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A KEY TO THE "X-SPECIES" OF NORTH AMERICAN FIDDLER CRABS (GENUS *UCA*)

by

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With 4 text-figures

Up to the late sixties of this century the number of species of the genus *Uca* occurring on the East and Gulf coasts of North America seemed rather well established. Usually ten species were listed: *U. burgersi* Holthuis (= *U. affinis* (Streets)), *U. leptodactyla* Rathbun, *U. minax* (Le Conte), *U. pugilator* (Bosc), *U. pugnax* (Smith), *U. rapax* (Smith), *U. speciosa* (Ives), *U. spinicarpa* Rathbun, *U. subcylindrica* (Stimpson) and *U. thayeri* Rathbun. Subsequently, however, some uncertainty arose about the number of fiddler crab species of the Gulf coast area. Barnwell (1968) mentioned an undescribed species from Ocean Springs, Mississippi, and Salmon and co-workers described no less than three new Gulf coast species of *Uca* (Salmon & Atsaides, 1968; Novak & Salmon, 1974). Meanwhile, the new names were used in ecological and other studies (e.g. Powers, 1975; Powers & Cole, 1976).

Crane (1975) was the first to re-examine the type material of two of these additional species. She decided to include them in her *Uca* monograph admitting subspecific rank to them. However, when trying to give a comprehensive differential diagnosis of the two new subspecies and all related forms Crane met with difficulties (most clearly expressed on p. 193 and p. 197 of the 1975 monograph). Furthermore, there are reasons to doubt the subspecies concept of Crane in general (see Von Hagen, 1976, and new data from Lewinsohn, 1977, and Frith & Frith, 1977).

These doubts as well as results of bioacoustic work with West Indian fiddler crabs (Von Hagen, 1975) induced the present author to question the taxonomic proposals of Crane (1975) as well as the original ones of Salmon and co-workers and to re-examine the holotypes, which was possible through the kindness of Dr. R. B. Manning, National Museum of Natural History (Washington).

In the present paper the results of this re-examination are not treated uniformly. The species most recently described, *U. panacea* Novak & Salmon, 1974, is only briefly mentioned here. In contrast to the drawings given by the authors (Novak & Salmon, 1974: 319, fig. 5) the gonopods of the holotype of *U. panacea* were found to be identical with those of *U. pugilator* (Bosc), nor was there any other morphological character that could serve for clearly separating the holotype of *U. panacea* from *U. pugilator*. One should, however, wait for the full evidence that Salmon and co-workers are going to display in several papers, apparently mainly relying on a concept of ethospecies. The evidence published so far (Salmon et al., 1978) is not convincing, because the investigations were not clearly centred on the zone of overlap of the two forms in question.

Despite of this, the case of *U. panacea* does not seem to be as intricate as the two other cases (*U. longisignalis* and *U. virens*), in which three to five species and more authors than the first-describing ones (Salmon & Atsaides, 1968) are involved and in which one is very far from the advanced stage of comparing possibly sibling forms. The main reason for the present confused situation is that, from the beginning, the two allegedly new species were not thoroughly compared to material of *U. minax* and *U. rapax*, respectively, but to a third form, i.e. *U. pugnax*, in each case. A morphological comparison of *U. longisignalis* with *U. minax* and of *U. virens* with *U. rapax* (as presented in figs. 2-4 of the present paper) should have caused the first-describing authors to desist from the creation of two new forms [1]).

Subsequently, in the course of their bioacoustic work, Salmon and co-workers (see Von Hagen, 1975, for references) casually compared some behavioural components of the synonymous forms *U. virens* and *U. rapax*. Owing to the great variability of these behavioural characters, however, these comparisons typically did not result in an elucidation of the taxonomic situation.

