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The nomenclatural status of the two “spiny-wristed” fiddler crabs: *Uca spinicarpa* Rathbun, 1900, and *U. hesperiae* Crane, 1975 (Crustacea: Brachyura: Ocypodidae)

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Abstract

A secondary homonymy is documented for *Gelasimus* [= *Uca*] *tetragonon* var. *spinicarpa* Kossmann, 1877 (a species from the Red Sea), and *Uca spinicarpa* Rathbun, 1900 (a species from the Gulf of Mexico). Although Kossmann’s usage of the nomen *spinicarpa* has chronological priority, a reversal of precedence is required by Article 23.9 of the Code since Kossmann’s use has not been applied as a valid name since the original publication in 1877, while Rathbun’s use of the name has been applied over 50 times in the last half century. The species Kossmann was most likely referring to is today known as *Uca hesperiae* Crane, 1975, a name which may be retained in light of the reversal of precedence.

Key words: *Uca vocans* complex, fiddler crabs, taxonomy, Kossmann

Introduction

The spiny-wristed fiddler crab, *Uca spinicarpa* Rathbun, 1900, is endemic to the Gulf of Mexico (Hopkins & Thurman 2010). The name was first introduced by Rathbun as part of a taxonomic key for North American grapsoid crabs, with characters derived from a specimen collected at Galveston, Texas. It was first fully described in her monograph on the grapsoid crabs of America (Rathbun 1918). There has rarely been any confusion or disagreement over the status of this species, and although Crane (1975) treated it as a subspecies of the closely allied *U. speciosa* (Ives, 1891), it has since been restored to specific status (Salmon *et al.* 1979; Barnwell & Thurman 1984). The type specimen is no longer extant, but Bezerra & Coelho (2010) recently redescribed this species in some detail. No other names have been applied to this species, and as its identity is clear, there is no reason at this time for a neotype designation.

Major revisions by Bott (1973) and Crane (1975) resulted in different phylogenetic groupings of *Uca* species, with each author using a different suite of generic (Bott) or subgeneric (Crane) names. Rosenberg (2001) supported recognition of most of Crane’s subgenera, although with many of Bott’s names having priority. Beinlich & von Hagen (2006) proposed a revised system of classification, recognizing some supraspecific taxa and synonymizing others, and this was used as a basis for the slightly modified synthesis used by Ng *et al.* (2008). According to this system the Atlantic species *Uca speciosa* (Ives, 1891) and *Uca spinicarpa* Rathbun, 1900, are both in the subgenus *Leptuca*.

The western calling fiddler crab, *Uca hesperiae* Crane, 1975, is the westernmost of the *Uca vocans* species-complex (*sensu* Crane 1975), viz. *U. borealis* Crane, 1975, *U. dampieri* Crane, 1975, *U. hesperiae* Crane, 1975, *U. neocultrimana* Bott, 1973, *U. vocans* (Linnaeus, 1758), *U. vomeris* McNeill, 1920, and the recently described *U. jocelynae* Shih, Naruse & Ng, 2010. These species are currently placed in the subgenus *Gelasimus* (see Ng *et al.*, 2008). Crane originally treated all of these as subspecies of *U. vocans*, but they have subsequently been given full species status (Rosenberg 2001; Beinlich & von Hagen 2006; Ng *et al.* 2008). With the exception of *U. hesperiae*, all are found predominantly in and around the western Pacific Ocean, with only *U. vocans* extending into the eastern part of the Indian Ocean. *Uca hesperiae* is found throughout the Indian Ocean, ranging from eastern South

Africa and Madagascar, along the east African coast, through India, to as far east as the western Malay peninsula where it overlaps with *U. vocans* (Crane, 1975). Prior to Crane, what is now *U. hesperiae* had been recorded as either *U. vocans* (Linnaeus, 1758), *U. marionis* (Desmarest, 1825), *U. cultrimana* (Adams & White, 1848) or *U. nitida* (Dana, 1851). *Uca marionis* and *U. cultrimana* are now regarded as junior synonyms of *U. vocans* sensu stricto, while *U. nitida* is a junior homonym of the fossil *Gelasimus nitidus* Desmarest, 1822.

