

Materials for a more stable subdivision of the genus *Uca* Leach¹

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The debate on a proper subdivision of the large genus *Uca* was initiated by the conflicting proposals of Bott (1973) and Crane (1975). In spite of recent computer-aided mending attempts, the overall situation (instability of *Uca* systematics and nomenclature) has not convincingly improved. Here we try to settle the debate by presenting a simple cladistic analysis *sensu* Hennig (1950) based on selected morphological characters supplemented by functional remarks and a few behavioural data resulting from fieldwork. All 94 species (except six) were examined, mostly by using the authors' collection of *Uca* (partly in Marburg and partly deposited in the Leiden Museum) and all species (see list in chapter 5) are assigned to one of the eight subgenera recognized: *Australuca*, *Cranuca* subgen. nov., *Gelasimus*, *Leptuca*, *Minuca*, *Paraleptuca*, *Tubuca*, *Uca* s. str. Some emphasis is laid on a differentiation within the synapomorphies selected: five “major unique inventions” (table 1) are delimited from normal apomorphic character states. The discussion is confined to zoogeographical conclusions, which refer to an early dispersal within “Wegener’s Indo-Atlantic Ocean” and which favour Australia as the centre of origin of the genus *Uca*.

Introduction

The genus *Uca* comprises about 94 species (see list of all species in chapter 5). There is an old practical division into “narrow-fronts” (about 38 species) and “broad-fronts” (about 56 species), which seems to have been sufficient for generations of *Uca* students and which attained formal character by Bott’s subgeneric taxa *Uca* s. str. (narrow-fronts) and *Minuca* (broad-fronts) in a paper on a collection of fiddler crabs from El Salvador (Bott, 1954). Serène (1973) and Guinot (1979) confirmed the biological sense of this division by pointing to the pleonal clasping apparatus (explained below), a key innovation uniting nearly all broad-fronts.

The usual reasons (not to be specified here) led to a further subdivision of the genus (Bott, 1973; Crane, 1975), which may be of some use on certain occasions, e.g. when somebody is watching fiddler crabs in the field and is surprised at seeing the enormous differences within the narrow-fronts (e.g. *U. seismella* and *U. capricornis* in North Australia) or within the broad-fronts (e.g. *U. leptodactyla* and *U. vocator* in the Caribbean).

Unfortunately, the two authors mentioned differed widely with respect to the limits of their new genera (Bott) or subgenera (Crane) and, equally unfortunately, the names of Crane were generally used though mostly invalid (Bott was earlier). Thus the situation was unstable in taxonomic respect as well as in nomenclature (von Hagen, 1976).

¹ On the 80th birthday of Professor Dr Rudolf Altevogt, a pioneer of *Uca* research.

While the present study was on the way, mainly two papers have provided *Uca* cladograms arising from molecular phylogeny analysis (sequences of 16s rDNA for 28 species; Levinton et al., 1996) and morphological phylogeny analysis (236 "discrete" characters of 88 species; Rosenberg, 2001), respectively.

The results of both papers refer to the contents of Crane's subgenera and their zoogeography, but only Rosenberg (2001: 851) made the attempt of a "reassessment of *Uca* subgeneric nomenclature". However, his pertinent Table 6 simply repeats the replacements of Crane's invalid names by the valid names of Bott (as far as necessary), which replacements are known since von Hagen (1976; in the case of *Gelasimus* corrected by Manning & Holthuis, 1981). The new branching systems relevant to the limits and contents of the subgenera have not been explicitly converted into a corrected system, especially not in the case of Crane's apparently paraphyletic "*Celuca*". Pertinent consequences are only shortly mentioned in the discussion among other suggestions (Rosenberg, 2001: 852).

In short, these papers (like many others based on computed cladograms) only put some question marks to the previous system, but leave taxonomists in their old difficulties. In view of this situation we attempt to present distinct definitions of all subgenera (tentative only in the New World broad-fronts), based on a differential weighting of a few characters. The weighting refers to the discreteness of characters as well as to their apomorphy and differentiates within apomorphies.

Animals and Methods

The 94 species of *Uca* recognized in the present paper are listed, with author names, in chapter 5. Of these, nearly all are present in the Collection von Hagen Marburg (abbreviated CVHM; exceptions are given below). This material, partly deposited in Leiden, was supplemented by several loans from the Leiden Museum of Natural History (RMNH), the U.S. National Museum Washington (USNM), the Hamburg Zoological Museum (ZSZM), the Paris Natural History Museum (MNHN) and the Senckenberg Museum Frankfurt/Main (SMFM).

As most of the material examined was mentioned in previous publications already, we give here, in an abbreviated form, only the pertinent data for the eight type species of the subgenera. For the rest, we present a list of the main collecting regions and collectors (including relevant publications) and comment on the species missing in the Marburg collection.

List of type species material of the eight subgenera (in the order of fig. 1)

- U. (Australuca) bellator*.— 1 ♂ (CVHM), Philippines, Manila. 4 ♂♂, 4 ♀♀ (RMNH D 1255), Java, Batavia.
U. (Tubuca) urvillei.— 1 ♂, 1 ♀ (CVHM), India, Vypeen Isld. (Cochin). 27 ♂♂, 4 ♀♀ (CVHM), Thailand, Ao Nam Bor (Phuket).
U. (Gelasimus) vocans.— 11 ♂♂, 2 ♀♀ (CVHM), Bali, Gilimanuk. 20 ♂♂ (CVHM), Philippines, Manila.
U. (Uca) major.— 5 ♂♂, 2 ♀♀ (CVHM) and 1 ♂, 1 ♀ (RMNH D 23035), Trinidad, Diego Martin R. 5 ♂♂, 10 ♀♀ (ZSZM K2991), Haiti.
U. (Cranuca) inversa.— 4 ♂♂ (CVHM), Oman, Salalah (Raysut). 1 ♂, 1 ♀ (CVHM), Egypt, Hurghada (Red Sea). 6 ♂♂ (CVHM), Egypt, Nabq (Sinai). 2 ♂♂ (CVHM), Madagascar, Belo-sur-Mer (Morondava).

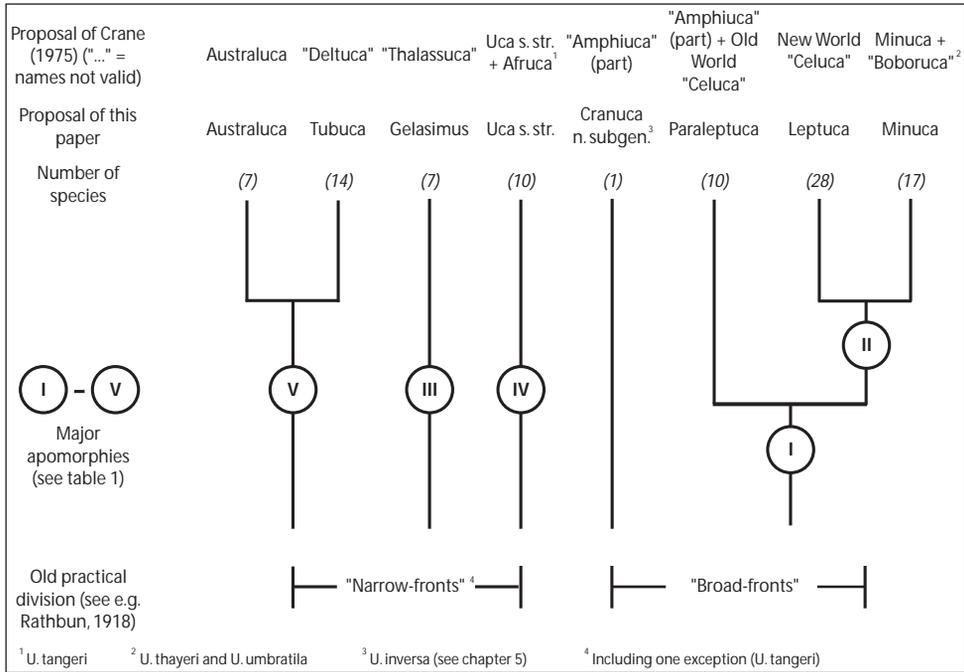


Fig. 1. Synopsis of Crane's (1975) subgeneric system and of the proposal of this paper. In the latter, invalid names used by Crane have been replaced (mostly by the earlier names of Bott, 1973), and the taxonomic units (with number of species in italics) have been corrected mainly according to the "major unique inventions" represented by Roman numerals (explained in table 1, depicted in fig. 3 and 4; I-V correspond to the order of reliability). The isolated *U. inversa* was found to be the only true "broad-front" without synapomorphy No. I and was ranked as a subgenus of its own (*Cranuca*). See figure 2 for the complete cladogram underlying the revised subgeneric system of the present paper and chapter 5 for species lists of all subgenera.

- U. (Paraleptuca) chlorophthalmus*.— 1 ♂ (CVHM), Mauritius. 3 ♂♂, 3 ♀♀ (MNHN), Mauritius, Grand Port. 8 ♂♂ (MNHN), Mauritius, Porte d'Esny.
- U. (Leptuca) stenodactylus*.— 40 ♂♂, 6 ♀♀ (CVHM) and 6 ♂♂, 2 ♀♀ (RMNH D 23057), Peru, Puerto Pizarro (Tumbes).
- U. (Minuca) mordax*.— 27 ♂♂, 22 ♀♀ (CVHM) and 1 ♂, 1 ♀ (RMNH D 23039), Trinidad, L'Ebranche R. 2 ♂♂ (CVHM), Brit. Guiana, Mahaicony Creek.

