Taxonomic revision of the wide-front fiddler crabs of the *Uca lactea* group (Crustacea: Decapoda: Brachyura: Ocypodidae) in the Indo-West Pacific

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**Abstract**

The Indo-West Pacific broad-front fiddler crabs, formerly attributed to the "*lactea* species-group" are revised. The subgenus *Uca* (*Austruca*) Bott, 1973, is here revived for accommodating the informal "*lactea* species-group". *Uca* (*Austruca*) presently covers 7 species, partly with a restricted regional distribution, of which one (*Uca cryptica* sp. nov. from Indonesia) is new to science.

**Key words:** Taxonomy, Ocypodidae, fiddler crabs, *Uca*, *Austruca*, *lactea* species-group

**Introduction**

Fiddler crabs (*Uca*) are a well-known group of Ocypodid crabs. They are mostly small, highly social, and are a conspicuous brachyuran element in the muddy, muddy-sand or sandy-mud intertidal flats, especially near mangroves, throughout tropical and subtropical regions of the world (Zeil *et al.* 2006; Barnes 2010). The species of *Uca* play important functional roles in coastal ecosystems in tropical and subtropical regions, hence a large amount of ecological work exists on the group (see Litulo 2005; Mokhtari *et al.* 2008). They show a remarkable social behaviour, particularly during courtship, which has been the subject of many studies (see Alen & Levinton 2007; Dayson 2008; How *et al.* 2008; Lailwaux *et al.* 2008). Despite these numerous studies, their systematics is still under dispute. To date Crane (1975) is the only and most comprehensive taxonomic work covering the complete genus. She proposed numerous subgenera and subspecies, but missed an earlier paper by Bott (1973) in which he had already introduced names for some of Crane's subgenera and species (von Hagen 1976). The fundamental difference between both systems is that Bott used the morphology of the male pleopods as prime classification character while Crane mostly referred to cheliped and carapace morphology, and included species with very different male pleopods as subspecies under one and the same species.

Rosenberg (2001) published a cladistic analysis on the basis of 236 morphological characters but failed to propose a new comprehensive system (Beinlich & von Hagen 2006). Beinlich & von Hagen (2006) were the first modern authors to propose a comprehensive system on the basis of Crane's, Bott's and Rosenberg's findings, with a list of all sugnereia recognised by them and including a list of the species and a new subgenus, *Uca* (*Cranuca*) for *Uca inversa* (Hoffmann, 1874). In spite of their clear proposals, Beinlich & von Hagen (2006) placed an additional question mark on the classification of the subgenus *Paraleptuca* Bott, 1973. The synapomorphies for *Paraleptuca* that were listed are not convincing, because they do not apply to all species, neither do other characters besides the broad front, being, however, not at all of a homogeneous breadth in all species. Furthermore, the subgenus *Paraleptuca* Bott, 1973, proposed by Beinlich & von Hagen (2006), seems to be potentially paraphyletic, as already suspected by these authors. Ng *et al.* (2008), in their comprehensive catalogue of Brachyura, followed the subgeneric system proposed by Beinlich & von Hagen...
The present study was started years ago by M. Türkay in collaboration with H.-L. Chen but was never finished for a number of reasons. R. Naderloo and M. Türkay, when revising the brachyurans of the coast of Iran, examined the complicated, still open problems of the broad-front Uca of the Indo-West Pacific. Because we have used the earlier input of our late colleague H.-L. Chen as a starting point, we found it appropriate to grant her authorship posthumously. Her memory will stay with this paper, which we dedicate to her memory.

Indeed, one of the most important morphological characters used in the present study are the median and lateral teeth of the gastric mill, the general morphology of which does not seem to be affected by the diet (Felgenhauer & Abele 1990), and was therefore proposed to be used in the systematics of brachyuran groups (see K. Sakai et al. 2006 for further discussion). The morphology of the median tooth of the gastric mill was found to be the most useful feature for distinguishing species in the lactea-group. Because of this we give a description and SEM-pictures of the median tooth of the gastric mill in all species of the group.

Here we revise the wide-front species of the Uca lactea-group using external morphological and gonopod characters and features of the gastric mills. Species of this group are readily characterised by the general shape of the first male pleopod, including a wide, blade-shaped endpiece, which is normally two-lobed dorsally, and by having a relatively small, dorsal palp. All species of the lactea-group were hitherto placed together with some others [U. bengali Crane, 1975, U. chlorophthalmus (H. Milne Edwards, 1837), U. crassipes (Adams & White, 1848), U. sindensis (Alcock, 1900) and U. triangularis (A. Milne Edwards, 1873)] in the subgenus Paraleptuca Bott, 1973 (Beinlich & von Hagen 2006). But regarding the characters of the first male gonopod particularly and some other synapomorphic characters, the lactea-group is fully distinct from other species of Paraleptuca. These characters include: 1) presence of special teeth on the cutting edges of fingers of the major chela of male, mainly subproximal teeth on both finger and subdistal tooth on fixed finger; 2) presence of a proximal oblique ridge and distal ridges on the inner surface of the major chela of male, which are parallel to dactyl base; 3) cutting edges of minor chela without any dentation; 4) presence of one postrolateral stria on the carapace; 5) characters of median and lateral tooth plates of the gastric mill; e.g. teeth on the median tooth are relatively large and distributed along more than half of the median tooth plate. The latter character is clearer and more important for separating this group from the remaining species of the genus, and subgenus Paraleptuca, in particular. The morphology of the gastric mill is furthermore a very helpful character for separating similar species within this group. Because of the clear synapomorphies that we could find for the lactea-group we separate these species from the subgenus Paraleptuca and revive the subgenus Austruca Bott, 1973, to accommodate them.

The subgenus Austruca was originally described by Bott (1973), in which he included two species U. lactea (De Haan, 1835), and U. annulipes (H. Milne Edwards, 1837). As all species of lactea-group revised here are genetically (Shih et al. 2009) and morphologically (present observations) closely allied, and are again assigned to the subgenus Austruca, to which they were formerly attributed. The remaining species of the subgenus Paraleptuca, as defined by Beinlich & von Hagen (2006), are completely different from those of the lactea-group (Naderloo & Türkay, ongoing study), and can be clearly included in the subgenus Paraleptuca proper.

The present study was started years ago by M. Türkay in collaboration with H.-L. Chen but was never finished for a number of reasons. R. Naderloo and M. Türkay, when revising the brachyurans of the coast of Iran, examined the complicated, still open problems of the broad-front Uca of the Indo-West Pacific. Because we have used the earlier input of our late colleague H.-L. Chen as a starting point, we found it appropriate to grant her authorship posthumously. Her memory will stay with this paper, which we dedicate to her memory.

While the manuscript of this revision was ready for submission, a paper by Shih et al. (2009), who studied the lactea-group using two mitochondrial genes, 16S rRNA and cytochrome oxidase subunit I, was published. The results of their study fully confirm our morphological findings: 1) the “Uca lactea species group”, as these authors called the unit, is monophyletic and thus our proposal to revive the subgenus Austruca Bott, 1973, is strongly supported; 2) the consistent morphological differences that we found for separating U. iranica Pretzmann, 1971, and U. albimana (Kossmann, 1877) from U. annulipes are backed by genetic differences.

The present paper aims at making these units morphologically identifiable and presenting background
information on the taxonomy and distribution of the species. Furthermore, a new species is described and assigned to the *U. lactea*-group under the subgenus *Uca (Austruca)* Bott, 1973.

**Material and methods**

For the taxonomic revision presented here, a large number of specimens deposited in the collections of different museums, as well as recently collected fresh material of *U. iranica* Pretzmann, 1971, and *U. albimana* (Kossmann, 1877) from the Persian Gulf and Gulf of Oman were examined. The majority of the material was from the Senckenberg Museum (Frankfurt a. M., Germany). Additional material from different collections, abbreviated as follows, was studied:

- **NHM** Natural History Museum (formerly British Museum of Natural History), London, UK
- **IOASQ** Institute of Oceanology of the Chinese Academy of Sciences, Qingdao, China
- **MNHN** Muséum national d’Histoire Naturelle, Paris, France
- **NHMB** Naturhistorisches Museum Basel, Switzerland
- **NHCY** Natural History Collection, Sanaa, Yemen
- **NHMW** Naturhistorisches Museum Wien, Vienna, Austria
- **NNM** Nationaal Natuurhistorisch Museum, Leiden, Netherlands
- **SMF** Senckenberg Museum, Frankfurt am Main, Germany
- **UZM** Universitets Zoologiske Museum, København, Danmark
- **ZMG** Zoologisches Museum, Göttingen, Germany
- **ZSM** Zoologische Staatssammlung, München, Germany
- **ZUTC** Zoology Museum, University of Tehran, Iran

Other abbreviations used in text are CL = carapace length, CB = carapace breadth, Ch.L = length of palm (from proximal part of palm to tip of fixed finger), and G1 = first pleopod of male. The terminology used here for the general descriptions mainly follows Crane (1975), and the description of the median and lateral teeth of the gastric mill follows K. Sakai *et al.* (2006).