Kossmann (1877), in his work on Crustacea from the Red Sea, described two new varieties of fiddler crabs: *Gelasimus* [= *Uca*] *annulipes* var. *albimana* and *Gelasimus tetragonon* var. *spinicarpa*. Kossmann's varieties were largely viewed as synonyms of the nominal species by other researchers around that time (e.g., De Man 1880; Kingsley 1880; Miers 1884, 1886). In her monograph on fiddler crabs, Crane (1975) treated *Gelasimus annulipes* var. *albimana* (Kossmann, 1877) as a junior synonym of *U. annulipes* (H. Milne Edwards, 1837), although Lewinsohn (1977) felt that *U. albimana* was morphologically distinct. Recent genetic and morphological work has given *Uca albimana* (Kossmann, 1877) full specific status (Shih *et al.* 2009; Naderloo *et al.* 2010).

As for Kossmann's "var. *spinicarpa*", Crane (1975: 80) said the following:

"Type Material of *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877. Red Sea. In the Rijksmuseum van Natuurlijk Historie, Leiden, under cat. no. 1493, is a single male with the following label: "*Uca tetragonon* (Herbst) var. *spinicarpus* Kossm. Kossmann 1880. Roode Zee." Measurements in mm: length 12; propodus 23. Examination shows this crab to be a young example of *Uca vocans*, leptochealous, with the claw probably regenerated. On the basis of this specimen, apparently identified by Kossmann and presented by him to the museum, the variety is here referred to the synonymy of *U. vocans*."

Although Crane did not specifically assign Kossmann's *spinicarpa* as a synonym of any particular one of her subspecies of *U. vocans*, nevertheless, based on her work it can only be *U. vocans hesperiae*. This is essentially the same conclusion of Lewinsohn (1977), Fransen *et al.* (1997) and Ng *et al.* (2008), all of whom suggest (either implicitly or explicitly) the likely synonymy of *Gelasimus tetragonon* var. *spinicarpa* (Kossmann, 1877) with *Uca vocans hesperiae* Crane, 1975. Although Rathbun (1897) had already recognized the nomenclatural priority of *Uca* over *Gelasimus* prior to her description of *U. spinicarpa*, her use of the specific name *spinicarpa* is a case of secondary homonymy because the original uses were with different generic group names (ICZN Articles 53.3, 57.3). If Crane's own assessment of the specimen *Gelasimus tetragonon* var. *spinicarpa* (Kossmann, 1877) is correct, that name would be the senior subjective synonym for *Uca vocans hesperiae* Crane, 1975. Although *U. spinicarpa* Kossmann and *U. spinicarpa* Rathbun are now attributed to different subgenera (the former to *Gelasimus* Latreille, 1817 and the latter to *Leptuca* Bott, 1973), this has no relevance to the homonymy (ICZN Article 57.4).

Thankfully for the sake of nomenclatural clarity, the lack of historical recognition for *Gelasimus tetragonon* var. *spinicarpa* (Kossmann, 1877) allows for a reversal of precedence. Following the International Code of Zoological Nomenclature, Article 23.9.1 states that "the prevailing usage must be maintained" when two conditions are met. First, "the senior synonym or homonym has not been used as a valid name after 1899," and second, "the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years." As for the first condition, *Gelasimus tetragonon* var. *spinicarpa* (Kossmann, 1877) has only been mentioned in the literature five times since its original publication:

(1) Crane (1975: 80), as already quoted above, regarded *Gelasimus tetragonon* var. *spinicarpa* (Kossmann, 1877) as a junior subjective synonym of *Uca vocans* (Linnaeus, 1758). Whether Crane was correct or not in her assessment, this does not represent a valid use of *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877.

(2) Lewinsohn (1977: 59), in treating *Uca tetragonon* (Herbst, 1790), lists Kossmann's name in the synonymy of *Uca tetragonon* (Herbst, 1790) but clearly does not regard it as synonymous when he wrote "non *Gelasimus tetragonon* var. *spinicarpa*—Kossmann, 1877: 52. Nach Crane (1975: 80) *U. vocans hesperiae* juv." This statement shows that Lewinsohn believed or suspected that *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, was conspecific and synonymous with *Uca* (*Gelasimus*) *vocans hesperiae* Crane, 1975. Despite the seniority of Kossmann's name, Lewinsohn (1977: 45, 58) nevertheless used the name *Uca vocans hesperiae* Crane, 1975, in the rest of his paper. Precisely why he chose to use Crane's junior name over Kossmann's senior one is unknown, but whatever the reason, this does not constitute a valid use of *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877.