List of main remaining material of the Marburg Collection (CVHM), summed up according to collecting regions, collectors and pertinent publications

Eastern Pacific.— Peru 1966 (R. Altevoigt, H.O. von Hagen), published by von Hagen (1968), partly deposited in Leiden (RMNH D 23043-23063); Ecuador and Colombia 1966 (R. Altevoigt, H.O. von Hagen); Costa Rica 1992 (B. Beinlich); Mexico 1995 (O. Eitan); California 1971 (H.W. Honegger). **Western Atlantic.**— Brazil 1983, 1986 (S. Götzfried), published by von Hagen (1987a); British Guiana 1966 (J. Darlington). **Caribbean:** Trinidad 1965/66, published by von Hagen (1970a), partly in Leiden (RMNH D 23034-23042); Jamaica 1991-1994 (M. Schuh, C. Schubart); Panama 1966 (H.O. von Hagen), partly in Leiden (RMNH D 25618-25619); Mexico and USA 1964-2000 (M. Salmon, G.W. Hyatt, C.L. Thurman, E. Fründ).

Eastern Atlantic (*U. tangeri*).— Spain 1955-1985 (R. Altevogt, H.O. von Hagen), partly published by von Hagen (1987b); Morocco 1963 (R. Altevogt), Senegal 1976, 1988 (R. Altevogt, S. Dietrich). **Indian Ocean**.— Sinai 1994 (C. Tautz-Kopania); Oman 1993 (S. Dietrich); Kenya 1972 (M. Nebelsick); Madagascar 1992 (J. Gronostay). India 1955-1976 (R. Altevogt); Sri Lanka 1983 (B. Beinlich); Thailand 1972, 1988 (N. Rieder, B. Beinlich); Malaysia 1984-1988 (S. Dietrich, B. Beinlich). **Western Pacific**.— Japan 1987 (T. Yamaguchi); Philippines 1980, 1995 (M.L. Dammann, A. & C. Bogusch); Java and Bali 1983-1994 (B. Beinlich, S. Dietrich, C. Tautz-Kopania); Australia (Darwin, Cairns, Brisbane) 1986-1990 (H.O. von Hagen), partly published by von Hagen & Jones (1989) and partly deposited in Leiden (RMNH D 51705-51718); Fiji Islands 1987 (K.D. Feussner).

Nine species are not represented in the Marburg collection. Of these, six (*U. acuta*, *U. borealis*, *U. formosensis*, *U. limicola*, *U. monilifera*, *U. typhoni*) were classified according to Crane's monograph (1975) or additional literature (see Shih et al., 1999 for *U. formosensis*). The remaining three were examined by the aid of the following Museum specimens:

U. (Minuca) brevifrons.— 4 ♂♂ (ZSZM K3051), Mexico, Salina Cruz.

U. (Minuca) herradurensis.— 1 ♂, 4 ♀♀ (SMFM 1865, 2135), El Salvador, La Herradura. 2 ♂♂, 3 ♀♀ (USNM 32320), Costa Rica, Boca del Jesus Maria.

U. (Paraleptuca) sindensis.— 9 ♂♂, 1 ♀ (Brit. Museum, London 1982.251), Kuwait, Al Memlhal (Doha). 13 ♂♂ (USNM 138046), Pakistan, Karachi. (Material also used by Collins et al., 1984).

Other ocypodids and mictyrids from the Marburg collection (CVHM), which were used for outgroup comparisons, are: *Dotilla myctiroides* (H. Milne-Edwards, 1852), *Macrophthalmus tomentosus* Souleyet, 1841, *Australoplax tridentata* (A. Milne-Edwards, 1873), *Heloecius cordiformis* (H. Milne-Edwards, 1837), *Ocypode cordimana* Desmarest, 1825, *O. cursor* (L., 1758), *O. fabricii* H. Milne-Edwards, 1837, *O. gaudichaudii* H. Milne-Edwards & Lucas, 1843, *O. quadrata* (Fabricius, 1787), *Mictyris longicarpus* Latreille, 1806.

The characters used for a simple cladistic analysis *sensu* Hennig (1950) are mostly morphological ones and are presented in semi-schematic drawings (figs 3-7). Wherever possible, we try to explain the function of a certain morphological construction or its alteration. A few behavioural data resulting from fieldwork are also included.

Some emphasis is laid on a differentiation within the synapomorphies discovered. The different types of synapomorphies referred to throughout the paper are explained in the first chapter of the results. This differentiation is the main reason for a portioned explanation of the reconstructed phylogenetic tree of *Uca* (extending from chapter 1 to chapter 4 of the results).

In addition to the main cladogram (fig. 2), there already exist specialized ones, i.e. analyses within the subgenera chosen (not completed for the New World broad-fronts). Though beyond the scope of the present paper and therefore omitted, these subgeneric trees are referred to in some passages, when the first branch within the subgenus is asked for.

Results

1. Major unique inventions defining reliable units

Differential weighting of characters is mainly the well-known distinction between apo- and plesiomorphic (derived and ancestral) characters or character states. How-

ever, this paper stresses the necessity to further differentiate between synapomorphies. There are several pertinent proposals of emphasizing certain traits: as “uniquely derived characters”, “unequivocal synapomorphies” or “key innovations” (see Rieppel, 1999 for a discussion). We choose the term “major unique inventions” and list the five ones detected in a special table (table 1, cf. figs 1, 3 and 4) with a special (Roman) number system indicating their importance.

The “supporting criteria” added as a second column in table 1 (cf. figs 3 and 4, Roman numerals with preceding “S”) are meant to indicate that the “major unique inventions” (table 1) are not the only common derived characters of the pertinent groups. However, with these supporting criteria we enter the category of “normal” synapomorphies, which are partly prone to compromises: S I is not an independent support, S III is missing in about ten per cent of the males, S IV is only a tendency (see parentheses).

The last column of table 1 gives the systematic units reliably defined by the characters mentioned in the first column, and in figure 1 the Roman numerals have been used to mark the upper branches of a corresponding cladogram, which is, at the same time, a synopsis of two systematic proposals as well as of the invalid and valid subgeneric names (see Introduction and von Hagen, 1976; Manning & Holthuis, 1981), and also the number of species.

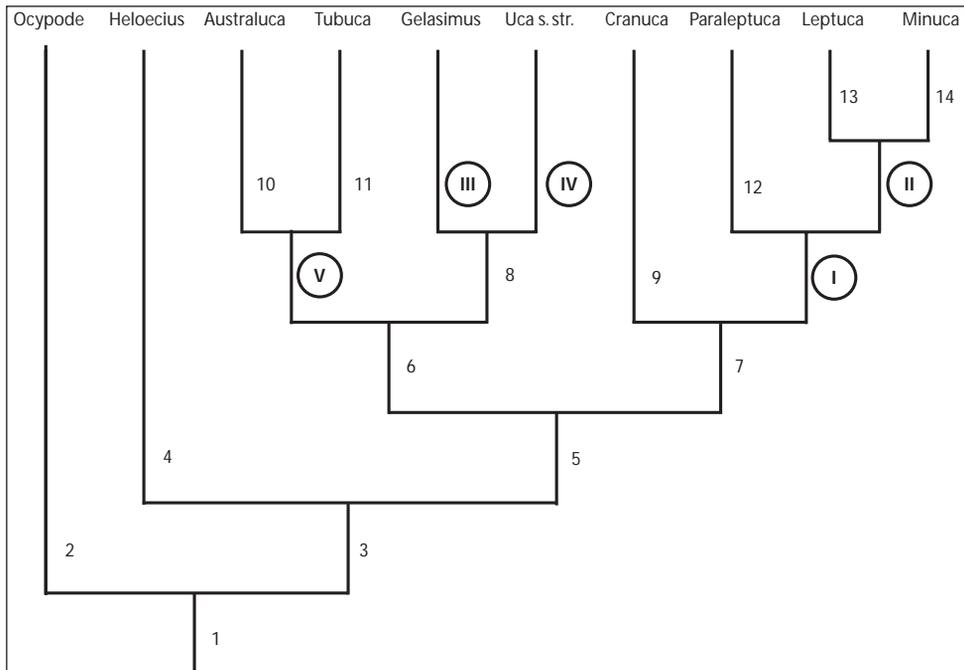


Fig. 2. Complete cladogram underlying the revised subgeneric system of figure 1, further supplemented by the branches leading to the remaining members of the Ocypodinae (*Ocypode* and *Heloecius*). All numerals refer to apomorphies, which are explained partly in table 1 (I-V) and partly by the character lists of chapter 2 (9-14) and chapter 4.1. (1-8), proceeding from top (terminal branches) to bottom (basal internodes). A partly alternative cladogram is given in figure 8.

The next three steps are: to define the remaining terminal branches of the cladogram by “normal” synapomorphies (chapter 2), to establish the number of subgenera (chapter 3) and to comment on the implications of the basal internodes of the cladogram (chapter 4).

2. Apomorphies of the remaining terminal *Uca* branches (fig. 2)

The first of the three tasks named at the end of the previous chapter is to define, by apomorphies, the terminal *Uca* branches not yet characterized in figure 1. This is done by the following survey using the branch numbers of figure 2. The pertinent character states (mostly depicted in fig. 5) are autapomorphies with respect to the subgeneric level, but synapomorphies of all species involved (except for *Cranuca*, which is monotypic). A complete list of species names for each subgenus is given in chapter 5.

