

PHYSIOLOGICAL INTER-RELATIONS OF DISPLAY AND LOCOMOTION IN FIDDLER CRABS : AN EVOLUTIONARY ASPECT*

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ABSTRACT

In general, the locomotory pattern of Decapod Crustacea can be regarded as representing the evolutionary old type of crosswise activation of ambulatories. In the highly evolved fiddler crabs of the genus *Uca* (Ocypodidae) this old locomotory pattern can still be traced though some of the ambulatories play a prominent role in the display parade, i.e., have become part of a different apparatus. While in all *Uca* species the chelipeds are used in waving, the extent of activating one or more pairs of ambulatories in display movements varies from species to species. Alternatively, waving the chelipeds is strictly correlated with locomotion in some species, while it has become almost fully independent from locomotion in others. This degree of correlation, viewed as neurophysiological interrelation of locomotion and display, seems to be an (additional) indicator of the evolutionary level of *Uca* species.

Based on motion picture analyses of several Old and New World forms of *Uca* the present paper reports the relevant findings on the Indian species *Uca vocans* (= *marionis*) and *U. annulipes*.

FIDDLER Crabs of the genus *Uca* (family Ocypodidae) represent the most highly evolved type of Decapod Crustacea. The ninety odd species of *Uca* are distributed in the warmer regions around the world where they inhabit the sandy and muddy stretches of backwaters, bays, lagoons and estuaries. In accordance with this wide spectrum of different habitats a rather intense speciation has apparently occurred which expresses itself among others in the various types of display of the large cheliped (visually or acoustically and vibrationally), the type of precopulatory behaviour, gross morphology and specific shapes of the gonopods. Ever since comparative morphological studies on *Uca* were started, one has tried to provide evidence for a proper arrangement of this *Uca*-diversity on a systematical and phylogenetical scale.

Thus, there is the broad grouping into the narrow-fronts and the broad-fronts (Rathbun, 1918 ; Crane, 1941) referring to the narrower or wider position of the eyestalks. Indeed, the 'tentative phylogeny' of American *Uca* species by Crane (1941) has several points in its favour. Another rather gross-morphological grouping was employed by Bott (1954) who thought that the genus *Uca* should be divided into a genus *Uca* sensu stricto and a genus *Minuca*, according to carapace size. However, in 1959 I indicated that this system could not be applied to the Afro-European *Uca tangeri*, which according to Bott's suggestion would belong to *Minuca* while having carapace dimensions of easily more than 30 mm width. Meanwhile, in the excellent paper by Von Hagen (1968) *U. minax* (Le Conte), *U. vocator* (Herbst) and *U. umbratila* Crane have also been shown not to fit in the system pro-

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posed by Bott. Hence, carapace morphology cannot be used in establishing a phylogenetic order of *Uca* species, nor does this apply to the more detailed morphology of the large cheliped (see Von Hagen, 1968, p. 404) or the gonopods. A comparative study of the morphology and function of mouthparts (spoon-tipped hairs and other seta-like structures of the maxillipeds) which play such an important role in the feeding process of *Uca* (Altevogt 1955, 1956; Schuster 1970) did not reveal any clues for a systematic or phylogenetic scale, either.

It can easily be said that the bulk of the more recent *Uca*-studies concerns ethological aspects of these crabs in the field, because there is a really vast range of waving, display and precopulatory behaviour patterns which provides an understandable temptation to authors for systematic scaling (Crane, 1941, 1943, 1957, 1958; Altevogt, 1955, 1957, 1958, 1959, 1969, 1970; Von Hagen, 1962, 1968, 1970). But what then should be regarded as 'higher' or 'lower' on this attempted scale:

Dancing by the male around the female and grasping her for mating above ground in a sort of rape (as in the Indian *Uca marionis=vocans*)?

Nicely and elaborately waving at the female and trying to induce her to follow the male to his burrow for underground mating (as in the Afro-European *Uca tangeri*, the Indian *U. annulipes*, and others)?

Waving towards the female and then gently grasping her back-to-back and carrying her to the male's burrow, releasing her near his burrow, he going in first and she following him for underground love (as in *Uca stylifera* from the Eastern Pacific)?

Waving near specially constructed 'shelters' (as in *Uca beebei*, *U. terpsichores* from the coasts of Peru and Ecuador)?

Waving emphasizing the lateral or vertical component of this particular movement (as in *U. vocans* and *U. annulipes*, respectively)?