(3) Yamaguchi (1994: 181), in his catalog of *Uca* specimens in the Leiden and British museums, listed the specimen studied by Crane from the Leiden museum (above) under the name *Uca vocans*: “1493 (♂ 1: R 1). Syntype of *Gelasimus tetragonon spinicarpa* Kossmann. Red Sea, 1880, R. Kossmann.” This is not a valid use of Kossmann’s name as he clearly treated it as a junior synonym of *Uca vocans*.

(4) Fransen *et al.* (1997: 152), in their catalog of Leiden types, list under the name *Uca vocans hesperiae* Crane, 1975, an extant syntype of *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, under its synonymy. Regarding this specimen they also state:

“Lewinsohn, 1977b: 58, 59, mentioned the specimen in the synonymy of *Uca tetragonon* as belonging to *Uca vocans hesperiae* Crane, 1975, probably because *U. vocans hesperiae* is the only subspecies of *Uca vocans* that has been reported from the Red Sea. If Crane is right, and if the two other syntypes of *U. tetragonon spinicarpa* also are *Uca vocans hesperiae*, the species group name *hesperiae* Crane, 1975, falls as a junior synonym of *spinicarpa* Kossmann, 1877.”

What is most important in this statement is the uncertainty of the authors. With two of the three syntype specimens unexamined, the synonymy of *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, and *Uca vocans hesperiae* Crane, 1975, is left as an open question, and their caveat about whether or not “Crane is right” means that this paper also cannot be regarded as a valid use of the name *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877.

(5) Ng *et al.* (2008: 240) directly list *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, as a junior subjective synonym of *Uca (Gelasimus) tetragonon* (Herbst, 1790). This is clearly not using Kossmann’s taxon as a valid name.

Thus, of the only five direct mentions of Kossmann’s name since 1899 (in fact, the only direct mentions since the original publication in 1877), not one uses *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, as a valid name, despite hints of its potential seniority over *Uca vocans hesperiae* Crane, 1975.

As for the second requirement of Article 23.9, the Appendix contains a list of over 50 publications between 1964 and 2013, from well over 10 authors, which refer to *Uca spinicarpa* Rathbun, 1900 (sometimes without specific authority, but always clearly with the intended usage toward the species from the Gulf of Mexico).

With both requirements of Article 23.9 met, the Code requires a reversal of priority, with *Uca spinicarpa* Rathbun, 1900, a **nomen protectum**, and *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, a **nomen oblitum**. Because the species have been considered congeneric since 1899, the requirement for replacement of the junior homonym to be referred to the Commission (ICZN Article 23.9.5) does not apply.

This action retains the prevailing usage of *Uca (Leptuca) spinicarpa* Rathbun, 1900, for the species from the Gulf of Mexico, and removes the availability of *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, for future use. Should *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, be proven to be a synonym of *Uca (Gelasimus) hesperiae* Crane, 1975, (as is currently suspected), the principle of priority would no longer apply, and Crane’s name would still be maintained for the species from the Indian Ocean and Red Sea.

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References

- Barnwell, F.H. & Thurman II, C.L. (1984) Taxonomy and biogeography of fiddler crabs (Ocypodidae: genus *Uca*) of the Atlantic and Gulf coasts of eastern North America. *Zoological Journal of the Linnean Society*, 81, 23–87.
- Beinlich, B. & von Hagen, H.-O. (2006) Materials for a more stable subdivision of the genus *Uca* Leach. *Zoologische mededelingen*, 80, 9–32.
- Bezerra, L.E.A. & Coelho, P.A. (2010) Redescription of the fiddler crab *Uca spinicarpa* Rathbun, 1900 (Decapoda: Ocypodidae). *Latin American Journal of Aquatic Research*, 38, 270–273.