List of apomorphies (cf. fig. 2, branches No. 9-14)

- 9 (*Cranuca*, only one species: *U. inversa*, fig. 5a)
 - Dactyl of major chela with huge triangular subdistal tooth.
 - Inner manus with very broad distal predactyl ridge, but without tuberculate oblique ridge as e.g. in fig. 5i.
- 10 (*Australuca*, mostly plesiomorphic compared with No. 11, not well defined by the apomorphies listed)
 - Male gonopod distally tapered, with long tubular projection (fig. 5b, parallel *U. (Tubuca) urvillei* and part of No. 12).
 - Two grooves on outer fingers of major chela (subdorsal groove of dactyl and supramarginal one of pollex) progressively reduced, beginning with *U. elegans* (see fig. 5f-h for details).
- 11 (*Tubuca*)
 - Juveniles conspicuously coloured, not cryptic as usual. Twofold ontogenetic colour change (examples given in von Hagen & Jones, 1989) resulting in juvenile, intermediate and adult colour stages (except in *U. rhizophorae*).
 - Sealing of burrow by thin disk of surface mud exactly fitting in burrow's mouth (photographs in George, 1985: 100).
- 12 (*Paraleptuca*)
 - Terminal flange of male gonopod prolonged: spadelike (fig. 5d, e, shortest in *U. sindensis*) or a very long tube (fig. 5c, parallel No. 10).
 - All subgroups (except *U. sindensis*) contain species (*U. annulipes*, *U. bengali*, *U. crassipes*, *U. triangularis*) the males of which often have a special device against excessive crossing of major chela tips, i.e. large proximal teeth on cutting edges (fig. 5i, 7g), one on dactyl and one on pollex (similar teeth in *Gelasimus* are rare and mostly confined to pollex, fig. 7h).
- 13 (*Leptuca*)

A heterogeneous, little investigated assembly of smaller New World species, some formerly doubtfully included in *Minuca* (see Crane, 1975), about one third with pleon segments No. 4-6 partly or fully fused (e.g. *U. leptodactyla*, fig. 5k).

14 (*Minuca*)

A rather homogeneous assembly of larger New World species with a jerking type of waving display (parallel some species of *Tubuca* and *Australuca*) and with a fixed carapace pattern of two postero-lateral striae (fig. 5l; cf. *Leptuca* with 0-2 striae).

A comparison of the apomorphies given for the branches No. 9-14 of figure 2 reveals that especially the subgenera *Australuca*, *Paraleptuca* and *Leptuca* are difficult to define (naming of exceptions, use of tendencies and of criteria with parallels in other subgenera). The reason is their in general more ancestral status: they stand for the heterogeneous plesiomorphic rest, when the more derived and coherent subgenera *Tubuca* and *Minuca* have been defined.

The question arises, whether *Australuca*, *Paraleptuca* and *Leptuca* are so heterogeneous that they should be subdivided into better-defined branches (cf. *Cranuca*) thus increasing the number of subgenera. This leads to the reflections of the following chapter.

3. Differential weighting of apomorphies and the number and limits of subgenera

In this chapter we have to explain the chosen number of subgenera, which is not in

Table 1. Synapomorphic characters defining five main branches of figure 1: major unique inventions (I-V) and pertinent supporting criteria (S I - S V) (cf. fig. 3 and 4).

| Main apomorphic characters | | |
|---|--|---|
| Major unique inventions | Supporting criteria | Systematic units defined by the characters listed |
| I: Pleonal clasping or locking apparatus (fig. 3b, c) | S I: Two morphological consequences of the new apparatus (fig. 3e) ¹ | "Broad-fronted" subgenera (<i>Paraleptuca</i> , <i>Leptuca</i> , <i>Minuca</i>), except <i>Cranuca</i> |
| II: Two huge brownish setae at base of median tooth of gastric mill (fig. 3g) | S II: Eyebrow (dorsal edge of the orbit) especially broad (fig. 3k) | New World "broad-fronts" (<i>Leptuca</i> and <i>Minuca</i> including <i>U. thayeri</i> and <i>U. umbratila</i>) |
| III: Median tooth of gastric mill with lateral rows of short setae (fig. 3h) | S III: More than 90% of the males "right-handed" (with regard to major cheliped) | Section of Old World "narrow-fronts" (<i>Gelasimus</i>) |
| IV: Spoon-tipped setae of 2 nd maxilliped with a proximal spine opposing the spoon (fig. 4a, b) | S IV: (Stylus on top of major eyestalk may occur in males, fig. 4c) | New World "narrow-fronts" (<i>Uca</i> s.str.) including <i>U. tangeri</i> |
| V: Carpus of major cheliped with delimited antero-dorsal area flattened to facilitate chela flexion (fig. 4e) | S V: Setae on merus of minor cheliped short and stiff (fig. 4g) | Remaining Old World "narrow-fronts" (<i>Tubuca</i> , <i>Australuca</i>) |

¹1. Loss of two ridges on first pleonal segment that prevent pleon from gliding back under rim of carapace.

2. Proximal shift of subterminal hair row on outer telson, probably to facilitate unlocking of pleon by aid of minor chela.

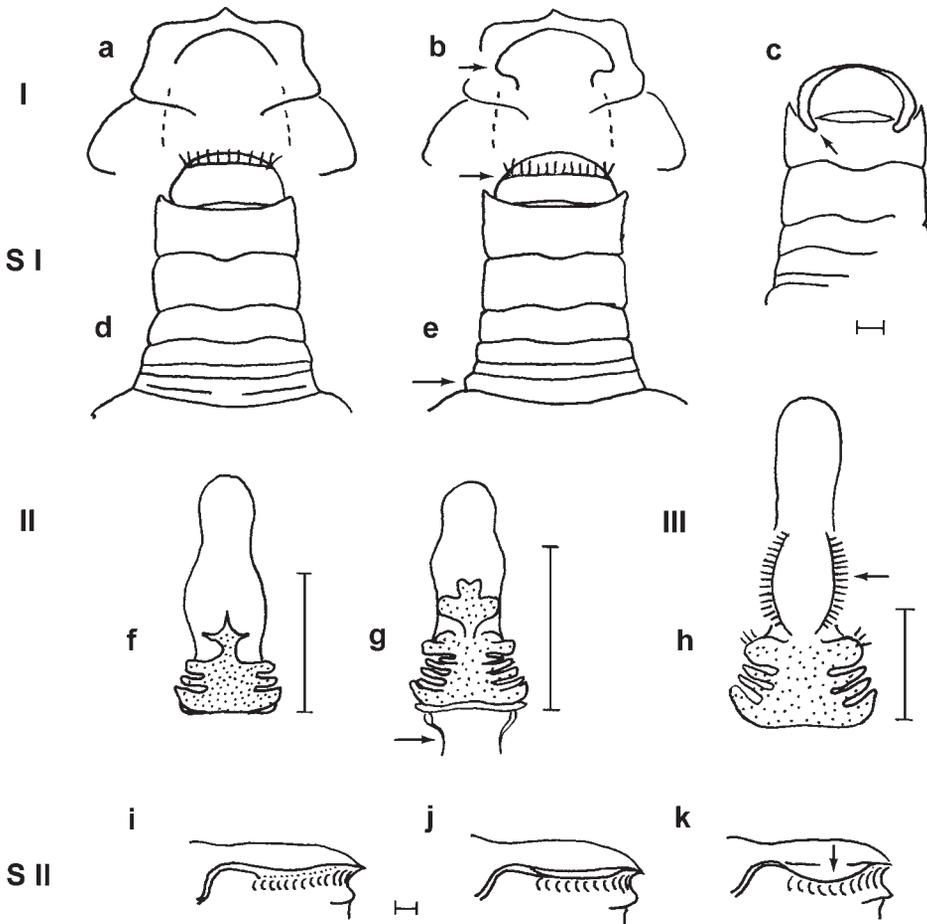


Fig. 3. Major unique inventions I-III and supporting criteria S I - S II, explained in table 1. Arrows point to apomorphic character states. All scales 1 mm. a, b, Thoracic cavity housing pleon, without (a) and with (b) ledges of locking apparatus; c, inner pleon (abdomen) of b with rectum removed to show projections of locking apparatus; d, e, outer pleon in narrow-fronted (d) and broad-fronted subgenera (e) with posterior rim of carapace at base; f, g, h, median tooth of gastric mill in *U. (Australuca) polita* (f), *U. (Leptuca) cumulanta* (g), and *U. (Gelasimus) vocans* (h); i, j, k, anterior view of left eyebrow in *Uca* s.str. (i), *Paraleptuca* (j), and *Minuca* (k).

accord with the proposal of Crane (1975) given in figure 1. Deviations refer to the number (eight instead of nine) as well as to the limits (mostly branches No. 9, 12, 13, 14 in figure 2) of the subgenera.

As explained in chapter 1, the “major unique inventions” (Roman numerals in table 1) are meant to define reliable taxonomic units and lack the compromises and complications of “normal” apomorphies. It is in the course of this reasoning that the proposal of the new subgenus *Cranuca* becomes understandable. Though nearly a “proper” broad-fronted species, *U. (Cranuca) inversa* lacks one of the most important inventions within the whole genus: the pleonal locking apparatus (I in table 1 and fig.