**Key to the species of *Uca lactea*-group**

1. Palm of the major chela with supramarginal groove adjacent to lower border in outer surface ......................... 2
   - Palm of the major chela without supramarginal groove adjacent to lower margin ........................................ 3

2. Subdistal tooth on cutting edge of immovable finger remarkably large, median tooth plate of the gastric mill with 5 differentiated teeth, apical flange of G1 wider than long, emarginated dorsally, palp reaching beyond base of endpiece ................................................................. *Uca (Austruca) perplexa*
   - Subdistal tooth on the cutting edge of immovable finger small, median tooth plate of the gastric mill with 6 teeth, 4 anterior ones nearly similar, apical flange of G1 about as long as wide, palp hardly reaching to base of endpiece ....... *Uca (Austruca) cryptica* sp. nov.
   - Subdistal tooth on the cutting edge of immovable finger small, median tooth plate of the gastric mill with 8 teeth, 6 anterior ones nearly similar, apical flange of G1 remarkably long, palp short, not reaching to base of endpiece ...... *Uca (Austruca) annulipes*

3. Apical flange of G1 short, palp remarkably long, reaching up to distal half of horny endpiece, median tooth plate of the gastric mill with 3 completely different-shaped teeth .................................. *Uca (Austruca) lactea*
   - Apical flange of G1 remarkably long, palp short, not reaching to base of endpiece, median tooth plate of the gastric mill with 4 to 8 teeth ............................................. *Uca (Austruca) mjoebergi*

4. Median tooth plate of the gastric mill with 4 teeth, two anterior ones nearly similar, G1 with distal part of stem remarkably bulged mesially, east Indian Ocean species ....................................................... 5
   - Median tooth plate of the gastric mill with 6 to 8 teeth, apical flange of G1 remarkably long, west Indian Ocean species .......................................................... *Uca (Austruca) lactea*

5. Lateral margin of carapace straight, median tooth plate of the gastric mill with 6 teeth, 4 anterior ones nearly similar,
but of different size ............................................................................................................... *Uca (Austruca) iranica*
- Lateral margin of carapace converging distally, median tooth plate of the gastric mill with 8 teeth, 6 anterior ones nearly similar ............................................................................................................... *Uca (Austruca) albimana*

**Systematic account**

*Uca (Austruca) albimana* (Kossmann, 1877)
(Figs. 1a–l, 4a, 6a–b)


*Uca (Celuca) lactea annulipes* — Crane 1975: 299, 301, 611. [part.: Red Sea material].

*Uca (Celuca) lactea albimana* — Lewinsohn 1977: 61–63.


*Uca lactea annulipes* — Hywel-Davies 1994: 37, 48.


**Lectotype.** 1 male {[SMF 9709] CL 6.8, CB 12.3, Ch.L 19.8 mm} Red Sea, 1874-75, leg. R. Kossmann.

**Paralectotypes.** 1 male, 1 female (SMF 17145), data as lectotype.


*Arabian Sea*: 3 males (NHM 1988:55), Oman, Dhofar, 20 km N. of Ras Sawqirah, Khor Fakr, 18° 19’N 56° 36’E, 10.11.1985, leg. J.B. Clarke; 1 male (NHCY 83), Yemen, Sokotra, N. coast, Khawr Qariyah, 12° 38.054’N 54° 12.568’E, muddy-sand, 10.02.1199, N. Simoes; 3 males, 1 female (NHCY 84), Yemen, Sokotra, W. coast, 12° 41.099’N, 53° 28.476’E, muddy-sand, bank of Wadi, 10.03.1999, M. Apel; 2 males (NHCY 85), Yemen, Sokotra, bank of Khawr, 12° 35.976’N 53° 46.44’E, muddy, 04.02.1999, N. Simoes; 3 males, 1 female (SMF 36907) Yemen, Sokotra, N. caost, Qadub-Mori, near Mori Lagune, 12° 38.446’N, 53° 56.137’E, muddy-sand, 05.02.1999; N. Simoes; 1 male (SMF 36908) Yemen, Sokotra, Khawr Qaryah, 12° 38.425’N, 54° 3.383’E, 07.04.1999, M. Apel; 7 males, 2 females (1 ovig.), 1 juv. (SMF 36909), Yemen, Sokotra, Qualansiyah Lagune, 12° 41.904’N, 53° 30.041’E, muddy-sand, 12.04.1999, M. Apel.

*Gulf of Oman*: 13 males, 1 female (SMF 26013), UAE, Fujairah, Khor Kalba, 25° 01’N 56° 21’E, mangroves, intertidal flat, sandy-mud substrate, 01.07.1995, M. Apel; 1 male (SMF 26014), UAE, Fujairah, Khor Kalba, 25° 01’N 56° 21’E, mangroves, intertidal flat, sandy-muddy substrate, 01.07.1995, M. Apel.


*Unknown locality*: 3 males (MNHN), 02.1933, leg. J. L. Dantan.
FIGURE 1. *Uca albimana* (Kossmann, 1877): a, c–f, i–j, lectotype male (SMF 9709); b, g, paralectotype females (SMF 17145); l ovigerous female (SFM 5698), Egypt.

a, infraorbital region of male; b, infraorbital region of female; c, major chela, outer surface; d, major chela, inner surface; e, merus of major chela, outer surface; f, merus of major chela, inner surface; g, minor chela, outer surface; i, minor chela, outer surface; k, tip of G1, mesial surface; j, tip of G1, lateral surface. l, genital opening of female.

**Diagnosis.** Front broad. Anterolateral borders of carapace moderately convergent. Major male chela palm without a supramarginal groove adjacent to lower border. G1 with palp relatively short, not reaching to base of horny endpiece; this last one flat, with flanges not inclined, longer than broad, suture displaced ventrally; terminal opening marked by a more or less distinct notch.

**Redescription.** Front broad, about 1/6.5 times as broad as carapace. Ventrolateral margin of carapace moderately convergent, distinctly crested, joining to posterolateral margin at base of exorbital triangle; posterolateral margin distinctly crested, extending curvedly backwards, ending at level of middle cardiac region; posterolateral striae short. Exorbital angle acutely triangular, directed forwards and inwardly; upper orbital margin sinuous, with two crests bordering narrow eyebrow; eyebrow getting narrower outwardly, inner
part less than 1/2 breadth of eyestalk in adjacent region; lower orbital margin regularly granulate, granules becoming larger outwardly (Fig. 1a), that of the paralectotype female with additional small granules, on middle part, at inner side of large granules (Fig. 1b).

Pterygostomian region (Fig. 1a) with regular feather-shaped bristles, becoming glabrous towards lower orbital region, two short longitudinal lines of bristles on anterior-inner portion.

Third maxilliped with merus about 1/3 length of ischium; longitudinal broad groove on outer surface of ischium and merus close to inner margin, bordered with short setae; long setae on inner margin of ischium and merus.

Major chela merus with transverse ridges on upper margin, finely granulate, becoming irregular distally; lower margin denticulate (Fig. 1e), denticles small, becoming larger distally; inner surface (Fig. 1f) with patch of relatively large granules distally on upper portion. Carpus about 1.5 times as long as broad, inner upper margin denticulate, small patch of feather-shaped setae on lower proximal and upper distal portions of inner surface. Outer surface of palm (Fig. 1c) smooth, without supramarginal groove; lower margin weakly granulate, with low granules, upper margin granulate, with relatively small granules; inner surface (Fig. 1d) with high oblique tuberculate ridge, tubercles large, becoming smaller distally; proximal ridge at dactylus base with large granules, distal ridge parallel to proximal one, with granules, low, relatively small. Dactylus about 1.3 to 1.4 times as long as palm, higher than fixed finger; proximal, median teeth on cutting edge of both fingers, median teeth relatively large, that of fixed finger slightly larger; fixed finger with subdistal tooth.

Small chela (Figs. 1g, i) with smooth ridge on outer surface, extending from lower distal part of palm to two third of fixed finger; cutting edge without tooth, gap between fingers as wide as adjacent dactylus, fixed finger slightly wider than dactylus.

Merus of walking legs with finely granulated transverse ridges on anterior margin, posterior margin minutely serrated; propodus 1.2 times as long as carpus; dactylus conical, as long as propodus; last leg with propodus as long as carpus; anterior margin of carpus and propodus slightly granulate.

Male abdomen tapering from segment 2 to 5, segment 6 with lateral margin nearly straight, length of segments 3-5 subequal.

G1 (Figs. 1j, k) with stem slightly bent in posterolateral direction, palp not reaching to base of horny endpiece; latter slightly longer than wide, distal margin convex, dorsal lobe large, reaching slightly beyond ventral lobe; terminal opening of sperm channel ventrally subdistal, in middle line of endpiece lobes; scarce feather-shaped setae along lateral margin, distally becoming longer and relatively dense, scarce short setae on palp.

Genital opening of female: direction of opercle edge parallel to median line of sternum.

Median tooth plate of the gastric mill (Fig. 4a) with 8 teeth, small gaps between them, two first ones massive, different in shape, 3–8 decreasing in size posteriorly, last one distally attached to basal plate; lateral tooth plate with 20–22 comb-shaped teeth.

**Distribution.** Red Sea, Gulf of Aden, Socotra, Arabian Sea, Oman (Dhofar), south Gulf of Oman, south-eastern Persian Gulf.