- Bott, R. (1973) Die verwandtschaftlichen Beziehungen der *Uca*-Arten (Decapoda: Ocypodidae). *Senckenbergiana biologica*, 54, 315–325.
- Crane, J. (1975) *Fiddler Crabs of the World: Ocypodidae: Genus Uca*. Princeton University Press, Princeton, NJ.
- Dana, J.D. (1851) Conspectus Crustaceorum quæ in Orbis Terrarum circumnavigatione, Carolo Wilkes e Classe Reipublicæ Foederatæ Duce, lexit et descripsit. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 5, 247–254.
- De Man, J.G. (1880) On some species of *Gelasimus* Latr. and *Macrophthalmus* Latr. *Notes from the Leyden Museum*, 2, 67–72.
- Desmarest, A.-G. (1822) Les crustacés proprement dits. In: Brongniart, A. & Desmarest, A.-G. (Eds.), *Histoire Naturelle des Crustacés Fossiles, sous les Rapports Zoologiques et Géologiques*. Levrault, F.-G., Paris, pp. 67–142.
- Desmarest, A.-G. (1825) *Considérations Générales sur la Classe des Crustacés, et description des espèces de ces animaux, qui vivent dans la mer, sur les côtes, ou dans les eaux douces de la France*. F. J. Levrault, Paris.
- Fransen, C.H.J.M., Holthuis, L.B. & Adema, J.P.H.M. (1997) Type-catalogue of the Decapod Crustacea in the collections of the Nationaal Natuurhistorisch Museum, with appendices of pre-1900 collectors and material. *Zoologische Verhandelingen*, 311, i–xvi, 1–344.
- Hopkins, M.J. & Thurman II, C.L. (2010) The geographic structure of morphological variation in eight species of fiddler crabs (Ocypodidae: genus *Uca*) from the eastern United States and Mexico. *Biological Journal of the Linnean Society*, 100, 248–270.
- Ives, J.E. (1891) Crustacea from the northern coast of Yucatan, the harbor of Vera Cruz, the west coast of Florida and the Bermuda Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 43, 176–207.
- Kingsley, J.S. (1880) Carcinological notes, No. II.—Revision of the Gelasimi. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1880, 135–155.
- Kossmann, R. (1877) *Zoologische Ergebnisse einer Reise in die Küstengegenden des Roten Meeres III. Crustacea*. Wilhelm Engelmann, Leipzig.
- Latreille, P.A. (1817) Gélasime, *Gelasimus* (Buffon). In: *Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'Agriculture, à l'économie rurale et domestique, à l'médecine, etc. Par une société de naturalistes et d'agriculteurs*. Deterville, Paris, pp. 517–520.
- Lewinsohn, C. (1977) Die Ocypodidae des Roten Meeres (Crustacea Decapoda, Brachyura). *Zoologische Verhandelingen*, 152, 45–84.
- Linnaeus, C. (1758) *Systema Naturæ* (10th ed. Vol. I).
- Miers, E.J. (1884) Collections from the Western Indian Ocean: Crustacea. In: *Report of the zoological collections made in the Indo-Pacific Ocean during the voyage of the H.M.S. 'Alert,' 1881–1882*, London, pp. 513–575.
- Miers, E.J. (1886) Report on the Brachyura collected by H.M.S. Challenger during the years 1873–76. In: *H.M.S. Challenger Reports*, London, pp. 1–362.
- Milne Edwards, H. (1837) *Historie naturelle des crustacés comprenant l'anatomie, la physiologie et la classification des ces animaux* (Vol. 2), Paris.
- Naderloo, R., Türkay, M. & Chen, H.-L. (2010) Taxonomic revision of the wide-front fiddler crabs of the *Uca lactea* group (Crustacea: Decapoda: Brachyura: Ocypodidae) in the Indo-West Pacific. *Zootaxa*, 2500, 1–38.
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*. Supplement 17, 1–296.
- Rathbun, M.J. (1897) A revision of the nomenclature of the Brachyura. *Proceedings of the Biological Society of Washington*, 11, 153–167.
- Rathbun, M.J. (1918) The grapsoid crabs of America. *United States National Museum Bulletin*, 97, 1–461.
- Rosenberg, M.S. (2001) The systematics and taxonomy of fiddler crabs: A phylogeny of the genus *Uca*. *Journal of Crustacean Biology*, 21, 839–869.
- Salmon, M., Ferris, S.D., Johnston, D., Hyatt, G.W. & Whitt, G.S. (1979) Behavioral and biochemical evidence for species distinctiveness in the fiddler crabs, *Uca speciosa* and *U. spinicarpa*. *Evolution*, 33, 182–191.
- Shih, H.-T., Kamrani, E., Davie, P.J.F. & Liu, M.-Y. (2009) Genetic evidence for the recognition of two fiddler crabs, *Uca iranica* and *U. albimana* (Crustacea: Brachyura: Ocypodidae), from the northwestern Indian Ocean, with notes on the *U. lactea* species-complex. *Hydrobiologia*, 635, 373–382.
- Shih, H.-T., Naruse, T. & Ng, P.K.L. (2010) *Uca jocelynae* sp. nov., a new species of fiddler crab (Crustacea: Brachyura: Ocypodidae) from the Western Pacific. *Zootaxa*, 2337, 47–62.
- Yamaguchi, T. (1994) Fiddler crabs of the genus *Uca* in the collections of three natural history museums in Europe. I. The specimens held by the Nationaal Natuurhistorisch Museum, Leiden and the National History Museum, London. *Calanus. Bulletin of the Aitsu Marine Biological Station*, 11, 151–189.