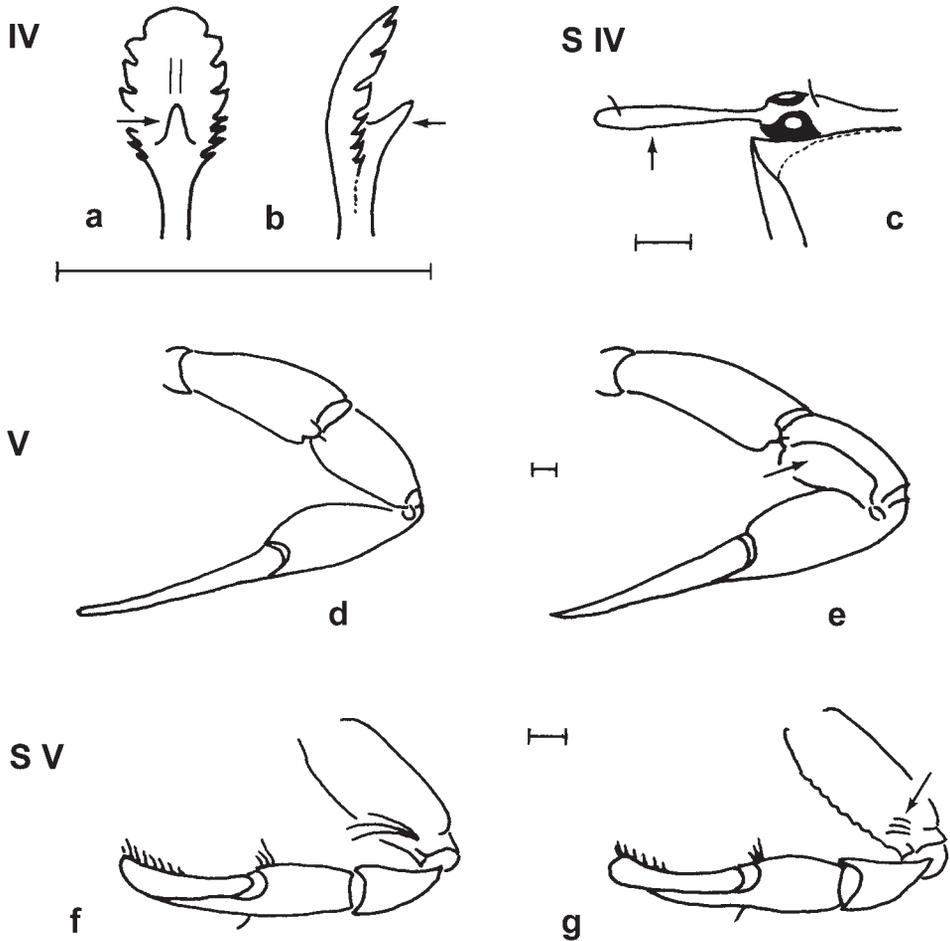


Fig. 4. Major unique inventions IV-V and supporting criteria S IV - S V, explained in table 1. Arrows point to apomorphic character states. All scales 1 mm. a, b. Top of spoon-tipped setae (on 2nd maxilliped in *Uca* s. str.) with proximal spine: view toward concave surface (a) and profile view (b); c, stylus on top of major eyestalk in male *U. (Uca) princeps* in dorsal view; d, e, left major cheliped in dorsal view without (d) and with (e) flattened area of carpus; f, g, tuft of serrated hair on inner merus of minor cheliped consisting of long and thin (f) and short and stiff setae (g).

3b, c) and is thus located between all main branches and best given a branch of its own.

This procedure is in accord with the common cladistic practice of taking the earliest subbranch of a certain branch, declaring it an "adelphotaxon" (term used by Ax, 1984 for sister taxon) of the main branch and giving it a name of its own (here *Cranuca*). However, generalizing this practice without the differentiation between major and minor apomorphies could easily result in an inflation of monotypic subgenera in *Uca*. A cladistic analysis (not yet published) within the subgenera chosen reveals no less than six additional isolated earliest branches that are either candidates for a new subgeneric

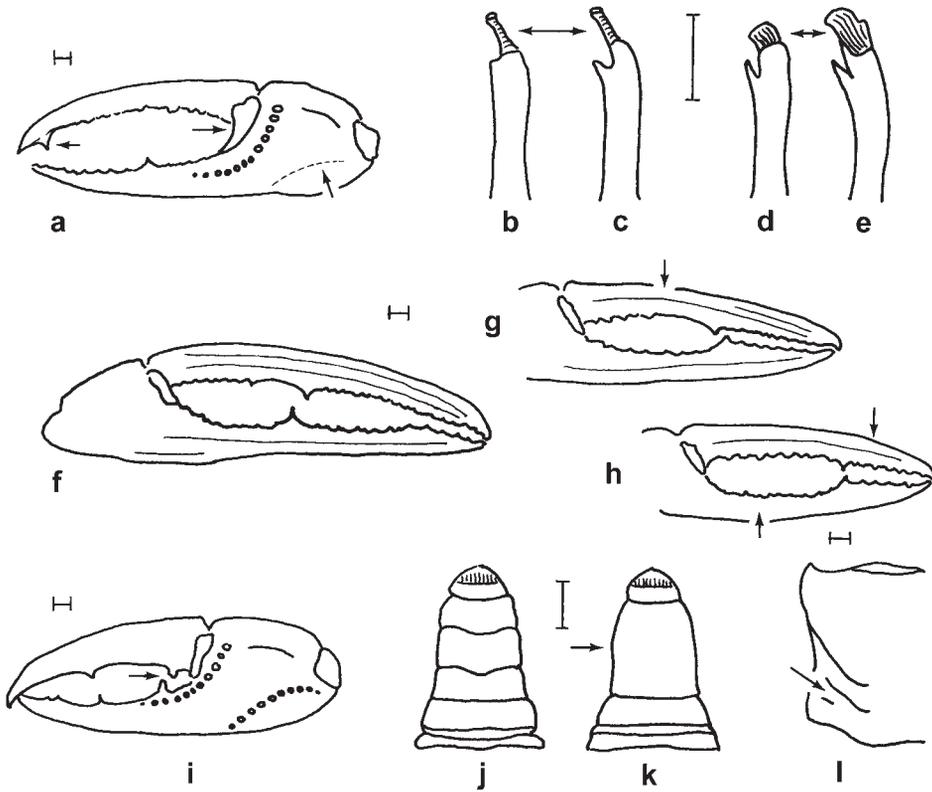


Fig. 5. Apomorphies defining the remaining terminal *Uca* branches (cf. fig. 2, branches with Arabic numerals 9-14, explained in chapter 2). Arrows point to apomorphic character states. All scales 1 mm. a, Inner major chela of *U. (Cranuca) inversa*; b-e, denuded tips of right male gonopods in lateral view: *U. (Australuca) elegans* (b), *U. (Paraleptuca) crassipes* (c), *U. (Paraleptuca) sindensis* (d), *U. (Paraleptuca) annulipes* (e); f, g, h, grooves of outer major chela in *Australuca*: *U. elegans* (f), *U. signata* (g), *U. longidigitum* (h); i, proximal teeth on cutting edges of major chela in *U. (Paraleptuca) bengali*; j, k, outer pleon of male *Leptuca*: *U. cumulanta* (j) and *U. leptodactyla* (k); l, postero-lateral striae of carapace in *Minuca*.

name (not the established one given here in parentheses) or have already been provided with a pertinent name: *U. (Gelasimus) dampieri*; *U. (Australuca) elegans*; *U. (Tubuca) rhizophorae*; *U. (Paraleptuca) sindensis*; *U. (Uca) tangeri* (ranked as *Afruca* by Crane, 1975); *U. (Minuca) thayeri* (ranked as "*Boboruca*" by Crane, 1975).

Taking *U. tangeri* as an example, one has to admit that it clearly represents the earliest branch of *Uca* s. str. and is aberrant in its front width and geography. But it has already the major invention of the subgenus, i.e. the proximal spine of its spoon-tipped setae (table 1). We decided to treat all six cases in the same manner, which means, to leave the first four as listed and to abandon *Afruca* and "*Boboruca*" as proposed earlier (Albrecht & von Hagen, 1981; von Hagen 1970b, 1987a).

A last problem connected with the number of subgenera is the case of *Paraleptuca*

and its controversial limits (see fig. 1 for a short synopsis of non-coincidences with Crane's proposal). The *Paraleptuca* problem is more complicated than those of *Afruca* and "*Boboruca*".

As stated earlier (chapter 2) the subgenus *Paraleptuca* is among the heterogeneous ones. Crane (1975) referred to this incoherence, when she created the new subgenus "*Amphiuca*" in order to separate *U. inversa*, *U. sindensis*, *U. chlorophthalmus* and *U. crassipes* from the remaining Old World broad-fronts (*U. triangularis* and *U. bengali* as well as the *U. lactea*-group), which she included into "*Celuca*".