As at present nobody can fully estimate the degree of intraspecific variation of e.g. sound production in *Uca*, it is necessary to centre on morphological characters, the variation of which is far better known in many cases. It must be admitted, however, that all species in question belong to the so-called "jerker-group" or *mordax*-group of New World fiddler crabs (for its greater

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[1]) This pertinent comparison was already suggested by Holthuis (1968, in litt.) who was the first to assume the synonymy of the two pairs of species mentioned above, when he examined part of the material involved prior to the publication of the paper of Salmon & Atsaides (1968). Unfortunately, *U. minax* was not mentioned at all by Salmon & Atsaides (1968) and *U. rapax* was only briefly treated in merely stating its distinctiveness from the two new forms (p. 287).

part identical with the subgenus *Minuca* sensu Crane, 1975), which was always said to be excessively variable even in their morphology. In respect to North America, the three species ending with an "x" (i.e. *U. minax, U. pugnax, U. rapax*) seem to be among the most difficult forms of this group. So it may be justified to call them "x-species" in a double sense.

It is the purpose of the present paper to show that some morphological characters are, nevertheless, reliable and lead to the result that the new taxonomic proposals of Salmon & Atsaides (1968) are not warranted, i.e. that *U. longisignalis* and *U. virens* can only be separated from *U. pugnax*, but not from *U. minax* and *U. rapax*, respectively. To avoid endless discussions of errors the results of the comparative work are mainly presented in the form of an illustrated key (using well-known and new characters) for the identification of the three North American x-species. Short lists of synonyms and of the material examined as well as a few remarks for each species are added.

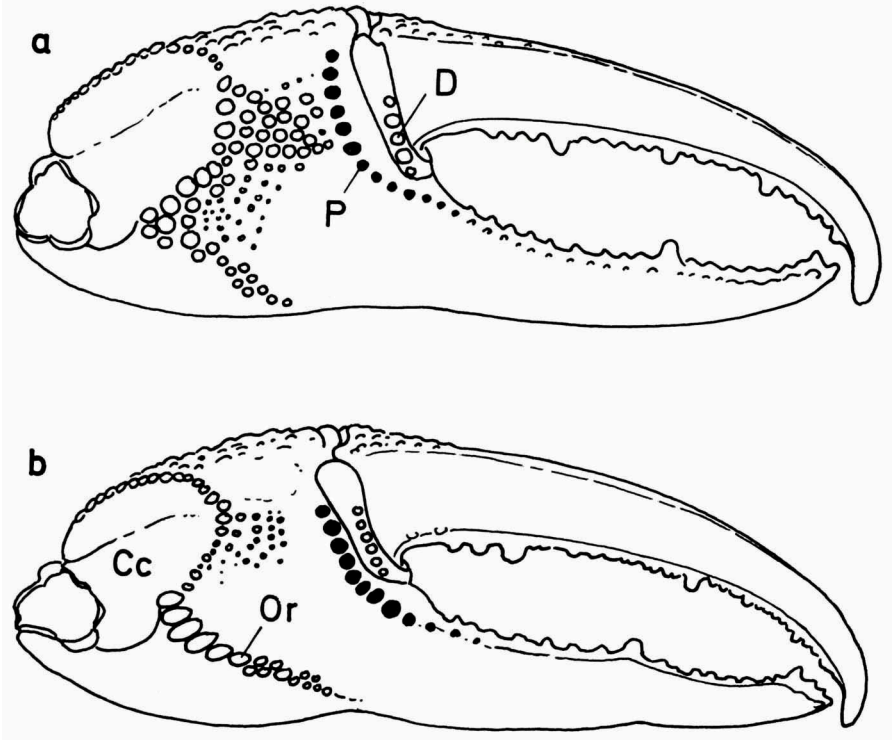

Fig. 1. Major chela of male in inner view. — a, *Uca burgersi* Holthuis; b, *Uca rapax* (Smith). Note semicircular divergence of proximal tuberculate ridge (P, drawn in black) from distal one (D) in (a) only. Cc, carpal cavity; Or, oblique tuberculate ridge.

There is a fourth species name ending with an "x", namely *U. mordax* (Smith). However, since the splitting of the former collective noun *U. mordax* (see e.g. Rathbun, 1918) by Holthuis (1959, 1967) the true members of this species are confined to South and Central America. All pertinent individuals from Florida and the Gulf coast belong to *U. burgersi* Holthuis. Though being a member of the difficult "jerker-group", *U. burgersi* is not worth to be mentioned here in detail, because the males of this species, at least with regard to North America, are identified very easily. They differ from the *minax-pugnax-rapax*-assemblage by the semicircular divergence of the proximal one of the two tuberculate ridges near the inner base of the movable finger (dactylus) of the major cheliped (fig. 1a, b).