**Remarks.** Crane (1975), like former authors, treated the present species as a synonym of *U. annulipes*. Lewinsohn (1977) was the first to point out the differences between both and thus separated the Red Sea populations under the subspecific name *U. lactea albimana*. We agree with the differences cited by Lewinsohn (1977), namely the lack of a supramarginal groove on the major chela and lack of a patch of setae on the lower distal portion of merus of the same chela in all specimens from the Red Sea and specimens from outside the Red Sea. Furthermore, a distinct difference is the median tooth of the gastric mill. *U. albimana* has 8 teeth on the median plate, whereas *U. iranica* has 6, which confirms the clear difference between these two species. We therefore consider both of them as having species rank. Regarding the median tooth of the gastric mill, *U. albimana* is more closely related to *U. annulipes*, as this last species has also 8 teeth on the median tooth (Figs. 4a, b). The most prominent difference is the shape of the second tooth, which is nearly elliptical in *U. annulipes*.

The material from Oman, Gulf of Oman, Persian Gulf and M. Jousseaume's material from Djibouti (Obock) belong to the typical *U. albimana*. This species is remarkably small-sized (the largest male [SMF
5698] from the Red Sea measures CL 8.5, CB 15.5, Ch.L 25.00 mm) in comparison to its more closely related and partly sympatric congeners U. annulipes and U. iranica. Lewinsohn (1977) also mentioned the small size of U. albimana in comparison to U. annulipes. This species are sympatric, with U. iranica in the southeastern Persian Gulf and western Gulf of Oman, but easily distinguished from U. iranica, apart from its fully different median tooth of the gastric mill, by having moderately convergent lateral margins, which are very slightly convergent, or nearly straight in U. iranica. Genetic evidence presented by Shih et al. (2009) supports our morphological findings as to the differentiation of these two species from each other and from U. annulipes.

**Uca (Austruca) annulipes** (H. Milne Edwards, 1837)
(Figs. 2a–h, 3a–e, 4b, 12a, b, c)


_Gelasimus lacteus_ — Krauss 1843: 14, 39. — Alcock 1900: 355 [specimens from Karachi] [not Ocypode (Gelasimus) lactea De Haan, 1835]


_Gelasimus annulipes var. lacteus_ — Ortmann 1894a: 759.


_Uca lacteus_ — Stebbing 1917: 16, pl. 4. [not Ocypode (Gelasimus) lactea De Haan, 1835].

_Austruca annulipes_ — Bott 1973: 322, fig. 13.

_Uca (Celuca) annulipes_ — Dai & Yang 1991: 467, pl. 3, fig. 362 (2).


**Lectotype.** 1 male (MNHN B11854), "Mer des Indes", leg. Reynaud.

**Paralectotype.** 1 male (MNHN B11884), data as lectotype.

**Other material.** _Mozambique:_ 1 male (ZH M K2913); 2 males (ZH M K11921), 03.08.1927; 1 male (SMF 17138), Beira, 03.09.1962; 1 male, 1 female (ZH M K12863), E. Africa (possibly Mozambique).

_Tanzania:_ 10 males (NHMB 576c), leg. La Roche, 1910; 4 males (SMF 5682), Dar Es Salam, 1899, leg. F. Winter; 8 males (ZSM), 09.1890, leg. Müller; 3 males, 1 female (ZH M K29767), 10.11.1967; 1 male (ZH M K2916), Bagamoyo, Lagoon. N. of the city, 26.06.1888, leg. F. Stuhlmann; 1 male (ZH M K3362), Kingani, near to ferry, mangroves, burrowing in muddy banks, 29.06.1888, leg. F. Stuhlmann; 9 males, 1 female (ZH M K2916), Kingani, near to ferry, Bagamoyo, flooding area, mud, 08.07.1888, leg. F. Stuhlmann; 3 males (ZH Ex K2993), Zanzibar; 31 males (ZH M K2898); 5 males (ZH M K2911); 5 males (ZSM); 8 males, 6 females (ZH M K2919), Lagoon, 20.04.1888, leg. F. Stuhlmann.

_Kenya:_ 71 males, 2 females (ZSM), Mombasa, leg. Wache; 1 male (ZH M K27111), river bank, 02.1957; 1
male (UZM), Mombasa Harbour, Kilindini, mangrove swamp, "Dana" Stat. 394; 1 male (SMF 17139),
between Mombasa and Malindi, Kilifi Creek, Manorani, 12.1985, leg. W. Baumeister; 19 males, 7 females
(SMF 9107), South of Malindi, Mida Creek, Island, mangroves, 10.1979, 1eg. M. Grasshoff; 5 males, 2
females (MNHN B11873), Gazi, 45 km S. Mombasa, shore, 1911, leg. Alluaud & Jeannel; 2 males, 1 female
(SMF 14921), Gazi, mangroves, 30.08.1985, leg. H. Thiel & H. Rumohr; 18 males, 6 females (SMF 35029),
S. Malindi, Minda, mangroves, 03.08.1989, H. G. Müller.

**FIGURE 2.** *Uca annulipes* (H. Milne Edwards, 1837): a, male (SMF 14921), Kenya; b, male (SMF), Malay Peninsula;
c, male (SMF 6692), Seychelles; d–f, male (ZSM), Kenya, Mombasa; g, male (SMF 5682), Tanzania, Dar Es Salam; h,
male (SMF 9854), Thailand.

a, infraorbital region; b, major chela, outer surface; c, major chela, outer surface (regenerated); d, major chela, inner
surface; e, merus of major chela, outer surface; f, merus of major chela, inner surface; g, minor chela, outer surface; h,
major chela, outer surface.

**Madagascar:** 1 male (MNHN B11880); 4 males (MNHN 11889); 1 male (MNHN B11892); 1 male, 1
female (MNHN B11894); 1 male (MNHN B11896); 20 females (MNHN B11904); 4 males (MNHN B11909);
1 male (MNHN B11910); 1 male, 1 female (MNHN B11913); 11 males (MNHN B11900), leg. Waterlot; 2
males (MNHN B11899), leg. G. Petit; 11 males, 3 females (SMF 5853), 1880, leg. Stumpf & Ebenau; 1 male
(SMF 5681), 1881, leg. A. Stumpf; 3 males, 1 female (MNHN B11890), Nossi Bé; 1 male (MNHN B11879), 6
males (MNHN B11880). 1 male (UZM), leg. A Crosnier; 1 male (MNHN B20241), id, 11.08.1953, 1eg. T.
Monod; 1 male (ZMH), 1883, leg. A. Stumpf; 2 males (SMF 17142), 07.06.1883, leg. A. Stumpf; 1 male, 1 female (MNHN B11893), Tamatave; 2 males, 2 females (MNHN 11898), Majunga Bay, 1926; 13.11.1962, leg. Arnoult; 2 males (MNHN B11902), Marondava, leg. Fauliatt; 4 males, 5 females (MNHN B11907), Ampalaza Bay, leg. G. Petit; 1 male (MNHN B11906), 2 males (MNHN B11908), Analalava, 1903, leg. E. HANTZ; 2 males (1 juv) (MNHN B12085), NW coast, Irohono, mangroves, 21.12.1965, leg. Betsch.

**Seychelles**: 5 males (SMF 6692), leg. R. Seréne; 14 males, 9 females (SMF 12944), Praslin, freshwater creek about 300 m. from sea, 16.05.1979, leg. M. Ackermann; 4 males (ZMH K32080), Mahé, 06.08.1979, leg. Martens & Gillandt; 2 males (SMF 17143), Port Gland (La Plaine Estate), mangroves, 09.09.1977, leg. H. Bosch.

**Mauritius**: 1 male (MNHN B11875), 1913, leg. P. Carie.

**Indian Ocean**: 2 males (SMF 110), leg. Reussmann; 6 males (ZSM), vend. Salmin.

**India**: 3 males (SMF 9739), vend. Salmin [ex. Mus. Heidelberg]; 17 males, 6 females (ZMH K2977); 5 males (ZMH K26900); 27 males, 2 females (ZMH K26913); 3 males (SMF 2343), 1 male (ZSM), Bombay, Bandra, shore, leg. R. Altevogt; 6 males (ZMH K26870), Alibag S. of Bombay, 28.11.1955, leg. G.A. Von Maydell; 11 males (ZMH Ex27091), 04.12.1955, leg. G.A. Von Maydell; 7 males, 4 females (UZM) Madras, "Galathea"-Expedition; 2 males (UZM), 04.1908, leg. Berg & Mathiassen; 1 male (UZM), Vellore, leg. Loeventhal; 1 male (MNHN B11878), Karikal, intertidal, 20.12.1940, leg. K. Lindberg; 5 males (UZM), Trankebar, "Galathea"-Expedition; 1 female (MNHN B11853), Vellar estuary near Porto Novo, 28.05.1980, leg. P. Noel; 1 female (MNHN B11881), Pondichery; 17 males, 4 females (MNHN B11888); 3 males, 1 female (ZMK ex Cr.1534), Nankauri.

**Sri Lanka**: 4 males, 2 females (SMF 7833). Negombo, mangroves, 02.04.1977, leg. R. König; 2 males (ZMH K30309), Bentota, river estuary; 2 males (ZMH K2912), 03.08.1909, leg. G. Duncker; 5 males (SMF 5692), Weligama-Bay, 04.02.1912, leg. O. Löw-Beer; 7 males (NHMB 576a), Trincomalee, 1886–1893, leg. Sarasin; 6 males (UZM), shore, 03.1889, leg. K. Rister.