We follow Crane's opinion only by placing *U. (Cranuca) inversa* in a subgenus of its own (see above) thus saving a small part of her "*Amphiuca*" under a new name. The rest of the Old World broad-fronts (*Paraleptuca*) is united by two synapomorphies (see No. 12 in chapter 2). Of little less importance is the detection of a synapomorphy with respect to the often neglected endostome (it ends in a relatively long sharp median spine) uniting two pairs of *Paraleptuca* species, which Crane (1975) separated by placing them partly in "*Amphiuca*" (*U. chlorophthalmus* and *U. crassipes*) and partly in "*Celuca*" (*U. triangularis* and *U. bengali*), although their similar (tubular) gonopods always suggested a closer relationship.

We finally want to make hesitate any author planning to remove the *U. lactea*-group (*U. albimanus*, *U. annulipes*, *U. lactea*, *U. mjoebergi*, *U. perplexa*) from *Paraleptuca* - perhaps because of their striking slenderness and agility in view of the "clumsier" rest of *Paraleptuca*. A pertinent subgenus would invariably inherit Bott's (1973) name *Austruca* (type species: *U. annulipes*) and a permanent confusion with *Australuca* seems inevitable.

4. Implications of the footing pattern

As all major morphological inventions and all *Uca* ends of the branches of the cladogram in figure 2 have been defined in chapters 1–3, the impression may arise that the material for the subgeneric subdivision of *Uca* has been completely presented. However, the basal branching pattern of figure 2 has some implications (conclusions about the ancestral *Uca* as well as about the monophyly of the genus), which will be treated after listing the synapomorphies for No. 1-8 of the cladogram:

4.1. Synapomorphies of basal internodes (cf. fig. 2, branches No. 1-8):

- 1 (Ocypodinae, comprising *Ocypode*, *Heloeicius* and *Uca*) (fig. 6a, b)
 - Hairy-edged pouch (leading into branchial cavity) between bases of 2nd and 3rd ambulatory leg.
 - Dorso-lateral margin of carapace present.
 - Male genital opening shifted from coxal at least to coxo-sternal position. *Heloeicius* (fig. 6b) has retained this state (Türkay, 1983: fig. 3).
- 2 (*Ocypode*)
 - Major cheliped with stridulatory apparatus: pars stridens on inner manus, plectrum on ischium (fig. 6c).
 - Male genital opening has shifted to advanced sternal position (fig. 6d) behind border separating 7th and 8th thoracic sternite (Guinot, 1979: fig. 53B).

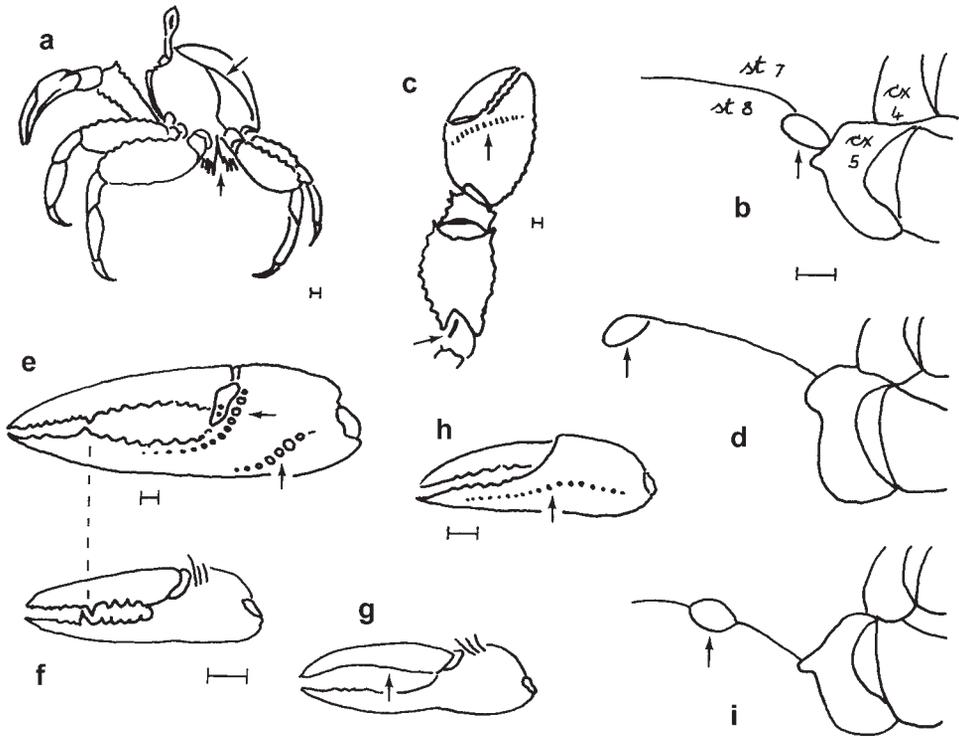


Fig. 6. Synapomorphies defining the basal internodes (cf. fig. 2, branches with Arabic numerals 1-5, explained in chapter 4). Arrows point to apomorphic character states. All scales 1 mm. a, Common traits of *Ocypodinae*: hairy-edged pouch between bases of 2nd and 3rd ambulatories, dorso-lateral margin of carapace (example: *Ocypode*); b, *Heloecius cordiformis*: male genital opening between coxa (cx) of 5th pereopod and 8th thoracic sternite (st); c, d, *Ocypode cursor*: stridulatory apparatus on inner major cheliped (c) and male genital opening in 8th thoracic sternite (d); e, f, *U. (Australuca) polita*: inner major chela (e) and female minor chela (f), dotted line separates corresponding chela sections; g, *U. (Paraleptuca) annulipes*: minor chela with teeth reduced; h, *Heloecius cordiformis*: oblique ridge on inner manus of chela in females and juvenile males; i, *U. (Gelasimus) tetragonon*: male genital opening on border between 7th and 8th thoracic sternite. (b adapted from Türkay, 1983; d and i from Guinot, 1979).

3 (*Heloecius* and *Uca* s. l.)

- A tuft of a few long serrated setae subdistally on inner merus of chelipeds in females (fig. 4f), in males confined to minor cheliped (*Uca*) or missing (*Heloecius*).
- Oblique tuberculate ridge on inner manus of major cheliped (*Uca* males, fig. 6e) or both chelipeds (*Heloecius* females and juvenile males, fig. 6h).
- Waving display also in females (Salmon, 1984; von Hagen 1993), lost mainly in *Uca* s. str. and in all broad-fronts (cf. No. 7).

4 (*Heloecius*)

- Male pachychelous, resulting in indistinct chela structures (compared with females).

- 5 (*Uca* s.l.)
- Male genital opening has (independently of *Ocypode*, Guinot, 1979) shifted to moderate sternal position (fig. 6i) right in the middle of border between 7th and 8th thoracic sternite (Guinot, 1979: fig. 53A).
 - Male extremely heterochelous. To keep heavy major cheliped in position when folded, a support (acting like pliers or a clamp) for the merus is formed by two normally tuberculate ridges on inner manus: the oblique ridge (cf. No. 3) and a proximal predactyl ridge (fig. 6e).
 - Carapace with one or two postero-lateral striae (fig. 5l, lost in *Uca* s. str. and a few species of other subgenera).
 - Outer fingers of major chela have lost prominent narrow ridges of ancestors (still present in outgroups like Dotillinae and Mictyridae), but have retained the adjoining space as grooves (fig. 5f), two on dactyl and one on pollex (pattern may be complete or in all stages of reduction).
 - Minor chela (at first more reminiscent of major chela, fig. 6f, i.e. with larger teeth on cutting edges, still present in *Australuca* and some females of *Tubuca*) with progressive reduction of teeth (fig. 6g).
 - Colour pattern of carapace originally with many or few horizontal stripes (fig. 7a, b, retained only in a few species of *Australuca*, *Tubuca* and *Paraleptuca*).
 - Waving display originally with diminishing waves regularly at the end of a wave series (still present in some species of *Australuca*, *Tubuca* and *Paraleptuca*).
- 6 ("Narrow-fronts")
- Front (i.e. tongue-like inter orbital region) stays moderately narrow as in *Heloecius* (fig. 7c) or becomes very narrow to spatuliform (extreme: *Uca* s. str., fig. 7d; functional explanation in von Hagen, 1970b; exception: *U. tangeri*).
 - Outer manus of major chela with large tubercles, which are largest in ventral part and especially near base of pollex (fig. 7f, h).
- 7 ("Broad-fronts")
- Front becomes broader than in *Heloecius* (fig. 7e).
 - Dactyl of major chela (originally of about the same length as pollex, fig. 7f) prolonged, bending hook-like around tip of pollex (fig. 7g).
 - Complete loss of female waving display (parallel in *Uca* s. str.).
- 8 (*Gelasimus* and *Uca* s. str.) (fig. 7h)
- Dactyl of major chela shortened, shorter than pollex.
 - Pollex (and sometimes also dactylus) of major chela dorsoventrally broadened and laterally flattened.
 - A special combination of waving display and locomotion (see Altevoigt, 1972; von Hagen, 1973), lost in some species.

4.2. Monophyly of the genus, definition of ancestral *Uca* and an alternative basal branching pattern

The number of seven synapomorphies for No. 5 of the above list (chapter 4.1.) is meant to stress the conception of *Uca* s. l. forming a monophylum (cf. doubts raised by Türkay in Salmon, 1983).