APPENDIX. Publications using *Uca spinicarpa* Rathbun, 1900 (or an unambiguous derivative), in the last 50 years (1964 through 2013)

- Abele, L.G. & Kim, W. (1986) *An Illustrated Guide to the Marine Decapod Crustaceans of Florida*. State of Florida Department of Environmental Regulation, Tallahassee, FL, 196 pp.
- Balbort, L. & Thurman II, C.L. (1997) Comparison of locomotor rhythms in sympatric *Uca* from the western Gulf of Mexico. *American Zoologist*, 37, 186A.
- Barnwell, F.H. (1986) Fiddler crabs of Jamaica (Decapoda, Brachyura, Ocypodidae, genus *Uca*). *Crustaceana*, 50, 146–165.
<http://dx.doi.org/10.1163/156854086x00179>
- Barnwell, F.H. & Thurman II, C.L. (1984) Taxonomy and biogeography of fiddler crabs (Ocypodidae: genus *Uca*) of the Atlantic and Gulf coasts of eastern North America. *Zoological Journal of the Linnean Society*, 81, 23–87.
<http://dx.doi.org/10.1111/j.1096-3642.1984.tb02558.x>
- Beinlich, B. & von Hagen, H.-O. (2006) Materials for a more stable subdivision of the genus *Uca* Leach. *Zoologische mededelingen*, 80, 9–32.
- Bezerra, L.E.A. & Coelho, P.A. (2009) Intraspecific variation in preserved specimens of the fiddler crabs *Uca panacea* and *Uca pugilator* (Decapoda: Ocypodidae). *Zoologia*, 26, 175–182.
<http://dx.doi.org/10.1590/s1984-46702009000100024>
- Bezerra, L.E.A. & Coelho, P.A. (2010) Redescription of the fiddler crab *Uca spinicarpa* Rathbun, 1900 (Decapoda: Ocypodidae). *Latin American Journal of Aquatic Research*, 38, 270–273.
<http://dx.doi.org/10.3856/vol38-issue2-fulltext-12>
- Castiglioni, D.d.S. & Negreiros-Fransozo, M.L. (2006) Ciclo reprodutivo do caranguejo violinista *Uca rapax* (Smith) (Crustacea, Brachyura, Ocypodidae) habitante de um estuário degradado em Paraty, Rio de Janeiro, Brasil. *Revista Brasileira De Zoologia*, 23, 331–339.
<http://dx.doi.org/10.1590/s0101-81752006000200004>
- Costa, T.M. & Negreiros-Fransozo, M.L. (2002) Population biology of *Uca thayeri* Rathbun, 1900 (Brachyura, Ocypodidae) in a subtropical South American mangrove area: Results from transect and catch-per-unit-effort techniques. *Crustaceana*, 75, 1201–1218.
<http://dx.doi.org/10.1163/156854002321518144>
- Costa, T.M., Silva, S.M.J. & Negreiros-Fransozo, M.L. (2006) Reproductive pattern comparison of *Uca thayeri* Rathbun, 1900 and *U. uruguayensis* Nobili, 1901 (Crustacea, Decapoda, Ocypodidae). *Brazilian Archives of Biology and Technology*, 49, 117–123.
<http://dx.doi.org/10.1590/s1516-89132006000100014>
- Crane, J. (1975) *Fiddler Crabs of the World: Ocypodidae: Genus Uca*. Princeton University Press, Princeton, NJ, 736 pp.
- deRivera, C.E. & Vehrencamp, S.L. (2001) Male versus female mate searching in fiddler crabs: A comparative analysis. *Behavioral Ecology*, 12, 182–191.
<http://dx.doi.org/10.1093/beheco/12.2.182>
- Di Benedetto, M. & Masunari, S. (2009) Estrutura populacional de *Uca maracoani* (Decapoda, Brachyura, Ocypodidae) no Baixo Mirim, Baía de Guaratuba, Paraná. *Iheringia Série Zoologia*, 99, 381–389.
<http://dx.doi.org/10.1590/s0101-81752005000400025>
- Felder, D.L. & Staton, J.L. (1994) Genetic differentiation in trans-Floridian species complexes of *Sesarma* and *Uca* (Decapoda: Brachyura). *Journal of Crustacean Biology*, 14, 191–209.
<http://dx.doi.org/10.2307/1548900>
- Fotheringham, N. & Brunenmeister, S.L. (1975) *Common Marine Invertebrates of the Northwestern Gulf Coast*. Gulf Publishing Company, Houston, TX, 197 pp.
- Hasek, B.E. & Rabalais, N.N. (2001) Settlement patterns of brachyuran megalopae in a Louisiana estuary. *Estuaries*, 24, 796–807.
<http://dx.doi.org/10.2307/1353171>
- Hopkins, M.J. & Thurman II, C.L. (2010) The geographic structure of morphological variation in eight species of fiddler crabs (Ocypodidae: genus *Uca*) from the eastern United States and Mexico. *Biological Journal of the Linnean Society*, 100, 248–270.
<http://dx.doi.org/10.1111/j.1095-8312.2010.01402.x>
- Johnson, P.T.J. (2003) Biased sex ratios in fiddler crabs (Brachyura, Ocypodidae): A review and evaluation of the influence of sampling method, size class, and sex-specific mortality. *Crustaceana*, 76, 559–580.
<http://dx.doi.org/10.1163/156854003322316209>
- Lim, S.S.L. (2006) Fiddler crab burrow morphology: How do burrow dimensions and bioturbative activities compare in sympatric populations of *Uca vocans* (Linnaeus, 1758) and *U. annulipes* (H. Milne Edwards, 1837)? *Crustaceana*, 79, 525–540.
<http://dx.doi.org/10.1163/156854006777584241>
- Lim, S.S.L. & Diong, C.H. (2003) Burrow-morphological characters of the fiddler crab, *Uca annulipes* (H. Milne Edwards, 1837) and ecological correlates in a lagoonal beach on Pulau Hantu, Singapore. *Crustaceana*, 76, 1055–1069.
<http://dx.doi.org/10.1163/156854003322753411>

