13582, Culebra Island, Panamá, coll. J. Christy, 2008. *Uca tetragonon*: 1 ♂ (12.8

mm), TMCD CHCD 526, Kenting, Pingtung, Taiwan, coll. H.-C. Liu & C.-H. Wang, 23 Sep. 1994. *Uca thayeri*: 1 ♂ (19.0 mm), 1 ♀ (16.3 mm), NCHUZOOL 13953, Hutchinson Island, Fort Pierce, Florida, USA, coll. C. Thurman, 6 Aug. 2003; 1 ♀ (23.4 mm), NCHUZOOL 13954, Anchieta, Espírito Santo, Brazil, coll. M. Tavares *et al.*, 3 Nov. 2006. *Uca umbratila*: 2 ♂♂ (16.2–21.0 mm), NCHUZOOL 13579, Diablo Heights mangroves, Panamá, coll. J. Christy, 2008. *Uca uruguayensis*: 1 ♂ (14.1 mm), 1 specimen not examined (only for DNA study), NCHUZOOL 13577, Samborombón, Argentina, coll. P.D. Ribeiro, 17 Mar. 2001. *Uca urvillei*: 1 ♂ (29.7 mm), ZRC 1999.1107, Poroani, Mayotte, 23 July 1998. *Uca cf. virens* (identified as *U. rapax*): 2 ♂♂ (19.5–18.6 mm), NCHUZOOL 13584, Ingleside Cove, Corpus Christi Bay, Texas, USA, coll. C. Thurman, 20 July 2000; 1 ♂ (17.0 mm), NCHUZOOL 13946, Money Bayou, Gulf County, Florida, USA, coll. C. Thurman, 14 Mar. 2001. *Uca victoriana*: 1 ♀ (12.2 mm), NCHUZOOL 13945, São Félix, Bahia, Brazil, coll. C. Thurman *et al.*, 5 Aug. 2009. *Uca vocans*: 1 ♂ (20.2 mm), NCHUZOOL 13667, 1 ♂ (23.1 mm), NCHUZOOL 13205, Bohol, Philippines, coll. H.-T. Shih, 2 Sep. 2003. *Uca vocator*: 1 ♀ (21.9 mm), NCHUZOOL 13948, Fortaleza, Ceara, Brazil, coll. C. Thurman & S. Faria, 8 June 2010.