The synapomorphies listed under No. 1, 3 and 5 comprise the essential characters of

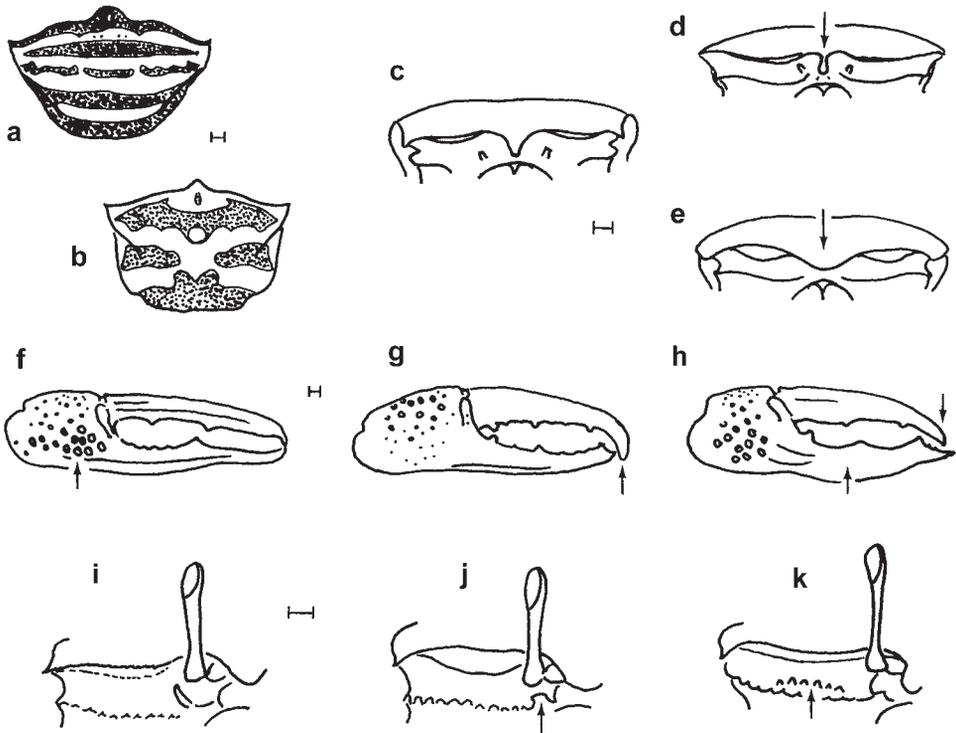


Fig. 7. Synapomorphies defining the internodes (cf. fig. 2 and 8) with Arabic numerals 5-8 (and 6') explained in chapter 4. Arrows point to apomorphic character states. All scales 1 mm. a, b, Ancient colour pattern with horizontal stripes in *U. (Paraleptuca) triangularis* (a) and *U. (Australuca) signata* (b); c, d, e, front (interorbital region of different width) in anterior view in *Heloecius cordiformis* (c), *U. (Uca) major* (d), and *U. (Minuca) mordax* (e), eyes omitted; f, g, h, outer major chela of *U. (Tubuca) urvillei* (f), *U. (Paraleptuca) annulipes* (g), and *U. (Gelasimus) vocans* (h); i, j, k, orbital armature in *U. (Uca) tangeri* (i), *U. (Leptuca) panamensis* (j), and *U. (Tubuca) urvillei* (k).

primordial or ancestral *Uca* and must not be repeated here. However in addition to the synapomorphies of the Ocypodinae (see No. 1), this ancestral *Uca* inherited the plesiomorphies of the subfamily, above all an isolated tubercle at the inner corner of the orbital floor (fig. 7d, i) serving to secure the eyestalk in its depressed position. Tubercles of this kind are found also in the outgroups (ocypodids of other subfamilies and micrityrids) as well as in *Heloecius* (fig. 7c) and all species of *Ocypode*.

In *Uca* the tubercle has vanished in all subgenera except *Uca* s. str. (a somewhat differently located equivalent in male *U. (Leptuca) panamensis* is considered a new character, fig. 7j). The question arises, why all other subgenera are able to thrive without this tubercle. They invented a provisional substitute (later replaced by other devices as broadening of eyebrow), namely one or more rows of tubercles, partly on mounds, behind the lower orbital border (fig. 7k). These, in turn, are normally missing in *Uca* s. str.

The different orbital armature mentioned was taken as a reason for trying an alternative cladogram with a partly different branching pattern (fig. 8), which at the same

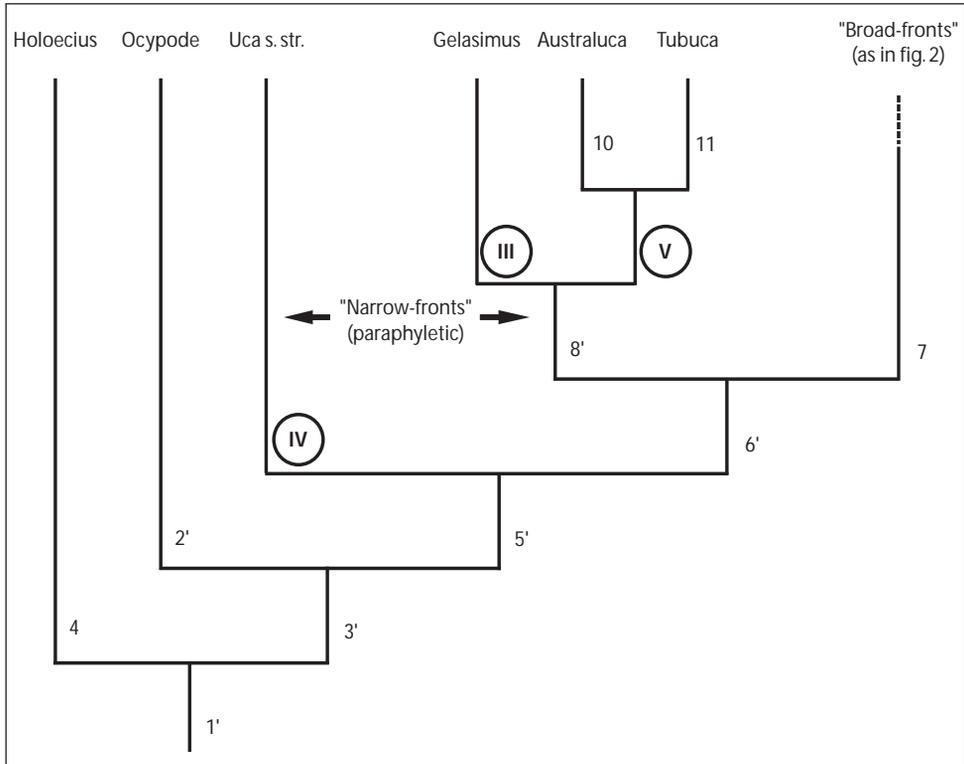


Fig. 8. Alternative cladogram with a partly different branching pattern (cf. fig. 2). Note the altered position of *Ocypode* (closer to *Uca*) and the now paraphyletic character of the “narrow-fronts”. The alternative does not affect the number and limits of the subgenera proposed.

time tests an alternative position of the genus *Ocypode* (closer to *Uca*). Branches with a new definition have been provided with a mark (e.g. 2'), for the remaining numbers (without marks) see chapter 4.1.

List of alternative synapomorphies (fig. 8):

- 1' (*Ocypodidae*)
 - A combination of No. 1 and No. 3 of fig. 2.
- 3' (*Ocypode* and *Uca*)
 - Invention of a proximal predactyl tuberculated ridge on inner manus of chela, used in a different manner in *Ocypode* and *Uca* later on.
- 2' (*Ocypode*)
 - Proximal predactyl ridge used as part of stridulating organ.
 - Loss of the three common characters of *Heloecius* and *Uca* (listed as No. 3 in fig. 2), possibly because of evolutionary shift into a new habitat (sandy beaches).
- 5' (*Uca* s.l.)
 - As No. 5 in fig. 2, but postero-lateral striae not yet present.

6' (All *Uca* subgenera except *Uca* s. str.)

- Loss of isolated tubercle at inner corner of orbital floor serving to secure depressed eyestalk. A provisional substitute (one or more rows of tubercles, partly on mounds, within orbita behind its lower border) is retained only in some species of *Australuca*, *Tubuca* and *Paraleptuca*.

- Carapace with one or two postero-lateral striae (fig. 5l) in most species.

8' (*Gelasimus*, *Australuca* and *Tubuca*)

- As No. 6 in fig. 2, parallel to No. IV; i.e. *Uca* s. str. independently acquired the same characters (narrow front and distribution of outer manus tubercles) as well as the traits shared with *Gelasimus* (No. 8 in fig. 2).

The alternative branching of fig. 8 renders the "narrow-fronts" a paraphyletic group and shifts the cladogram somewhat nearer to the proposals of Levinton et al. (1996) and Rosenberg (2001), but has to cope with a relatively large number of parallels (see No. 8') and secondary losses (see No. 2'). The alternative does not affect the number and limits of the subgenera proposed and does not question the monophyly of the genus, nor the pattern of early dispersal (see below, fig. 9).

5. Taxonomic survey with list of all species

Crane (1975) listed 91 forms (species and several subspecies) of *Uca*. Because of inconsistencies of her subspecies concept (see von Hagen, 1976) most subspecies were treated as species by subsequent authors. We follow this trend - in a few cases (*U. crassipes*, *U. hirsutimanus*, *U. longisignalis*) with some hesitation only, because they may be ranked as subspecies of *U. chlorophthalmus*, *U. bellator* and *U. minax*, respectively.