- Litulo, C. (2005a) Population biology of the fiddler crab *Uca annulipes* (Brachyura: Ocypodidae) in a tropical East African mangrove (Mozambique). *Estuarine, Coastal and Shelf Science*, 62, 283–290.
<http://dx.doi.org/10.1016/j.ecss.2004.09.009>
- Litulo, C. (2005b) Population structure and reproductive biology of the fiddler crab *Uca urvillei* (Brachyura: Ocypodidae) in Maputo Bay (south Mozambique). *Journal of Natural History*, 39, 2307–2318.
<http://dx.doi.org/10.1080/00222930500101688>
- Mace, D.S. Jr. & McGraw, L. Jr. (1985) A confirmation of the occurrence of *Uca minax* LeConte (Ocypodidae) in Texas. *Southern Naturalist*, 30, 148.
<http://dx.doi.org/10.2307/3670669>
- Mangum, C.P. & Greaves, J. (1996) Hemocyanins of the genus *Uca*: Structural polymorphisms and native oligomers. *Journal of Experimental Marine Biology and Ecology*, 199, 1–15.
[http://dx.doi.org/10.1016/0022-0981\(95\)00154-9](http://dx.doi.org/10.1016/0022-0981(95)00154-9)
- Mouton, E.C. Jr. & Felder, D.L. (1995) Reproduction of the fiddler crabs *Uca longisignalis* and *Uca spinicarpa* in a Gulf of Mexico salt marsh. *Estuaries*, 18, 469–481.
<http://dx.doi.org/10.2307/1352365>
- Mouton, E.C. Jr. & Felder, D.L. (1996) Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. *Estuaries*, 19, 51–61.
<http://dx.doi.org/10.2307/1352651>
- Nabout, J.C., Bini, L.M. & Diniz-Filho, J.A.F. (2010) Global literature of fiddler crabs, genus *Uca* (Decapoda, Ocypodidae): Trends and future directions. *Iheringia Série Zoologia*, 100, 463–468.
<http://dx.doi.org/10.1590/s0073-47212010000400019>
- Nabout, J.C., Terribile, L.C., Bini, L.M. & Diniz-Filho, J.A.F. (2010) Phylogenetic autocorrelation and heritability of geographic range size, shape and position of fiddler crabs, genus *Uca* (Crustacea, Decapoda). *Journal of Zoological Systematics and Evolutionary Research*, 48, 102–108.
<http://dx.doi.org/10.1111/j.1439-0469.2009.00531.x>
- Nickol, B.B., Heard, R.W. Jr. & Smith, N.F. (2002) Acanthocephalans from crabs in the southeastern US, with the first intermediate hosts known for *Arhythmorhynchus frassoni* and *Hexaglandula corynosoma*. *Journal of Parasitology*, 88, 79–83.
[http://dx.doi.org/10.1645/0022-3395\(2002\)088\[0079:afcits\]2.0.co;2](http://dx.doi.org/10.1645/0022-3395(2002)088[0079:afcits]2.0.co;2)
- Pérez-Campos, R.A., Rodríguez-Canul, R., Pérez-Vega, J.A., González-Salas, C. & Guillén-Hernández, S. (2012) High serotonin levels due to the presence of the acanthocephalan *Hexaglandula corynosoma* could promote changes in behavior of the fiddler crab *Uca spinicarpa*. *Diseases of Aquatic Organisms*, 99, 49–55.