In each of its four sections the key starts with characters also suitable to

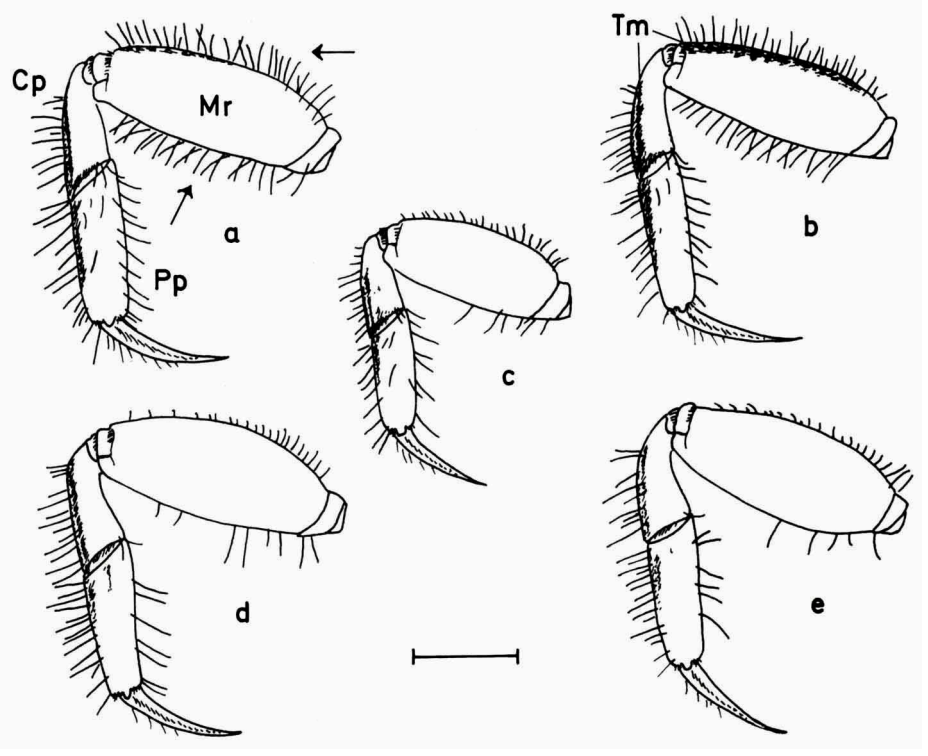

Fig. 2. Left third walking leg (fourth peraeopod) of male in posterior view. — a, *Uca minax* (Le Conte), eastern Florida; b, *Uca minax* (Le Conte), Mississippi (holotype of *U. longisignalis* Salmon & Atsaides); c, *Uca pugnax* (Smith), eastern Florida; d, *Uca rapax* (Smith), Trinidad; e, *Uca rapax* (Smith), Texas (holotype of *U. virens* Salmon & Atsaides). Cp, carpus; Mr, merus; Pp, propodus; Tm, tomentum (pile); arrows point to long setae of merus. Scale 5 mm.

identify females (except when stated otherwise). It should be mentioned, however, that the identification of a single female remains a difficult task. Even the tubercle posterior to the female gonopore looks rather similar in each of the three cases.

The illustrations (figs. 1-4) supporting the key are semi-schematic. "Left-handed" males, i.e. males with their major cheliped on their left side, were used in each of the drawings. With the exception of *U. pugnax* most males were of comparable size (carapace width 20-22 mm).