**Thailand**: 4 males (UZM), 07.02.1920; 38 males, 3 females (UZM); 6 males, 1 female (UZM), 1915, leg. Fogh; 1 male (SMF 9854), Phuket, W. coast, several 100 m. upstream, intertidal zone, 1981, leg. J. Kaden; 1 male (UZM), Terutao Isl., estuary, 01-02.03.1966 [5th Thai Dan. Exped., Stat. 1149].

**Malaysia**: 1 male (ZMG 102), W. coast of Malay Peninsula, 1894, leg. Sturm; 5 males (SMF), Malay Peninsula, 1901, leg. M. Jensen; 1 male, 3 females (UZM), 3 males (UZM), Telok Merban, shore, 22.08.1937, leg. C.W. Frank; 3 males, 2 females (UZM), Pinang, "Galathea"-Expedition, leg. Reinhardt; 2 males, 1 female (ZSM), shore, 17.12.1912, leg. Haberer.

**Singapore**: 1 male (ZSM), 1906, leg. Schauinsland; 1 male (SMF 6685), 2.01.1972, leg. R. Seréne; 6 males (ZMH K3073), 3 males (ZMH K3204), Changi, 10.1900, leg. G. Duncker; 1 male (UZM), Pulau Tekong, south coast, sandy mudflat, 28.05.1951, "Galathea"-Expedition, stat. 351.

**Indonesia**: 1 female (ZSM), Java, Soetji near Grisee; 7 males (ZSM), 2 males, 1 female (UZM), Tjilatjap; 2 males (NHMB 576b), Celebes, Makassar, 1894, leg. Sarasin.

**China**: 1 male (IOASQ), Hainan Island, Gangmen, 05.12.1955, leg. Liu.

**Japan**: 1 male (SMF 34768), Ogasawara (Bonin Islands), T. Sakai.

**Wrong or doubtful localities**: 4 males (ZSM), Chile, leg. Wessel; 1 male (ZMH K3205), W. Africa, 1911, leg. W. Michaelsen.

**Unknown locality**: 25 males, 1 female (MNHN B11865); 2 males (1 Chelip of male) (MNHN B11877); 42 males, 3 females (MNHN B11886); 1 male (MNHN B11895); 2 males (MNHN B11901); 6 males (MNHN B11903); 1 male (MNHN B11905); 1 male (MNHN B11911); 1 male (MNHN B11937); 4 males (UZM); 1 male (ZMH Ex K6748); 1 female (ZMH); 2 males, 5 juv. (SMF 17144).

**Diagnosis.** Front broad. Anterolateral borders of carapace moderately convergent. Major male chela (Figs. 2b–d) with palm bearing a supramarginal groove adjacent to lower border, which very often is beset with short bristles. G1 (Figs. 3a–e) with palp relatively short, sometimes reaching to base of horny endpiece (Figs. 3b, c); this last one flat, with flanges not inclined, longer than broad, mainly due to the largely protruding dorsal lobe; suture displaced ventrally; terminal opening marked by a more or less distinct notch. Female genital opening as in *U. albimana*. 

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**TERMS OF USE**

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Distribution. Indian Ocean: from East Africa to the Indo-Malayan archipelago, excluding the Red Sea and the Persian Gulf, western Pacific: Borneo, Celebes, Lombok, Sumbawa, Flores, Phillipines, Hainan Island of China, probably ranging up to Ogasawara (Bonin) Islands.

Remarks. Crane (1975) treated this species as a subspecies of *U. lactea*. We do not think that species with such different pleopods do interbreed and therefore assign a species rank to Crane’s subspecies. This is also the case of *U. perplexa, U. lactea* and *U. cryptica* sp. nov., which are described herein. In the Persian Gulf populations hitherto referred to as *U. annulipes* the G1s are within the range of variability of *U. annulipes* (see Figs. 3b–e, or Crane 1975: fig. 65D). However, the anterolateral borders of the carapace consistently do not converge in contrast to the convergent anterolateral borders in *U. annulipes* from outside the Persian Gulf. Furthermore, they have a completely different form of the median tooth of the gastric mill (see Figs. 4b, 7a). In this respect *U. annulipes* resembles much more *U. albimana*, by having 8 teeth on the basal plate of the
median tooth, while the Persian Gulf populations have only 6. Therefore we separate these last ones under the name *U. iranica* Pretzmann, 1971, which we rank as a morphologically closely related but distinct species. *U. albimana* (Kossmann, 1877) and *U. mjoebergi* Rathbun, 1924, are easily distinguishable from *U. annulipes* by lacking the supramarginal groove of the large cheliped. Regarding the form of the median tooth of the gastric mill (Fig. 4b), *U. annulipes* is closely related to *U. albimana* rather than to *U. mjoebergi*, the latter having a fully different morphology in the median tooth. Therefore these two taxa are treated as full species here. Shih et al. (2009), based on genetic evidence, identified two species, *U. albimana* and *U. annulipes* as good species, and assigned them together with *U. iranica* in the same clade, which can be well supported by morphological findings.

Small variations on the apical portion of the G1 of *U. annulipes* are observed in specimens from different localities (see Figs. 3b–e), but these differences are not considerable as all have the same pattern by having a short palp not reaching to the base of endpiece, a long apical flange, distally two lobed, and in all cases the dorsal lobe is larger than ventral one. There is another noteworthy feature not noticed in earlier studies. The gap of the small chela in males is always narrower than the breadth of the adjacent dactylus in all specimens from Thailand, farther east than India (Fig. 2h). In East African samples, a certain number of specimens have a very broad gap (Fig. 2g), being superior to the breadth of the adjacent dactylus. However, this character is not consistent in that particular area. This probably can be the beginning of a differentiation of western and eastern Indian Ocean forms that may be taking place, as the character is asymmetrically distributed. Because of the missing consistency we do not advocate any taxonomic separation at the present time. As may be expected, the identification of females of wide-front *Uca* related to *U. annulipes* is very difficult and seems impossible in most forms. We have examined the small chelae of females, which showed no differences between different species, as well as the female genital opening. Of all the species, only *U. perplexa* is slightly different by the orientation of the genital opening.

**FIGURE 4.** Median tooth plate of the gastric mill, ventral face. a, *Uca albimana* (Kossmann, 1877), male (SMF 26018); b, *Uca annulipes* (H. Milne Edwards, 1837), male (SMF 9107).
**Uca (Austruca) cryptica** sp. nov.  
(Figs. 5, a–k, 7b, 8b)

**Holotype.** 1 male (ZSM), Indonesia, West Flores, mangroves, coll. date and collector unknown.

**Paratypes.** 1 male [(SMF 17167) CL 8.5, CB 15.9 mm], Phillipines, Naawan, ded. K. Sakai; 2 males (NHMW), Indonesia, Celebes, 01.1894, leg. Wolf.

**Diagnosis.** Front broad. Anterolateral margin moderately convergent (Fig. 5a). Major male chela palm with supramarginal groove, partly beset with setae (Fig. 5e). G1 with palp, relatively short, hardly reaching to base of horny endpiece (Fig. 5i). This last one flat, with flanges not inclined, about as broad as long, strongly bent in lateral direction, forming much smaller angle with the stem. Inclination of endpiece is much stronger than in any other species of the lactea-group, Position and displacement of suture as in U. annulipes (Figs. 5i-j). Median plate of the gastric mill with 6 teeth (Fig. 7b).

**Description.** Carapace smooth. Front broad (about 1/7 times as broad as carapace). Venterolateral margin of carapace moderately convergent (Fig. 5a), distinctly crested; posterolateral margin distinctly crested, extending curvedly backwards, ending in level of central cardiac region; posterolateral striae short. External orbital angle acute, long triangular, directed antero-externally, tip very slightly incurved frontally. Upper orbital border sinuous, with two crests bordering eyebrow, in its broadest part about 1/3 breadth of eyestalk. Lower orbital border (Fig. 5b) regularly granulate, with granules increasing in size from inner to outer part. Pterygostomian regions beset regularly with feathered bristles, becoming scarce towards lower orbital border (Fig. 5b).

Third maxillipeds with merus 1/3 length of ischium. longitudinal broad groove on ischium and merus, close to inner margin, bordered with short setae; long setae along inner margin of ischium, merus.

Major chela merus (Fig. 5c) with scarce granules on anterior upper portion of outer surface; inner dorsal margin with large granules; lower margin denticulate, denticles becoming large dorsally (Fig. 5d). Carpus definitively longer than broad, outer surface smooth, anterior upper margin with a row of granules, alternating in size; inner surface with scattered granules. Palm (Fig. 5e) with outer surface minutely granular; lower margin with row of large granules; supramarginal groove adjacent to lower margin, beset with short setae; inner surface (Fig. 5f) with oblique tuberculate ridge, high, with large granules; proximal ridge at dactylus base parallel to distal one, both strongly tuberculate. Dactylus high in proximal part, higher than fixed finger; both fingers with enlarged proximal tooth; subdistal tooth on fixed finger. Small chela (Fig. 5g) with smooth ridge on outer surface, extending from lower distal end of palm to proximal two thirds of fixed finger; without teeth on cutting edge of fingers, gap large, broader than adjacent dactylus.