After the appearance of Crane's monograph a small number of additional species was described. Of these, some were synonymized with known taxa, but six were accepted as new by several authors: *U. panacea* Novak & Salmon, 1974; *U. marguerita* Thurman, 1981; *U. elegans* and *U. hirsutimanus* George & Jones, 1982; *U. intermedia* von Prahl & Toro, 1985; *U. victoriana* von Hagen, 1987a. A seventh form was favoured by Lewinsohn (1977) as being separate from *U. annulipes*, namely *U. albimana* (Kossmann, 1877).

These seven additional taxa have to be balanced with four taxa that should be deleted from Crane's list:

- *U. australiae* Crane, 1975: a doubtful taxon based on one mysterious male (George & Jones, 1982),
- *U. minima* Crane, 1975: = juveniles of *U. signata* (see George & Jones, 1982),
- *U. virens* Salmon & Atsides, 1968: = *U. rapax* (see von Hagen, 1980; Barnwell & Thurman, 1984),
- *U. leptochela* Bott, 1954: = juveniles of *U. festae* (von Hagen, unpublished).

In all, additions and deletions result in 94 species, which can be arranged as follows (a few names are provided with special remarks in parentheses):

Australuca Crane, 1975

Type species: *U. bellator* (Adams & White, 1848)

- | | |
|--|---|
| <i>U. bellator</i> (Adams & White, 1848) | <i>U. longidigitum</i> (Kingsley, 1880) |
| <i>U. elegans</i> George & Jones, 1982 (transferred from <i>Tubuca</i> by von Hagen & Jones, 1989) | <i>U. polita</i> Crane, 1975 |
| <i>U. hirsutimanus</i> George & Jones, 1982 | <i>U. seismella</i> Crane, 1975 |
| | <i>U. signata</i> (Hess, 1865) |

Tubuca Bott, 1973Type species: *U. urvillei* (H. Milne-Edwards, 1852)

- | | |
|--|--|
| <i>U. acuta</i> (Stimpson, 1858) | <i>U. formosensis</i> Rathbun, 1921 |
| <i>U. arcuata</i> (de Haan, 1835) | (transferred from <i>Gelasimus</i> by Shih et al., 1999) |
| <i>U. capricornis</i> Crane, 1975 (= <i>U. pavo</i> George & Jones, 1982) | <i>U. paradussumieri</i> Bott, 1973 (= <i>U. spinata</i> Crane, 1975) |
| <i>U. coarctata</i> (H. Milne-Edwards, 1852) | <i>U. rhizophorae</i> Tweedie, 1950 |
| <i>U. demani</i> Ortmann, 1897 | <i>U. rosea</i> (Tweedie, 1937) |
| <i>U. dussumieri</i> (H. Milne-Edwards, 1852) | <i>U. typhoni</i> Crane, 1975 |
| <i>U. flammula</i> Crane, 1975 | <i>U. urvillei</i> (H. Milne-Edwards, 1852) |
| <i>U. forcipata</i> (Adams & White, 1848) | |

Gelasimus Latreille, 1817Type species: *U. vocans* (Linnaeus, 1758)

- | | |
|--|-------------------------------------|
| <i>U. borealis</i> Crane, 1975 | <i>U. tetragonon</i> (Herbst, 1790) |
| <i>U. dampieri</i> Crane, 1975 | <i>U. vocans</i> (L., 1758) |
| <i>U. hesperiae</i> Crane, 1975 | <i>U. vomeris</i> McNeill, 1920 |
| <i>U. neocultrimana</i> Bott, 1973 (= <i>U. pacifensis</i> Crane, 1975) | |

Uca s. str. Leach, 1814Type species: *U. major* (Herbst, 1782)

- | | |
|---|--|
| <i>U. heteropleura</i> (Smith, 1870) | <i>U. monilifera</i> Rathbun, 1914 |
| <i>U. insignis</i> (H. Milne-Edwards, 1852) | <i>U. ornata</i> (Smith, 1870) |
| <i>U. intermedia</i> von Prael & Toro, 1985 | <i>U. princeps</i> (Smith, 1870) |
| <i>U. major</i> (Herbst, 1782) | <i>U. stylifera</i> (H. Milne-Edwards, 1852) |
| <i>U. maracoani</i> (Latreille, 1802-1803) | <i>U. tangeri</i> (Eydoux, 1835) |

Cranuca **subgen. nov.**

(fig. 5a)

Diagnosis.— The most ancestral broad-fronted *Uca*, still lacking a pleonal clasping apparatus (table 1) contrary to the data of Rosenberg (2001: 867, no. 221). (The only

other species combining a broad front and the lack of the apparatus, *U. tangeri*, is a member of the well-defined subgenus *Uca* s. str.).

Type species.— *U. inversa* (Hoffmann, 1874).

Description and type material.— see Crane (1975: 105-107).

Only one species.— *U. inversa* (Hoffmann) (not *U. sindensis* (Alcock)).

Paraleptuca Bott, 1973

Type species: *U. chlorophthalmus* (H. Milne-Edwards, 1837)

U. albimana (Kossmann, 1877)

(see Lewinsohn, 1977)

U. annulipes (H. Milne-Edwards, 1837)

U. bengali Crane, 1975

U. chlorophthalmus (H. Milne-Edwards, 1837)

U. crassipes (Adams & White, 1848)

U. lactea (de Haan, 1835)

U. mjoebergi Rathbun, 1924

U. perplexa (H. Milne-Edwards, 1852)

U. sindensis (Alcock, 1900)

U. triangularis (A. Milne-Edwards, 1873)

Leptuca Bott, 1973

Type species: *U. stenodactylus* (H. Milne-Edwards & Lucas, 1843)

U. batuenta Crane, 1941

U. beebei Crane, 1941

U. crenulata (Lockington, 1877)

U. coloradensis (Rathbun, 1893)

U. cumulanta Crane, 1943

U. deichmanni Rathbun, 1935

U. dorotheae von Hagen, 1968

U. festae Nobili, 1902

U. helleri Rathbun, 1902

U. inaequalis Rathbun, 1935

U. latimanus (Rathbun, 1893)

U. leptodactyla Rathbun, 1898

U. limicola Crane, 1941

U. musica Rathbun, 1914

U. oerstedii Rathbun, 1904

U. panacea Novak & Salmon, 1974

U. panamensis (Stimpson, 1859)

(transferred from *Minuca*)

U. pygmaea Crane, 1941

(transferred from *Minuca*)

U. pugilator (Bosc, 1802)

U. saltitanta Crane, 1941

U. speciosa (Ives, 1891)

U. spinicarpa Rathbun, 1900

U. stenodactylus

(H. Milne-Edwards & Lucas, 1843)

U. subcylindrica (Stimpson, 1859)

(transferred from *Minuca* by

Barnwell & Thurman, 1984)

U. tallanica von Hagen, 1968

U. tenuipedis Crane, 1941

U. terpsichores Crane, 1941

U. uruguayensis Nobili, 1901

Minuca Bott, 1954

Type species: *U. mordax* (Smith, 1870)

U. argillicola Crane, 1941

(transferred from *Leptuca*
by Levinton et al., 1996)

U. marguerita Thurman, 1981

U. minax (LeConte, 1855)

U. mordax (Smith, 1870)

| | |
|--|--------------------------------------|
| <i>U. brevifrons</i> (Stimpson, 1860) | <i>U. pugnax</i> (Smith, 1870) |
| <i>U. burgersi</i> Holthuis, 1967 | <i>U. rapax</i> (Smith, 1870) |
| (= <i>U. panema</i> Coelho, 1972) | <i>U. thayeri</i> Rathbun, 1900 |
| <i>U. ecuadoriensis</i> Maccagno, 1928 | <i>U. umbratilis</i> Crane, 1941 |
| <i>U. galapagensis</i> Rathbun, 1902 | <i>U. victoriana</i> von Hagen, 1987 |
| <i>U. herradurensis</i> Bott, 1954 | <i>U. vocator</i> (Herbst, 1804) |
| <i>U. longisignalis</i> Salmon & Atsides, 1968 | <i>U. zacaе</i> Crane, 1941 |

6. Discussion: zoogeographical conclusions

6.1. Present views

There are three major zoogeographical hypotheses with respect to the origin of the genus *Uca*. The primary center of dispersal was either

1. the Indo-West Pacific region or
2. the shores of the whole Tethys (the circumtropical sea of late Mesozoic to Lower Miocene) or
3. the New World.

Crane (1975) discussed all three opinions and rightly chose the first one. Unfortunately, she connected it with some additional assumptions:

- An exchange with the New World via the tertiary Bering Strait region: stock members of *Gelasimus* (and perhaps *Australuca*) migrating east and part of Crane's "*CelUCA*" (i.e. part of *Paraleptuca*) returning west.
- Intertidal ascent of *Uca* habitats and correlated development of behavioural complexity increasing with distance from the centre of origin, thus highest in the New World and re-imported into the Old World only by the return of "*CelUCA*" mentioned above.

The critics of Crane's concept (Salmon & Zucker, 1988; Levinton et al., 1996; Sturmbauer et al., 1996) opposed to these additional assumptions and rightly so: the present paper confirms e.g. that there was never a return from America (i.e. any return of *Lep-tuca* and *Minuca* united by synapomorphy II of table 1) to the Indo West Pacific.