Key

1. Merus of second and third walking leg very hairy: at least (in females) anterior lower margin on its whole length covered with very long hair bristles (setae), their length corresponding to the length of hair of carpus and pro-

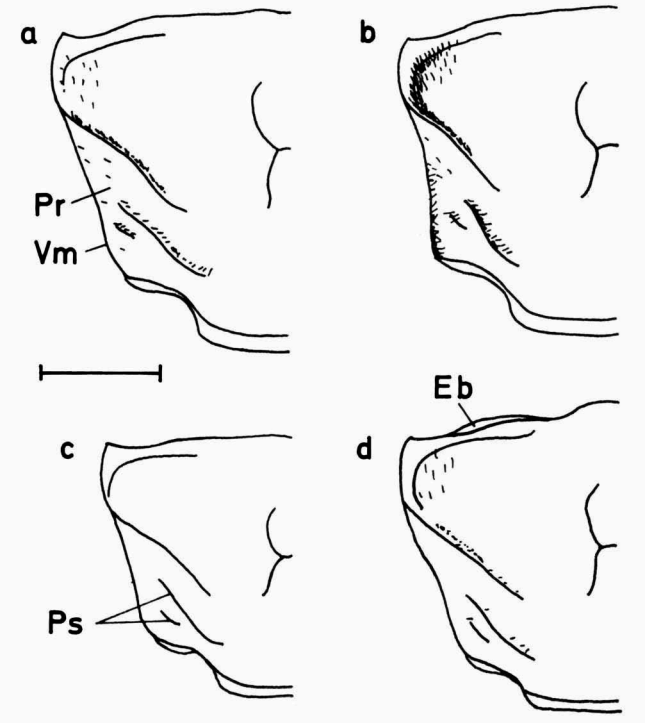

Fig. 3. Carapace of male in lateral-dorsal view. — a, *Uca minax* (Le Conte), eastern Florida; b, *Uca minax* (Le Conte), Mississippi (holotype of *U. longisignalis* Salmon & Atsaides); c, *Uca pugnax* (Smith), eastern Florida; d, *Uca rapax* (Smith), Trinidad. Eb, eyebrow; Pr, postero-lateral region; Ps, postero-lateral striae; Vm, vertical lateral margin. Scale 5 mm.

podus. In males (fig. 2a, b) setae of this long type usually also on upper and posterior lower margin of merus. Short soft hair of pterygostomian region penetrates beyond the vertical lateral margin of carapace into the postero-lateral region forming virtual fields (in females) or conspicuous rows on the postero-lateral striae (in males, fig. 3a, b), often together with pile (pubescence, tomentum). Front (measured at the spot where upper and lower margins of eyebrow meet) very broad: clearly more than one third of maximum carapace width. (Eyebrow nearly vertical as in *U. pugnax*). Sub-