Second to fifth pereiopods with merus having convex borders, granular crests on anterior margin (Fig. 5h); remaining joints smooth. Dactyls moderately curved.

Sternum smooth, transverse lines not reaching midline, longitudinal line present in thoracic segments 6-8. Episternites not completely separated from respective sternites.

Male abdomen tapering from segments 2 to 5, segment 6 with subparallel margin; length of all segments between 3 and 6 subequal.

G1 with stem (Fig. 5i) slightly bent in dorso-lateral direction; palp rather short, hardly reaching to base of horny endpiece. This last one about as long as broad, flat, with flanges not inclined, distal border oblique (Fig. 5j), with terminal opening of sperm channel in midline; dorsal lobe reaching slightly beyond ventral one; whole endpiece bent in lateral direction, thus forming rather small angle with stem, its inclination is much larger than in any other species of the lactea-group. Suture of sperm channel displaced ventrally from base to tip (Fig. 5k).

Median tooth plate of the gastric mill (Fig. 7b) with 6 teeth; two first ones massive, different in shape; 3-5 decreasing in size distally; third one clearly narrow, large gap between it and second and third teeth; 4 and 5 nearly in the same size, small gap between them; last one shorter, attached to plate dorsally. Lateral tooth plate (Fig. 8b) with 17 comb-shaped teeth.

**Distribution.** Up to now only known from Indonesia and the Philippines.
FIGURE 5. *Uca cryptica* sp. nov. Holotype male (ZSM): a, lateral margin of carapace; b, infraorbital region; c, merus of major chela, outer surface; d, merus of major chela, inner surface; e, major chela, outer surface; f, major chela, inner surface; g, minor chela, outer surface; h, last walking leg (right); i, G1, lateral surface; j, apical part of G1, lateral surface; k, apical part of G1, mesial surface.
**Remarks.** The new species is distinct from any other lactea-group members by the peculiar shape of its G1, particularly the strongly inclined endpiece. There are other characters that allow its identification. The presence of a supramarginal groove on the major male chela palm leads to the exclusion of all similar species except *U. annulipes* and *U. perplexa*. It is distinguishable from these two species by the fact that the new species lacks a tuft of setae on the lower anterior corner of the merus of the large chela, which is present in *U. perplexa* and *U. annulipes*. As only the holotype and two paratypes (NHMW) can be compared in this respect, the Philippines paratype lacking the large chela, the identification has always to be determined by examining the G1. Regarding the median tooth of the gastric mill (Figs. 7a, b), this species is closely related to *U. iranica* by having 6 teeth on the median plate, but readily distinguishable from all other members of the group. Considering the general features of the apical part of the G1 and median tooth plate of the gastric mill, *Uca cryptica sp. nov.* can be properly attributed to Clade W (this clade already includes *U. albidabana*, *U. annulipes* and *U. iranica*) proposed by Shih *et al.* (2009).

Nothing is known about the biology and ecology of the new species, and very few specimens are known.

**Etymology.** We name it *cryptica* to point out the fact that it was hidden among numerous museum specimens and still remained undiscovered.

**Uca (Austruca) iranica** Pretzmann, 1971  
(Figs. 6, c–f, 7a, 8a, 9a–k)


*Austruca lactea annulipes* — Clayton 1986: 86–88, fig. 3.  

**Holotype.** 1 male (NHMW 3788), Iran, Bandar-Abbas, 1970, leg. Pretzmann & Bilek.


**UAE:** 3 males (SMF 26026), Ras al Khaimah, mangroves, N. Rams, 25°50′N, 55°00′E, sandy-muddy substrate, high intertidal, 10.07.1995, leg. M. Apel; 7 males, 2 females (SMF 26027), Ras al Khaimah, inner...


**FIGURE 6.** *Uca albimana* (Kossmann, 1877): a,b, Red Sea, Yemen, Abuzaher; b, posterior view; c–f, *Uca iranica* Pretzmann, 1971; c, Persian Gulf, Qeshm Island, Naghasheh; d, posterior view; e, Persian Gulf, UAE; f, Persian Gulf, Qeshm Island, Naghasheh, carapace with different colour pattern. Photo credits: a, b, e by M. Apel; c, d, f by R. Naderloo.
FIGURE 7. Median tooth plate of the gastric mill, ventral face: a, *Uca iranica* Pretzmann, 1971, male (SMF 34650); b, *Uca cryptica* sp. nov., paratype (SMF 17167).


**Diagnosis.** Front broad. Anterolateral borders of carapace weakly arched, nearly straight. Major male chela palm without supramarginal groove adjacent to lower border, but shallow depression near base of fixed finger. G1 and female genital opening as in *U. annulipes*.

**Redescription.** Front broad, about 1/6.5 times as broad as carapace. Venterolateral margin of carapace (Figs. 6d, 9a) very slightly convergent, nearly straight, distinctly crested; posterolateral margin crested, extending curvedly backwards, ending about in level of middle cardiac region; posterolateral striae short, shortly behind posterolateral margin, slightly lower that latter. Exorbital angle triangular, directed forward; upper orbital margin sinuous, with two crests (lower one faintly crested), bordering narrow eyebrow, getting strongly narrower outwardly, inner part less than 1/2 breadth of eyestalk in adjacent region; lower orbital margin regularly granulate, granules becoming larger on outer one third portion (Fig. 9b).

Pterygostomian region with regular feather-shaped bristle near third maxilliped, becoming glabrous towards lower orbital margin, one longitudinal line of bristle on low-laid antero-inner portion.

Third maxilliped with merus about 1/3 length of ischium; longitudinal broad groove on ischium, merus, close to inner margin, bordered with short setae; long setae on inner margin of ischium, merus.
Major chela merus (Fig. 9d) with transverse ridges on upper margin, finely granulate; inner upper margin distally elevated, granulate; lower margin denticulate, denticles becoming larger distally (Fig. 9c). Carpus about 1.5 times as long as broad, inner upper margin denticulate, 3, 4 proximal denticles remarkably large; outer surface, inner surface and lower margin smooth, glabrous. Outer surface of palm (Fig. 9e) smooth, without supramarginal groove, with shallow depression near base of fixed finger; lower margin weakly granulate, with low granules, upper margin granulate, proximal portion with dense short setae at inner surface; inner surface (Fig. 9f) with high, oblique and tuberculate ridge, granules large, becoming smaller distally; proximal ridge at dactylus base with large granules, distal ridge parallel to proximal one, with granules low, relatively small. Dactylus more than 2 times as long as palm, slightly wider than fixed finger, with subproximal tooth, median teeth nearly in middle; fixed finger with large median tooth on proximal third, located between proximal and middle teeth of dactylus when fingers are closed, subdistal tooth small.

Small chela (Fig. 9g) with smooth ridge on outer surface, extending from lower distal end of palm to proximal two third of fixed finger; cutting edge without tooth, dactylus slightly wider than gap between fingers, gap getting narrower distally, fixed finger slightly higher than dactylus proximally.

Merus of walking legs with finely granulated transverse ridges on anterior margin, posterior margin serrated on proximal half; propodus 1.2 times as long as carpus, propodus of last leg slightly shorter than carpus (Fig. 9h); dactylus conical, as long as propodus; row of brown bristles on anterior and posterior surface of propodus and dactylus, those of dactylus longer.

Male abdomen tapering from segments 2 to 5; segment 6 with lateral margin nearly straight; length of segments 3–5 subequal; segments 5 and 6 of nearly equal length.
G1 (Fig. 9i) with stem bent in posterolateral direction, palp not reaching to base of horny endpiece; latter slightly longer than wide, distal margin convex, dorsal lobe large (Fig. 9k), reaching slightly beyond ventral lobe; terminal opening (Fig. 9j) of sperm channel subdistal ventrally, in midline of endpiece lobes; feather-shaped setae along lateral margin, distally longer, scarce short setae on palp. Genital opening of female as in *U. albimana*.

Median tooth plate of the gastric mill (Fig. 7a) with 6 teeth, with relatively large gaps between them, two first ones massive, different in shape, 3–5 nearly of same size, 6 shorter; lateral tooth plate (Fig. 8a) with 18 comb-shaped teeth.

**FIGURE 9.** *Uca iranica* Pretzmann, 1971: holotype male (NHMW 3788), a, lateral margin of carapace; b, infraorbital region; c, merus of major chela, inner surface; d, merus of major chela, outer surface; e, major chela, outer surface; f, major chela, inner surface; g, minor chela, outer surface; h, last walking leg, left; i, G1, laterla surface; j, apical part of G1, lateral surface; k, apical part of G1, mesial surface.

Remarks. Pretzmann (1971) originally described the species as a subspecies of *U. annulipes* from the Persian Gulf. He recorded both *U. annulipes* and *U. iranica* from the same locality in Bandar-Abbas. The main characteristics given by Pretzmann (1971) to distinguish the two forms were mainly limited to the morphology of the large chelae. Apparently he assigned specimens with chela without large teeth on the cutting edge of the fingers (mainly regenerated form) to his subspecies *U. annulipes iranica*, but in the material examined here both species of *U. iranica* and *U. annulipes* have broadly the same type of chela. Such differences in the major chelae, which in reality refer to the peculiarities of regenerated pincers, are described also by Yamaguchi (1973) for *Uca lactea*. We also include in *U. iranica* the specimens from Bandar-Abbas assigned to *U. annulipes* proper by Pretzmann (1971). Crane (1975) did not mention or discuss the species.