<http://dx.doi.org/10.3354/dao02453>
- Powers, L.W. (1977) A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico. *Contributions in Marine Science*, 20, 1–190.
- Pralon, B.G.N. & Negreiros-Fransozo, M.L. (2008) Relative growth and morphological sexual maturity of *Uca cumulanta* (Crustacea: Decapoda: Ocypodidae) from a tropical Brazilian mangrove population. *Journal of the Marine Biological Association of the United Kingdom*, 88, 569–574.
<http://dx.doi.org/10.1017/s0025315408000453>
- Raz-Guzman, A. & Sanchez, A.J. (1992) Registros adicionales de cangrejos braquiuros (Crustacea: Brachyura) de Laguna de Términos, Campeche. *Anales del Instituto de Biología Universidad Nacional Autónoma de México, Serie Zoología*, 63, 29–45.
- Rosenberg, M.S. (2000) The Comparative Claw Morphology, Phylogeny, and Behavior of Fiddler Crabs (Genus *Uca*). In: *Ecology and Evolution*. State University of New York at Stony Brook, Stony Brook, NY, pp. 182.
- Rosenberg, M.S. (2002) Fiddler crab claw shape variation: A geometric morphometric analysis across the genus *Uca*. *Biological Journal of the Linnean Society*, 75, 147–162.
<http://dx.doi.org/10.1046/j.1095-8312.2002.00012.x>
- Salmon, M. & Atsides, S.P. (1968a) Behavioral, morphological and ecological evidence for two new species of fiddler crabs (genus *Uca*) from the Gulf Coast of the United States. *Proceedings of the Biological Society of Washington*, 81, 275–290.
- Salmon, M. & Atsides, S.P. (1968b) Visual and acoustical signalling during courtship by fiddler crabs (genus *Uca*). *American Zoologist*, 8, 623–639.
<http://dx.doi.org/10.1093/icb/8.3.623>
- Salmon, M., Ferris, S.D., Johnston, D., Hyatt, G.W. & Whitt, G.S. (1979) Behavioral and biochemical evidence for species distinctiveness in the fiddler crabs, *Uca speciosa* and *U. spinicarpa*. *Evolution*, 33, 182–191.
<http://dx.doi.org/10.2307/2407375>
- Salmon, M. & Horch, K.W. (1972) Acoustic signalling and detection by semiterrestrial crabs of the family Ocypodidae. In: Winn, H.E. & Olla, B.L. (Eds.), *Behavior of Marine Animals Vol. 1. Invertebrates*. Plenum Press, New York, pp. 60–96.
- Suzawa, Y., Yong, H.-S. & Murai, M. (1993) Genetic differentiation of Malaysian fiddler crabs (genus *Uca*). *Comparative Biochemistry and Physiology*, 105B, 529–533.
[http://dx.doi.org/10.1016/0305-0491\(93\)90084-i](http://dx.doi.org/10.1016/0305-0491(93)90084-i)
- Thurman II, C.L. (1979) *Fiddler crabs of the Gulf of Mexico*. University of Minnesota, pp. 301.