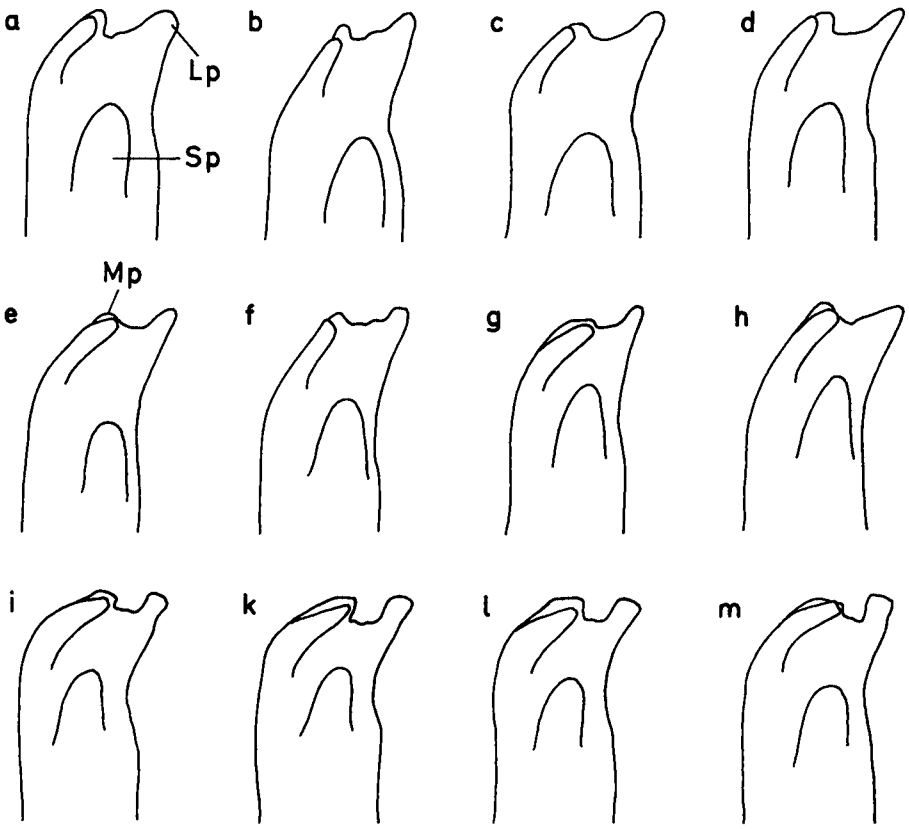

Fig. 4. Contours of tip of right first male gonopod in sternal (anterior) view (brought to about equal size, setae omitted). — a-d, *Uca minax* (Le Conte): a, eastern Florida; b, Louisiana; c, Mississippi (holotype of *U. longisignalis* Salmon & Atsaides); d, Virginia. — e-h, *Uca pugnax* (Smith): e, eastern Florida; f, g, New York; h, "USA". — i-m, *Uca rapax* (Smith): i, Puerto Rico; k, Trinidad; l, Texas (holotype of *U. virens* Salmon & Atsaides); m, Curaçao. Lp, lateral terminal projection; Mp, mesial terminal projection; Sp, subterminal palp.

terminal process (palp) of male gonopod inclined sternally, not in contact with shaft (inclination not visible in fig. 4). Tip of gonopod otherwise rather variable (fig. 4a-d, similar to *U. pugnax*, fig. 4e-h). Palm of major cheliped uses to be extremely coarsely tuberculate on upper half of outer surface, fixed finger frequently rather high throughout, little tapering and suddenly cut distally. Carapace up to 38 (width) × 25.2 mm (length) . . . *Uca minax*

1′. Merus of second and third walking leg less hairy (fig. 2c-e), especially its lower margins, which bear mainly proximally a few distantly set bristles of the long type. Dorsal setae of merus in males and females much shorter than those of carpus and propodus. At most a few scattered hairs on the postero-lateral striae of carapace (fig. 3c, d), though tomentum may be present sometimes. Front not very broad (one third of carapace width or less). Subterminal palp of male gonopod more or less in contact with shaft, not clearly slanting sternally. Outer surface of palm of major cheliped less coarsely tuberculate, fixed finger normally tapering gradually, rather slender distally 2

2. Eyebrow (elongate field above dorsal margin of orbit) inclined, therefore nearly fully visible in dorsal view (fig. 3d). Tip of male gonopod not very variable, its lateral terminal "horny" projection proximally not wider than distally in sternal view (fig. 4i-m). Notch between lateral and mesial projection sharply cut and often nearly rectangular, frequently not much wider than lateral projection. Oblique ridge on inner surface of palm of major cheliped usually strongly protruding and frequently marked with very large tubercles near carpal cavity (fig. 1b). Carapace up to 34 × 21.5 mm . . . . . *Uca rapax*

2′. Eyebrow nearly vertical, not or almost not visible in dorsal view (fig. 3c). Tip of male gonopod (fig. 4e-h) variable, but its lateral projection usually proximally wider than distally. Notch between the two terminal projections not subrectangular but asymmetrically v-shaped. Oblique ridge on inner surface of major chela not strongly protruding, its tubercles of normal size. Fixed finger rather straight, little curved upwards distally. Carapace up to 22.7 × 14.9 mm . . . . . *Uca pugnax*

Abbreviations used in the following section: CVHM, Collection Von Hagen, Marburg; RMNH, Rijksmuseum van Natuurlijke Historie (Leiden, Netherlands); USNM, United States National Museum (Washington); ZSZM, Zoologisches Staatsinstitut & Zoologisches Museum (Hamburg).

Uca minax (Le Conte, 1855)

Gelasimus minax Le Conte, 1855: 403.
Uca minax — Rathbun, 1918: 389.

Uca longisignalis — Salmon & Atsaides, 1968: 279.
Uca (Minuca) minax — Crane, 1975: 176.
Uca (Minuca) rapax longisignalis — Crane, 1975: 197.