As stated under the remarks for *U. annulipes*, all examined specimens clearly differ from *U. annulipes* and *U. albimana* by the shape of the anterolateral borders. Regarding the median tooth of the gastric mill, this species is clearly different from the two former, but is similar to *U. cryptica* sp. nov. by having 6 teeth on the median tooth of the gastric mill (Figs. 7a, b). In contrast, the lateral tooth of the gastric mill of *U. iranica* is different from *U. cryptica* sp. nov. and allied to *U. albimana* and *U. annulipes*, as *U. iranica* has a narrow lateral tooth plate with about 18 comb-shaped teeth.

*Uca (Austruca) lactea* (De Haan, 1835)
(Figs. 10a–f, 11a–c, 14a, 15a, 18a, b)

Ocypode (*Gelasimus*) lactea De Haan 1835: 54, Pl. 15, fig. 5.


*Ucca (Celuca) lactea* — Dai & Yang 1991: 466, fig. 236 (1), pl. 49 (2).

Paralectotypes. 3 males, 1 female (ZMG 105), Japan, leg. P. von Siebold. [exchanged with Leiden Museum in 1880]; 1 male (MNHN B11967); 1 male (MNHN B11964), [exchanged with Leiden Museum].


K Sakai; 1 male, 1 female (SMF 35009), Kochi, Shimantogawa River, 01.08.1996, K. Sakai; 5 males, 2 females (SMF 35010), Amakusa Island, Kyushu, 04.1974–05.1981, Y. Ono, ded. K Sakai; 1 male, 1 female (SMF 35011), Kochi, Irino, Okata-cho 01.08.1996, K. Sakai.

**Taiwan:** 1 male (SMF 8813) W. coast, Mai Liao, 23° 47'N, 120° 11'E, sandy-mud flat, 02.08.1977, leg. J. Dörjes; 1 male, 2 females (juv.) (SMF 8814), 07.09.1977, leg. J. Dörjes; 1 male (UZM), Tanshui River NW. of Taipei [ex Mus.Milano, 20.02.1922]; 2 Chelas (ZSM), Amping, leg. Haberer; 1 male (ZSM), Takao, 06.1903, leg. Haberer.

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**FIGURE 10.** *Uca lactea* (De Haan, 1835): a, b, c, f, paralectotype male (ZMG 105), Japan; d, e, male (SMF 1813), Taiwan: a, infraorbital region; b, major chela, inner surface; c, major chela, outer surface; d, major chela, inner surface; e, major chela, outer surface; f, G1, lateral surface.
China: 26 males, 5 females (ZMH K6755); 2 males (MNHN B11963); 2 males (ZSM); 3 males (MNHN B11966), leg. M. Callery; 10 males, 3 females (ZMH Ex K3100), 04.09.1919; 13 males, 3 females (ZMH ex K3156), 28.10.1910, leg. G. Siemssen; 1 male (IOASQ), Shajiang, 03.03.1957, leg. Fan & Xu; 4 males, 1 female (ZMH Ex K3154), Fuzhou, 13.06.1903, leg. G. Siemssen; 2 males (IOASQ), Quanzhou, Shengpu, 21.06.1975, leg. H.L. Chen; 2 males, 2 females (IOASQ), Tongan, Xiaodeng, N. of Xiamen, 02.04.1982, leg. H.L. Chen; 5 males, 1 female (MNHN B11965), Xiamen, 07.1925, leg. C.F. Wang; 2 males, 2 females (SMF 17158), Xiamen, Zhongzhai, 26.05.1982, leg. H.L. Chen; 1 male, 1 female (SMF 17159), Dongshan, Beinan, 26.05.1975, leg. H.L. Chen; 1 male (IOASQ); 2 males, 1 female (SMF 17160), Hainan, Haikou, Cangtonqian, 07.06.1958, leg. J.Y. Liu; 1 male, 1 female (IOASQ); 2 males (SMF 17162), Haikou, Beigang, 06.06.1958, leg. J.Y. Liu; 1 male (SMF 17161), Beili, 12.07.1957, leg. J.Y. Liu.

Diagnosis. Front broad. Anterolateral borders moderately convergent. Palm of major male chela without supramarginal groove adjacent to lower border. G1 (Fig. 10f) with palp long, reaching up to distal half of horny endpiece; this last one has inclined flanges, but no strong torsion (Fig. 11c); terminal opening at base of deep emargination of distal margin (Fig. 11b). Genital opening of female (Fig. 11a) and thus also direction of the opercle's edge slightly oblique in respect to median line of sternum.

Distribution. Korea, Japan, Taiwan, China, northern Vietnam. The northern limit in China is in Zhejiang Province, Ise Bay in Japan. Southwards the species reaches Hainan Island, China and northern Vietnam.

**FIGURE 11.** *Uca lactea* (De Haan, 1835): a, female (SMF 17159) Taiwan; b, c, paralectotype male (ZMG 105), Japan; a, genital opening; b, apical part of G1, lateral surface; c, apical part of G1, mesial surface.

Remarks. The species is easily recognisable by the peculiar shape of the G1, especially the large size of the palp. *U. lactea* may easily be distinguished from *U. perplexa*, with which it may be sympatric at least in the Ryukyu Islands, by the lack of a supramarginal groove on the major chela palm as well as by the weakness of the subdistal tooth on the fixed finger of the same limb (Figs. 10b–e), which is more prominent in *U. perplexa* and makes it easily distinguishable from its congener.

The southern distribution of this species is not well known. This applies especially to the Ryukyus, from which it was reported by T. Sakai (1976). Although Sakai mentioned the presence of *U. lactea* in the Ryukyus, but he did not list *U. perplexa* from Japan. Sakai probably ignored Crane's record of *U. perplexa* in the Ryukyus. Crane (1975), however, only recorded *U. perplexa* from this area and our material also belongs to this species. On the contrary, we have not seen any specimen of *U. perplexa* from China. The same applies to our few specimens from Taiwan, which all belongs to *U. lactea*, although the species has been recorded from Taiwan several times (see Ng *et al.* 2001). It has to be checked if *U. perplexa* and *U. lactea* exclude each other.
or if they are sympatric in part of their range. The factors limiting the distribution of the two species also remain unknown. The median tooth of the gastric mill of *U. lactea* (Fig. 14a) is unique among all member of the *U. lactea*-group, but slightly similar to *U. perplexa* rather than others. But regarding the form of the lateral tooth plate of the gastric mill (Fig. 15a) and the number of teeth on it, numbering 22 and being comb-shaped, ally the species with *U. annulipes* and *U. albimana*.

*Uca (Austruca) mjoebergi* Rathbun, 1924  
(Figs. 12d–f, 13a–j, 14b, 15b)

*Uca mjoebergi* Rathbun 1924: 9.  
*Uca lactea mjoebergi* — Crane 1975: 299, figs. 17A–C, 19O–P, 54H, 69B.  

**Material examined. Indonesia:** 1 male (NNM 32589), Indonesia, Irian Jaya (= Western New Guinea), mangroves near Kampong Madong, between Mokmer and Bosnek, SE Biak, 20.02.1955, leg. L.B. Holthuis; 34 males, 14 females (UZM), 1 male (SMF 17163), Banda-Isles, Lontor, Coast near Lavvande, 06.06.1922, "Dan. Expedition to the Kei Islands, 1922"; 2 males, 1 female (UZM), same locality and expedition, 07.06.1922.  
**Australia:** Northern Territory: 2 males (NHMB 574C), Port Darwin, leg. E. Handschin. —Western Australia: 10 males, 13 females (ZMH), 2 males, 2 females (SMF 17155), Broome, mangroves, 24.11.1975, leg. G. Hartmann & G. Hartmann-Schröder; 10 males, 2 females (ZMH); 2 males (SMF 17156), Harbour, 1 km E. of Onslow, about 500 m. from mouth of Beadon Creek, 07.06.1975, leg. G. Hartmann & G. Hartmann-Schröder; 12 males, 4 females (ZMH), Exmouth, external side of peninsula, Reef near Tantabiddy Creek, 11.10.1975 or Carnavon, Pelican Point, inner beach with mangroves, 13.10.1975, leg. G. Hartmann & G. Hartmann-Schröder.  
**Western Samoa:** 1 male (SMF 5676), Upolu, vend. Mus. Goddefroy [this locality is probably wrong].

**Diagnosis.** Front broad. Anterolateral borders of carapace slightly convergent. Palm of major male chela (Figs. 13c, d) without supramarginal groove adjacent to lower margin; oblique ridge at inner surface low. G1 generally as in *U. annulipes*, but horny endpiece comparatively broader, directed remarkably in a dorsolateral direction (Fig. 13e), mesial border of stem between palp and endpiece bulging outward.