- Thurman II, C.L. (1984) Ecological notes on fiddler crabs of south Texas, with special reference to *Uca subcylindrica*. *Journal of Crustacean Biology*, 4, 665–681.
<http://dx.doi.org/10.2307/1548080>
- Thurman II, C.L. (1987) Fiddler crabs (genus *Uca*) of eastern Mexico (Decapoda, Brachyura, Ocypodidae). *Crustaceana*, 53, 94–105.
<http://dx.doi.org/10.1163/156854087x00664>
- Thurman II, C.L. (1998) Evaporative water loss, corporal temperature and the distribution of sympatric fiddler crabs (*Uca*) from south Texas. *Comparative Biochemistry and Physiology*, 119A, 279–286.
[http://dx.doi.org/10.1016/s1095-6433\(97\)00424-8](http://dx.doi.org/10.1016/s1095-6433(97)00424-8)
- Thurman II, C.L. (2000) Variance in osmoregulation among sympatric fiddler crabs, genus *Uca*, from Texas. *American Zoologist*, 40, 1234–1235.
- Thurman II, C.L. (2001) Osmoregulation by *Uca* from the temperate coasts of eastern North America. *American Zoologist*, 41, 1607.
- Thurman II, C.L. (2002) Osmoregulation in six sympatric fiddler crabs (genus *Uca*) from the northwestern Gulf of Mexico. *Marine Ecology*, 23, 269–284.
<http://dx.doi.org/10.1046/j.1439-0485.2002.02785.x>
- Thurman II, C.L. (2003a) Osmoregulation by six species of fiddler crabs (*Uca*) from the Mississippi delta area in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*, 291, 233–253.
[http://dx.doi.org/10.1016/s0022-0981\(03\)00138-2](http://dx.doi.org/10.1016/s0022-0981(03)00138-2)
- Thurman II, C.L. (2003b) Osmoregulation in fiddler crabs (*Uca*) from temperate Atlantic and Gulf of Mexico coasts of North America. *Marine Biology*, 142, 77–92.
- Thurman II, C.L. (2004a) Osmoregulation in fiddler crabs: A review. *Integrative and Comparative Biology*, 44, 652.
- Thurman II, C.L. (2004b) Unravelling the ecological significance of endogenous rhythms in intertidal crabs. *Biological Rhythm Research*, 35, 43–67.
<http://dx.doi.org/10.1080/09291010412331313232>
- Thurman II, C.L. (2005) A comparison of osmoregulation among subtropical fiddler crabs (*Uca*) from southern Florida and California. *Bulletin of Marine Science*, 77, 83–100.
- Thurman II, C.L., Faria, S.C. & McNamara, J.C. (2013) The distribution of fiddler crabs (*Uca*) along the coast of Brazil: implications for biogeography of the western Atlantic Ocean. *Marine Biodiversity Records*, 6, 1–21.
<http://dx.doi.org/10.1017/s1755267212000942>
- Utrera-López, M.E. & Capistrán-Barradas, A. (2013) New record and range expansion of the narrow-fronted fiddler crab *Uca (Uca) major* (Herbst, 1782), from the state of Veracruz, Mexico. *Crustaceana*, 86, 367–371.
<http://dx.doi.org/10.1163/15685403-00003164>
- von Hagen, H.-O. (1980) A key to the "X-species" of North American fiddler crabs (genus *Uca*). *Zoologische mededelingen*, 55, 88–96.
- Yamaguchi, T. (1994) Fiddler crabs of the genus *Uca* in the collections of three natural history museums in Europe. 1. The specimens held by the Nationaal Natuurhistorisch Museum, Leiden and the National History Museum, London. *Calanus. Bulletin of the Aitsu Marine Biological Station*, 11, 151–189.
- Yamaguchi, T. (2001) The breeding period of the fiddler crab, *Uca lactea* (Decapoda, Brachyura, Ocypodidae) in Japan. *Crustaceana*, 74, 285–293.
<http://dx.doi.org/10.1163/156854001505523>