Material examined. — Gulf coast: Mouth of Mississippi, Louisiana, May 1905, W. Schwinghammer, ZSZM, 13 males. Ocean Springs, Mississippi, 23 June 1967, M. Salmon and S. P. Atsaides, USNM, 1 male (holotype of *U. longisignalis*). Port St. Joe, Florida, 1971, H. W. Honegger, CVHM, 2 males, 1 female. "Amerika", 11 March 1917, J. Umlauff, ZSZM, 28 males, 1 female.

East coast: Harborton, Chesapeake Bay, Virginia, 28 September 1952, L. B. Holthuis, RMNH, 3 males. Flagler Beach, eastern Florida, 7 August 1970, G. W. Hyatt, CVHM, 2 males, 1 female.

Remarks. — Individuals from the Gulf coast usually have more tomentum on their ambulatories (fig. 2b) and on the lateral portions of their carapace (fig. 3b) than East coast specimens (figs. 2a, 3a). Considering the evolutionary tendency of "detomentation" in New World *Uca* (Von Hagen, 1970), this fact supports the view that *U. minax* originated on the Gulf coast and secondarily invaded the East coast. It is not certain whether, at present, the populations of the two regions are isolated from each other. Perhaps the Key West record (2 males in Harvard Museum) is not as questionable as it is thought by Crane (1975: 178). On the other hand, the species is recorded not farther south than Bulow Creek (north of Daytona Beach, Miller, 1968) on the East coast of Florida.

Uca pugnax (Smith, 1870)

Gelasimus pugnax Smith, 1870: 131.
Uca pugnax — Rathbun 1918: 395.
Uca (Minuca) pugnax pugnax — Crane 1975: 203.

Material examined. — East coast: Cold Spring Harbor, New York, 1899, G. Duncker, ZSZM, 39 males, 3 females. Flagler Beach, eastern Florida, 7 August 1970, G. W. Hyatt, CVHM, 3 males. "USA", 1937, Dr. Ladiges, ZSZM ,1 male.

Remarks. — In the past, *U. pugnax* was always considered very closely related to *U. rapax*. As judged from the similarity of their gonopods it may, however, be the smaller sister species of *U. minax*, the latter having only secondarily invaded the area of *U. pugnax*, i.e. the temperate zone of the East coast of North America. In contrast to earlier statements of Rathbun (1918), *U. pugnax* seems to have been always confined to this coast.

Uca rapax (Smith, 1870)

Gelasimus rapax Smith, 1870: 134.
Uca pugnax rapax — Rathbun, 1918: 397.
Uca rapax — Tashian & Vernberg, 1958: 89.
Uca virens Salmon & Atsaides, 1968: 281.
Uca (Minuca) rapax rapax — Crane, 1975: 196.

Uca (*Minuca*) *pugnax virens* — Crane, 1975: 203.

Material examined. — Gulf coast: Tampico, Mexico, 17 October 1902, M. Heimreich, ZSZM, 1 male. Port Aransas, Texas, 17 June 1967, M. Salmon and S. P. Atsaides, USNM, 1 male (holotype of *U. virens*).

West Indies: Montecristi, Dominican Republic, August 1935, P. Thumb, ZSZM, 9 males, 3 females. Boquéron, Puerto Rico, 17 August 1969, G. W. Hyatt, CVHM, 2 males, 1 female. Trinidad, 1965/66, CVHM, 36 males, 22 females. Caracas Baai, Curaçao, 27 September 1951, G. Krefft, ZSZM, 6 males, 1 female.

Remarks. — This species is widely distributed on tropical and subtropical Atlantic shores and islands of the two Americas (Von Hagen, 1970). The tip of the male gonopod was accurately figured in posterior and lateral view by Chace & Hobbs (1969: 215, fig. 73a, b). Unfortunately, the gonopod drawings of *U. rapax* in Crane's monograph (1975: 381, fig. 67) are misleading.