**Distribution.** Australia: Northern Territory and Western Australia, New Guinea (where it probably is sympatric with *U. annulipes*), central Indonesia (Sulawesi Tenggara, Pulau Kaledupa) sympatric with *U. perplexa* (Barnes 2010).  
**Remarks.** The most reliable characters to recognise this species is the shape of the G1, especially the curb in the distal part of stem adjacent to the horny endpiece as well as its convexity, of course with a certain amount of variability (see Figs. 11f–i). It is easily distinguished from *U. perplexa* by the lack of the supramarginal groove at the outer surface of the palm of the large male chela. From *U. annulipes* it can be also easily distinguished by this last character. All Australian specimens examined are typical both in the shape of the G1 and the palm of the male chela. In the examined specimens also the oblique ridge on the inner surface of large male chela palm is typically low as described by Crane (1975) and George & Jones (1982). In *U. annulipes* this crest is typically high, but there is a certain amount of variability in this character, so that it cannot be used as good discrimination character. In the specimens from the Banda Archipelago different forms of G1 were found, exhibiting some variations from typical *U. annulipes* to typical *U. mjoebergi* (see Fig. 11f–i). The specimen from New Guinea identified by Crane (1975) as *U. mjoebergi* is quite typical in the major chela. Regarding the features of median and lateral teeth of the gastric mill, this species is readily separated from all other members of this group. The median tooth plate (Fig. 14b) has four teeth, the two first ones being variable in size, the third and fourth ones nearly equal, one very small tooth attached dorsally to the basal plate. The lateral tooth plate (Fig. 15b) is typical in having a shoe-shaped form, with 17 comb-shaped teeth. *U. mjoebergi* has a local distribution in northern and Western Australia (Davie 2002). There are
also specimens from western New Guinea, where it is likely sympatric with *U. annulipes*. More recently, Barnes (2010) recorded this species from Sulawesi Tenggara in central Indonesia in sympaty with four different species of fiddler crabs, including *U. perplexa* from the present group. These records from outside Australia extend its distribution north to South East Asia, but still within Wallacea.

**FIGURE 12.** *Uca annulipes* (H. Milne Edwards, 1837): a, b, Mozambique, Inhaca Island; c, Thailand, Phuket, Ao Tang Kheng. d–f, *Uca mjoebergi* Rathbun, 1924: d, Indonesia, Sulawesi Tenggara; e, f, Australia, Darwin Island. Photos credits: a, b, e, f by T. Detto (The Australian National University); c by S. Komai (Natural History Museum and Institute, Chiba, Japan); d by R.S.K. Barnes (Cambridge University).
FIGURE 13. *Uca mjoebergi* Rathbun, 1924. a–e, male (SMF 17156), Western Australia, 1 km E. Onslow; f–i, males (ZUM), Banda Islands; j, female (SMF 17155), Western Australia, Broome. a, merus of major chela, outer surface; b, merus of major chela, inner surface; c, major chela, outer surface; d, major chela, inner surface; e, G1, lateral surface. f, g, h, i, apical part of G1, lateral surface; j, genital opening of female.

*Uca (Austruca) perplexa* (H. Milne Edwards, 1852)
(Figs. 16a–g, 17a, b, 18c–f)

*Gelasimus perplexus* H. Milne Edwards 1852: 150.
*Uca annulipes* var. *orientalis* — Nobili 1901: 13, 14, fig. A. — Maccagno 1928: 36, fig. 21.
*Uca lactea* — Musgrave 1929: 342, 343 [as *lacteae*]. — Boone 1934: 199, pl. 103.

**Uca (Celuca) lactea lactea** — T. Sakai 1976: 608. [part.]

**Uca (Celuca) lactea annulipes** — T. Sakai 1976: 608. [non Gelasimus annulipes H. Milne Edwards, 1837.]

**Uca lactea perplexa** — Shih et al. 1999: 170.


**Material examined.**

**India:** 1 male (UZM), Nicobar Islands, leg. Reinhardt, "Galathea"-Expedition.

**Thailand:** 1 male (UZM), Malay Peninsula, 1915; 1 male (UZM), Koh Chang, stony coast at low water, 01.1900, leg. T. Mortensen.

**Cambodia:** 4 males, 1 female (UZM), Lam Ngob, mangrove swamp, 23–27.12.1899, leg. T. Mortensen.

**Japan:** 1 male (SMF 35021), exact locality unknown, ded. K. Sakai; 1 male (SMF 35022), exact locality unknown, ded. K. Sakai; 1 male, 1 female (SMF 35023), exact locality unknown, ded. K. Sakai; 3 males (SMF 35024), Ryukyu Islands, Kabira, Ishigaki Island, November 1971, coll. Sakurai, ded. K. Sakai; 2 females (SMF 35018), Amami-Oshima, Tekebu, 24.07.1966, ded. K. Sakai; 4 males (SMF 35025), Okinawa, ded. K. Sakai; 50 males, 24 females (1 ovig.) (SMF 35012), Ryukyu Archipelago, Yaeyama Islands, Ishigaki-jima, April 1973, leg. Y. Ono, ded. K. Sakai; 3 males, 3 males (SMF 35019), Ryukyu Archipelago, Yaeyama

![FIGURE 14. Median tooth of the gastric mill, ventral face. a, Uca lactea (De Haan, 1835), male (SMF 17161); b, Uca mjoebergi Rathbun, 1924, male (SMF 17163).](image-url)

**FIGURE 15.** Lateral tooth of the gastric mill, mesial face. a, *Uca lactea* (De Haan, 1835), male (SMF 17161); b, *Uca mjoeberti* Rathbun, 1924, male (SMF 17163).

**Singapore:** 4 males (UZM), Putan Sudang, tidal zone, bottom coral reef, 19.05.1951 ["Galathea"-Expedition. Stat. 337.]

**Indonesia:** 2 males (SMF 5680), Sumatra, Sipora, leg. Maass; 1 male (ZMG 101), Noordwachter Isl. (Pulo Sebiri) E. of Lampong, 04-05.1885, leg. J. Brock; 1 male (UZM), Padang, leg. Djellerus; 2 males (ZSM), Java, 1929; 3 males (MNHN B12006), 1 male (MNHN B12008), 1 male (MNHN B12009), 1 male (MNHN B12010), Jakarta, leg. Blecker; 7 males, 1 female (UZM), Tjilatjap; 3 males, 1 female (UZM), Soelyi, mangrove beach, 01.04.1909, "T. Mortensne's Java expedition"; 1 male (ZMG 100), Borneo, Pontianac, 1894, leg. Storm; 1 male (MNHN), E. coast, delta of Makaham river, Senipah, 10.1986, leg. Detrieux; 3 males (NHMB 575), Celebes, Kema, 1894, ded. Sarasin; 6 males (ZSM), W-Flores, mangrove beach; 1 male (UZM), Banda Archipelago, Lontor, coast near Lavvande, sand, 06.06.1922, "Danish expedition to Kei Islands 1922"; 1 male (MNHN B11882), Aroe islands, 06.1959, leg. Lorquin; 3 males (ZMG 99), Molucca Archipelago, Ambon, 07–09.1885 leg. J. Brock; 4 male (SMF 5677), Ternate, 1894, leg. W. Kükenthal; 1 male (NNM 32609), W. New Guinea, Mangroves near Kampong Mandong, between Mokmer and Bosnek, SE Biak, 20.03.1955, leg. L. B. Holthuis.

**Papua New Guinea:** 1 male (NHMB 574d), Bismarck Archipelago, Tatau Island near New Ireland, 1933,
ded. A. Bühler; 5 males (ZMH K5768), New Britain, Gazelle Peninsula, Blanche bay, W. coast of volcanic island, 04.08.1908, leg. G. Duncker.

FIGURES 16. Uca perplexa (H. Milne Edwards, 1852): a, male (UZM), Indonesia, Soelyi; b–f, male (UZM), Cambodia, Lam Ngob; g, female (SMF 17146) Japan, Ryukyu Islands. a, major chela, outer surface; b, major chela, outer surface; c, major chela, inner surface; d, G1, lateral surface; e, apical part of G1, lateral surface; f, apical part of G1, mesial surface; g, genital opening of female.
FIGURE 17. *Uca perplexa* (H. Milne Edwards, 1852). male (ZMG 99), Indonesia, Moluccas. Tooth plates of the gastric mill: a, median tooth plate, ventral face; b, lateral tooth plate, mesial face.

**Australia**: 1 male (SMF 17149), Queensland, Bribie Island, N. of Brisbane, W. coast, Banksia beach, mangroves at Dux creek, 31.05.1980, leg. M. Türkay; 10 males, 2 females (ZMH), 3 males (SMF 17148), Tannum Sands 25 km from Gladstone, sand mangroves, 28.01.1976, leg. G. Hartmann & G. Hartmann-Schröder; 1 male (SMF 17158), Innisfail, 28.04.1957, leg. H. Felten; 4 males, 1 female (SMF 17150), Yarabah NE of Cairns, beach, sand mangroves, 06.06.1980, leg. M. Türkay; 3 males, 2 females (SMF 17151), Yule point near Port Douglas, N. of Cairns, mangroves, 08.06.1980, leg. M. Türkay.