But at the same time, Salmon and Zucker (1988) revived the Tethys hypothesis mentioned above. This can be called an evasive action, because little is gained by the assumption that a continuous uniform Tethyan fauna with both narrow- and broad-fronts existed from the beginning. What was before the beginning? Even if there are "dangers of postulating evolution from a centre of origin" (Levinton et al., 1996: 117), such a postulate is a usual topic in zoogeography.

Consequently, the same authors concede that, though they favour the hypothesis of Salmon & Zucker (1988), they must insist on the ancestral status of *Uca* s. str. (including *U. tangeri* = *Afruca* Crane), which appears from their analysis of 16 S rDNA. This ancestral status of *Uca* s. str. leads the authors in a parallel paper to an Atlantic centre of origin: "We suggest that the ancestors of all fiddler crabs may have arisen in the Proto-Atlantic" (Sturmbauer et al., 1996: 10856), i.e. on the East Coast of America and the West Coast of Africa, which means that, finally, the third hypothesis (see above) has been revived.

We think that, surprisingly, a certain synthesis of all hypotheses mentioned will be

possible with the aid of Wegener's Indo-Atlantic Ocean (see following section 6.2.). However, a few premises have to be discussed first:

With respect to the 16 S rDNA analysis of Levinton et al. (1996) mentioned, some reserve is necessary. Cases of incongruence between morphological and DNA characters are frequent in literature meanwhile, especially when the molecular data set is not based on an advanced type of handling the pertinent sensitive methods. In the case of the paper mentioned (Levinton et al., 1996), the problem of long-branch-attraction (see e.g. Wägele, 2001) seems to have not been taken into account. The result is a common branch of the ocyropodid *Scopimera* and the gecarcinid *Cardisoma* (!) and an alleged affinity of *Macrophthalmus latifrons* Haswell, 1881, and *Heloeccius cordiformis* (H. Milne Edwards, 1837). The long-branch-effect can be responsible for an assumed special affinity of *Uca* s. str. and *Ocyropode* as well. The most improbable result however, is the ranking of *Gelasimus* ("Thalassuca" Crane) in the midst of the broad-fronted "*Celuca*", which would mean that the "key innovation" (pleonal apparatus, table 1) has been secondarily lost in *Gelasimus*.

The more recent computer analysis of 236 morphological characters of *Uca* (Rosenberg, 2001) consistently ranks *Gelasimus* nearer to the Indo-West Pacific narrow-fronts (see also Suzawa et al., 1993). But unfortunately, Rosenberg's paper is not an independent source with respect to the ranking of the subgenus *Uca* s. str. The author states himself: "...the results of the Levinton et al. (1996) and Sturmbauer et al. (1996) studies were followed, the subgenera *Uca* and *Afruca* sensu Crane were used to root the tree." (Rosenberg 2001: 847).

6.2. Wegener's Indo-Atlantic Ocean

The scarcity of *Uca* fossils renders any reconstruction of the genus' early dispersal very difficult. *U. (Uca) maracoani antiqua* from Pará, Brazil (Brito, 1993) is the earliest member known and the only fossil fiddler of the Miocene. One can, however, combine this fossil subspecies with those recent species that form isolated early branches (mentioned in chapter 3 and in the legend of fig. 9) and record this assemblage together with *Heloeccius* in a map of the lower Tertiary. The pertinent drawings (fig. 9) consider narrow-fronts (left) and broad-fronts (right) separately. The position of the continents in upper Eocene (adapted from Stanley, 1994) was chosen, because *Uca* is still typically associated with certain species of mangroves (*Rhizophora*, *Avicennia*, *Sonneratia*) that appeared in the late Eocene of West Australia (palynological evidence compiled in Specht, 1981).

The *Uca* entries in the two maps of figure 9 form a "garland" of species on the shores of two smaller oceans, which can be tied together as "Wegener's Indo-Atlantic Ocean" and which suggest a southern route (around South Africa) of early dispersal, at least in the case of the narrow-fronts (left map). As for the broad-fronts, some early descendants of *Paraleptuca* may have used the Tethys (before its closure by the North drift of Africa during middle Miocene) for a passage to the Caribbean region to create the more derived New World broad-fronted subgenera *Leptuca* and *Minuca*, which seem to have secondarily invaded the area of the New World members of *Uca* s. str. When no longer taken as a subgenus of its own, *U. thayeri* (see chapter 3) is probably the oldest member of *Minuca*, but the earliest branch of *Leptuca* is not clear. Abbreviations of the subge-

neric names (L and M) have been used in both cases (see right map of fig. 9).

Why should one refer to a Tethyan passage for these two New World subgenera and not to the southern route as before? Because of the two brownish setae at the base of the gastric mill (II in table 1, cf. fig. 3g). This synapomorphy of all New World broad-fronts is unique with respect to the huge dimensions it has in *Leptuca* and *Minuca*. However, the setae have very thin "golden" precursors. Of all Indo-West Pacific broad-fronts, only *U. (Cranuca) inversa* and *U. (Paraleptuca) sindensis* have preserved these precursory structures (von Hagen, unpublished) and these two species still are to be found as "guardians" near the former eastern portals of the Mediterranean section of the Tethys, i.e. on the shores of Arabia and East Africa and Kuwait to Pakistan, respectively (right map of fig. 9).

In all, Wegener's Indo-Atlantic Ocean and the Tethyan supplement make it easier to understand the dispersal of the genus. The old puzzle, how the *Uca* migrants overcame the formidable barrier of the East Pacific, is no question any longer. They never crossed the Pacific, but travelled West, starting from Australia.

Australia as the centre of origin in the strict sense was already favoured by Crane (1975: 439), who at first supposed a Malaysian origin of the genus (Crane, 1956), but

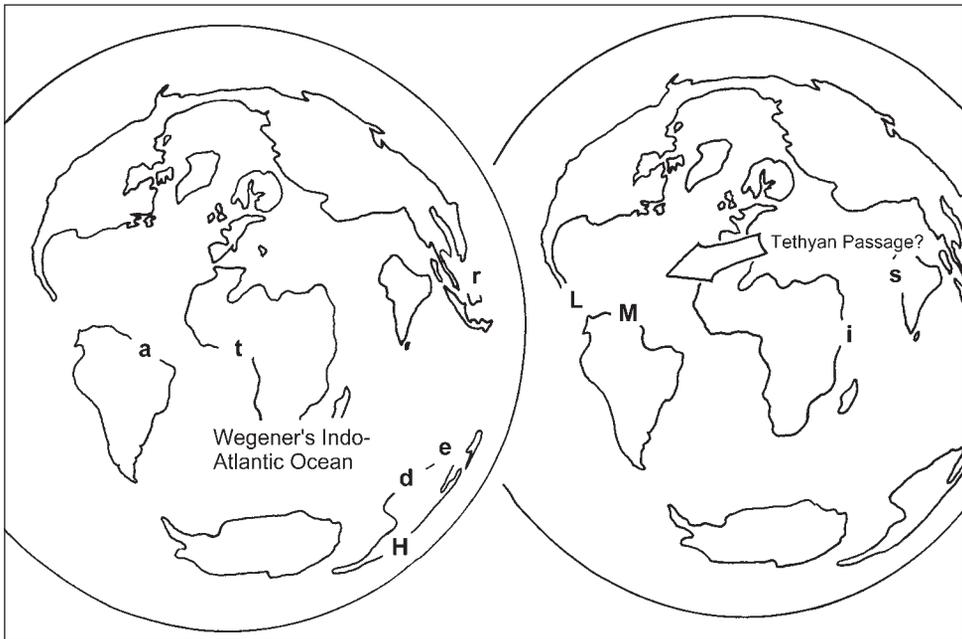


Fig. 9. Hypothetical reconstruction of the early dispersal of the genus *Uca*. The most conservative members of recent subgenera, the oldest *Uca* fossil and *Heloecius* have been "implanted" in maps of the lower Tertiary (adapted from Stanley, 1994). Travelling West and North from the "land of *Heloecius*" (Australia, see text), ancient *Uca* colonized the shores of what can be called "Wegener's Indo-Atlantic Ocean" (shown for the "narrow-fronts" in the left map). The "broad-fronts" (right map) may have used a Tethyan passage for secondarily invading the area of New World *Uca* s.str.— a, †*U. (Uca) maracoani antiqua* (Miocene); d, *U. (Gelasimus) dampieri*; e, *U. (Australuca) elegans*; i, *U. (Cranuca) inversa*; r, *U. (Tubuca) rhizophorae*; s, *U. (Paraleptuca) sindensis*; t, *U. (Uca) tangeri*.— H, *Heloecius*; L, *Leptuca* (oldest member not known); M, *Minuca* (oldest member probably *U. thayeri*).

later called Australia's North West coast "the most conservative area, judging by the morphology of the local *Uca*".

Von Hagen (2000) discussed some further evidence in favour of the whole continent of Australia, which was the first centre of certain mangrove trees (see above) and which still harbours, besides *Heloeccius*, the bulk of the *Australuca* species. These unite early stages of sound evolution (von Hagen, 2000), display with diminishing waves (see chapter 4.1.) and waving in females (von Hagen, 1993) with several morphological pleiomorphies like minor chelae with large teeth, remnants of the ancestral colour pattern of horizontal carapace stripes, grooves of the outer major chela, rows of tubercles within the orbit and a relatively simple gastric mill (figs. 6f, 7b, 5f, cf. 7k, 3f).

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