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Zusammenfassung

Neubeschreibungen von Winkerkrabben-Arten von der Golf-Küste der Vereinigten Staaten haben in jüngster Zeit eine systematisch und nomenklatorisch unklare Situation geschaffen, die durch die *Uca*-Monographie von Crane (1975) nicht beseitigt wurde und die vor allem den wissenschaftlichen Umgang mit der ohnehin schwierigen „Ruckwinker-" oder *mordax*-Gruppe weiter erschwert. Eine Nachuntersuchung des Typus-Materials der Neubeschreibungen ergab, daß sie nicht berechtigt sind. Anstelle einer aufwendigen Diskussion der Irrtümer und ihrer Ursachen wird ein Bestimmungsschlüssel für die drei schwierigsten nordamerikanischen Arten (*U. minax, U. pugnax, U. rapax*) aufgestellt und durch entsprechende Synonymie-Listen ergänzt.

Literature

Barnwell, F. H., 1968. The role of rhythmic systems in the adaptation of fiddler crabs to the intertidal zone. — Am. Zoologist, 8: 569-583.

Chace, F. A. & H. H. Hobbs, 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. — Bull. U.S. Nation. Mus., 292: 1-258.

Crane, J., 1975. Fiddler crabs of the world. Ocypodidae: genus Uca. — Princeton: University Press.

Frith, D. W. & C. B. Frith, 1977. Range extensions of fiddler crabs (Decapoda, Brachyura, Ocypodidae) in the north-western Malay Peninsula area. — Crustaceana, 32: 100-102.

HAGEN, H. O. VON, 1970. Verwandtschaftliche Gruppierung und Verbreitung der karibischen Winkerkrabben (Ocypodidae, Gattung Uca). — Zool. Meded. Leiden, 44: 217-235.

——, 1975. Klassifikation und phylogenetische Einordnung der Lautäußerungen von Ocypodiden und Grapsiden (Crustacea, Brachyura). — Z. zool. Syst. Evolut.-forsch., 13: 300-316.

——, 1976. Review: J. Crane, Fiddler crabs of the world. — Crustaceana, 31: 221-224.

HOLTHUIS, L. B., 1959. The Crustacea Decapoda of Suriname (Dutch Guiana). — Zool. Verhand. Leiden, 44: 1-296.

——, 1967. On a new species of Uca from the West Indian region (Crustacea, Brachyura, Ocypodidae). — Zool. Meded. Leiden, 42: 51-54.

LE CONTE, J., 1855. On a new species of Gelasimus. — Proc. Acad. nat. Sci. Philad., 7: 402-403.

LEWINSOHN, CH., 1977. Die Ocypodidae des Roten Meeres (Crustacea Decapoda, Brachyura). — Zool. Verhand. Leiden, 152: 45-84.

MILLER, D. C., 1968. Some thermal requirements of fiddler crabs of the temperate and tropical zones and their influence on geographic distribution. — Am. Zoologist, 8: 459-469.

NOVAK, A. & M. SALMON, 1974. Uca panacea, a new species of fiddler crab from the Gulf coast of the United States. — Proc. Biol. Soc. Wash., 87: 313-326.

POWERS, L. W., 1975. Fiddler crabs in a nontidal environment. — Contrib. Mar. Sci., 19: 67-78.

POWERS, L. W. & J. F. COLE, 1976. Temperature variation in fiddler crab microhabitats. — J. exp. mar. Biol. Ecol., 21: 141-157.

RATHBUN, M. J., 1918. The grapsoid crabs of America. — Bull. U.S. Nation. Mus., 97: 1-461.

SALMON, M. & S. P. ATSAIDES, 1968. Behavioral, morphological and ecological evidence for two new species of fiddler crabs (genus Uca) from the Gulf coast of the United States. — Proc. Biol. Soc. Wash., 81: 275-290.

SALMON, M., G. HYATT, K. MCCARTHY & J. D. COSTLOW, JR., 1978. Display specificity and reproductive isolation in the fiddler crabs, Uca panacea and U. pugilator. — Z. Tierpsychol., 48: 251-276.

SMITH, S. I., 1870. Notes on American Crustacea. No. 1. Ocypodoidea. — Trans. Conn. Acad. Arts Sci., 2: 113-176.

TASHIAN, R. E. & F. J. VERNBERG, 1958. The specific distinctness of the fiddler crabs Uca pugnax (Smith) and Uca rapax (Smith) and their zone of overlap in northeastern Florida. — Zoologica (N.Y.), 43: 89-92.