**Solomon Islands**: 2 males (MNHN B11968).

**Vanuatu**: 2 males (MNHN B7917), New Hebrides, 03.10.1971, leg. R. Seréne.

**New Caledonia**: 6 males (MNHN B12011); 4 males (MNHN B12013), 1862; 2 males (MNHN B12007), 1903, leg. A. Milne Edwards; 1 male (MNHN B20301), St. 26, 26.09.1978; 1 male (UZM), mouth of Duinbea river, mangrove swamp, 04.12.1928 [*"Dana"*-Station 3618]; 3 males (MNHN B20307), 22.09.1978; 22 males (MNHN B9473), Route de Ocou, 4 km from Noumea, 08.08.1971, leg. R. Seréne.

**Fiji**: 1 male (Ex ZMH K3184); 3 males, 3 females (UZM), Nukumarareko Isl., Suva Bay, 18° 07’S, 178° 24’E, below high water mark on dry sand, leg. T. Wolf.

**Tonga**: 1 male (ZMH K2914); 2 males (UZM), Nukualofa, intertidal, 01.1956, leg. Mischele.

**Samoa**: 1 male (ZMH K2909); 1 male (ZMH K2915); 4 males (SMF 5675), 1904, leg. Hauck; 1 male (SMF 17153), Upolu, vend. Mus. Goddefroy.

**Pacific Ocean**: 1 male (UZM), Mus. Goddefroy, ded. Wroblewsky; 1 male (ZMK Cr.1528), 1876, leg. G. Jantzen.
FIGURE 18. Uca lactea (De Haan, 1835): a, b, Japan, Wakayama Prefecture, Wakayama City Waka River estuary; b, anterior view; c–f, Uca perplexa (H. Milne Edwards, 1852): c, Japan, Ryukyu Islands, Iriomote Island, Urauchi River estuary; d, the same specimen in displaying position; e, Indonesia, Papua, Mimika; f, posterior view. Photo credits: a, b by T. Koga (Wakayama University, Japan); c, d by S. Komai (Natural History Museum and Institute, Chiba, Japan); e, f by A. Darmawan (Indonesian Institute of Sciences).

Wrong or doubtful localities: 1 male (ZNIH K2938), "South Atlantic".
Unknown locality: 4 males (ZMH K6748), vend. J. Umlauf, 04.03.1914.

Diagnosis. Front broad. Anterolateral borders moderately convergent. Major male chela with palm
bearing a supramarginal groove adjacent to lower border, beset with short setae (Figs. 16a, b). G1 (Fig. 16d) with palp long, clearly reaching beyond base of horny endpiece; this last one has inclined flanges, strongly folded towards dorsal direction in comparison to the stem (Fig. 16f); terminal opening of sperm channel at base of shallow emargination of the distal margin (Fig. 16e). Genital opening of female (Fig. 16g) and thus also direction of opercle edge oblique in respect to median line of sternum.

**FIGURE 19.** Distribution pattern of seven species of the subgenus *Uca* (*Austruca*) Bott, 1973 according to recent data.

**Distribution.** Eastern Indian Ocean (from the Nicobar Is. eastward), western and central Pacific Ocean as far north as the Ryukyu Islands to Amami-Oshima. In Australia, the species is distributed throughout the east coast reaching its southern limit around Trial Bay in southern New South Wales.

**Remarks.** Crane (1975) reported one or two intermediate individuals from north-central Philippines, and believed that these emerged from hybridization between *U. perplexa* and *U. annulipes*. She referred mainly to the intermediate form of the G1 of these specimens, and mentioned that interbreeding occurs between these two species in Sunda Shelf. Subsequently, Barnwell (1980) examined specimens of *U. perplexa* and *U. annulipes* from Jakarta, Indonesia, and found three different forms contributing to *U. perplexa*, *U. annulipes* and an intermediate form. He believed that all three are distinct species, but this intermediate form never has been described as a new species. We examined numerous specimens of *U. perplexa* from different locations within its distribution as far as South Australia and Japan, including areas where it was thought to occur sympatrically with *U. annulipes*. *Uca perplexa* deserves specific rank, as G1 and the female genital opening are in all cases different from *U. annulipes* and allies, also from *U. lactea* and *U. mjoeberti*. The strong torsion of the endpiece, together with its prominent emargination is especially distinctive in *Uca perplexa*. The corresponding shape of the female genital opening also allows the recognition of females. The median tooth plate of the gastric mill is a further character that is used to separate this species from its congeners. We,
therefore, do not agree with Crane’s (1975) hypothesis that interbreeding occurs between *U. perplexa*, and *U. annulipes*. However, *U. perplexa* is morphologically more similar to *U. lactea* than to *U. annulipes*. They share similarities in the G1, major chela of the male and the morphology of the median tooth plate of the gastric mill. Genetic results of Shih *et al.* (2009) support this idea by grouping *U. perplexa* with *U. lactea* in the same clade (Clade E by Shih *et al.* 2009). They also treated *U. perplexa* as a good species as did George & Jones (1982).

**Discussion**

This revision shows that the species of the subgenus *Uca* (*Austruca*) are unevenly distributed throughout the Indo-West Pacific region (Fig. 19). Careful comparison reveals that there are regionally restricted species in contrast to broadly distributed ones. At least some of these narrowly distributed species must be the result of regional speciation.

*Uca* (*Austruca*) *annulipes* has the widest range, present from East Africa to the Ogasawara (Bonin) Islands. *Uca* (*A.*) *perplexa* also has a wide range, from the eastern Indian Ocean to French Polynesia. All the remaining species show a more restricted distribution. *Uca* (*A.*) *albimana* is the only species of the subgenus in the Red Sea, presumably well adapted to the high salinity conditions, confirmed by the fact that it also occurs in the highly saline south-western Persian Gulf (Apel & Türkay 1999). *Uca* (*A.*) *iranica* is restricted to the Persian Gulf, including the northern regions that can be quite cold in winter, with water temperatures in coastal regions usually around 10°C, occasionally to 7°C in Kuwait (Sheppard *et al.* 1992) or even 4°C in Qatar (Shinn 1976). In contrast, summer temperatures can be around 39°C (Sheppard *et al.* 1992). This, in combination with high salinity, makes the Persian Gulf a peculiarly harsh marine environment, especially in the north, where *U. (A.)* *iranica* is the only species of the subgenus, presumably well adapted to these extremes and excluding other related species except *U. (A.)* *albimana* in the warmer south-western Gulf. This is best explained as the result of local speciation of both species originating from a basal *annulipes*-stock. This is supported by the genetic relationships shown by Shih *et al.* (2009, Fig. 2), in which *U. annulipes*, *U. albimana* and *U. iranica* are closely related as members of a single clade (Clade W). It is remarkable that the *U. annulipes* specimens used for the genetic analyses are from localities far away from the western Indian Ocean (China, Thailand and Malaysia) and still cluster together with the two others from far west and northwest (there is obviously a mistake in the labeling of fig. 2 in Shih *et al.* (2009) in which *U. iranica* and *U. annulipes* are reversely labeled). It is much more difficult for the remaining species of the subgenus to suggest an origin in correlation with ecological or zoogeographical conditions. An exception may be the eastern Asia *U. (A.) lactea*, which is restricted to temperate and subtropical conditions and therefore might also be the result of a local speciation. If the cladogramm in Shih *et al.* (2009) is taken into account, the basal stock here could be the more widespread *U. (A.) perplexa*. It is noteworthy that *U. mjoebergi* does not cross the Wallace line and therefore is not a Wallacean element (see also Barnes 2010). For *U. (A.) cryptica* n. sp., there is not much information in order to attribute it to a specific biogeographic group. This species is so far only known from Indonesia. The Indo-Malayan Archipelago is a biodiversity hotspot (Roberts *et al.* 2002). Of the subgenus, 4 of 7 species are known from that area while the remaining 3 are restricted to marginal regions.

The present study has also offered the possibility of comparing morphological against genetic character distribution and emerging systems. The genetic cladogramm in Shih *et al.* (2009) is exactly parallel with what we have found in gonopod and gastric mill characters. All other external characters such as cheliped and carapace morphology do not fit the genetic results. Concerning the gonopod morphology, the phylogenetic value for classifications has been on numerous times (e. g., Türkay 1975; Guinot 1979; Brandis *et al.* 1999). For the gastric mill this phylogenetic value is more surprising. It has, however, after its introduction as a character by Yang (1986), been successfully used by K. Sakai *et al.* (2006) and proved a very powerful tool in generic classification, fully in line with gonopodial and other complex character systems. It is again clearly parallel with gonopod morphology and genetic grouping, and it should be used as a routine character in crab systematics.
Acknowledgements

This work would not have been possible without the extensive material borrowed from the collections of several museums listed in the abbreviations under “Materials and methods”. We are thankful to curators who placed this material at our disposal. We are grateful to M. Apel (Museum Mensch und Natur, Munich, Germany) R.S.K. Barnes (Cambridge University, England), D.L. Rahayu (Indonesian Institute of Sciences), T. Komai (Natural History Museum and Institute, Chiba, Japan), T. Koga (Wakayama University, Japan), and P. Backwell (The Australian National University) for providing us with color photos from living animals. We also extend our thanks to the staff of Crustacean section of the Senckenberg Museum, in particular, P. Friesleber, K. Pietratus and F. Mause, who provided us with material and related literature during the study. Special help was received from Kristin Pietratus, who collated the information of the extensive material, its localities and catalogue numbers.

We are greatly indebted to DAAD (German Academic Exchange Service) for financial support in the form of Ph.D. scholarship for R. Naderloo.

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