This short survey of behavioural and ecoethological characteristics shows how difficult it is to group them objectivistically. This applies also if one compares the various patterns of waving proper. Here one finds the simple up-and-down movement of the large claw in front of the body (as in *U. batuenta*), which movement can be temporally altered to a slow up and a rapid down-movement (as in *U. princeps*). Moreover, there is the 'jerking type' of waving the large claw in a series of definite jerks to the highest position (as in *U. galapagensis*), the waving with a more or less pronounced vibratory component accompanying the waving actions (as in *U. mertensi*, *U. inaequalis*, *U. tangeri*). Then—and this type does not exhaust the wide range of waving patterns in *Uca*—some species wave their large claw only while activating their ambulatories, while others wave only while remaining in place (*U. vocans*, *U. stylifera* representing the first type, *U. tangeri*, *U. annulipes* the second). Finally, there is the extraordinary type of rotation waving, as in *U. insignis* which, while standing on tiptoes raise their large cheliped as high as possible and start rotating it. This extraordinary sight which one can experience in the Eastern Pacific is probably surpassed only by that most absurd looking type of 'waving' of an as yet undescribed *Uca* species from the Gulf of Guyaquil (Ecuador; Altevogt, 1966 unpublished): here waving has apparently been competitively pushed to a mere holding-up the bleached cheliped in a statuesque pose. How, then, can that rich diversity of structure and function of the *Uca* world be grouped and arranged?

We hope that the following aspect may prove as another, and may be important, means of scaling *Uca* species phylogenetically.

Since our first studies on *Uca* (Altevogt, 1955, 1957) in India we have tried to take motion pictures of as many *Uca* species as possible in as many as possible different situations, levels of excitation and sexual arousal for later evaluation. This material was collected by using a Bolex H16 and Bolex Reflex movie camera employing 24 frames per second and, where necessary, slow motion technique up to 64 frames per second. In the laboratory, these movies were frame-to-frame analysed so that the succession of claw- and leg-movement could be followed up in detail by enlarged drawings from the single frames. In this manner we have covered some 20 species of *Uca* from the Eastern Pacific, the Caribbean, Northwest Africa, the Red Sea, and India. To these must be added five more *Uca* species studied by my former collaborator H.-O. Von Hagen on the Isle of Trinidad. Some of these films have been published by the Institut für den Wissenschaftlichen Film, Göttingen, West Germany (see list of films attached to the end of this paper). Quite a number of people have helped me in gathering this material, of whom a few should be mentioned here: repeatedly I enjoyed financial help from the Deutsche Forschungsgemeinschaft, the Gesellschaft zur Förderung der Westfälischen-Wilhelms-Universität, the Institut für den Wissenschaftlichen Film, Göttingen, and the Deutsche Ibero-Amerika-Gesellschaft, Hamburg. Special thanks are due to my wife, Dr. med. Rosamunde Altevogt, who fully shared the work on several tropical trips, and to Dr. R. Korte. I am indebted to H. Kinne, who did a good deal of movie-analysing, and to Miss A. Hapel, again for analyses and drawing.

Realising that in ascending phyletic series a gradual reduction of homonomous metamery and corresponding organs takes place, to which a gradual reduction of neurophysiological patterns (viewed as innervation, activation etc.) is correlated, one finds that the less pronounced this correlation is the more highly evolved is the structure in question, and vice versa. It is a well established fact that neurophysiological connections are a very stable mechanism and that they show a high degree of persistency in the ascending phylogenetic ladder. This aspect, then, should also apply to the locomotory apparatus of Arthropods in general and of Decapod Crustacea in special. This would mean that one has to look at the type of locomotion in Decapods and find out its possible alteration as soon as—apart from the maxillipeds and other mouthparts as transformed ambulatories—the chelipeds had given up their locomotory function. Hence, in primitive cheliped-bearing crustaceans the neural activation of these chelipeds should be strongly correlated with the activation of ambulatories. On the other hand, in the most highly evolved Decapods, handling and moving and waving these chelipeds should have become almost or fully independent of locomotion. Between these two extremes all species in question should be properly lined up in an order justified by phylogeny. Phyletic reduction of ambulatories in arthropods is evident in Chilopoda where *Geophilus* has 40 to 60 pairs of walking legs, *Cryptops* 21, and *Lithobius* 15 pairs of ambulatories. It is important to note, that in an animal with many legs (as *Geophilus*) the balance of the body on the left and right legs is easily maintained even then, when there is some disorder on the left or the right side, or when some legs on either side are missing. This maintenance of body-balance becomes more critical the more the number of legs is reduced, because with fewer legs the support and balance of the body can only be maintained by an equal number of legs on either side having contact to the ground at the given moment. Correspondingly, the neural co-ordination of ambulatories in the three animal types mentioned shows the important transition from the Annelid type of innervation (as in *Geophilus*) to the typical Arthropod type

(as in *Lithobius*) where the legs are innervated and activated in a pairwise correlation apart from that older and persisting innervation in an anterior-posterior sequence (Fig. 1).

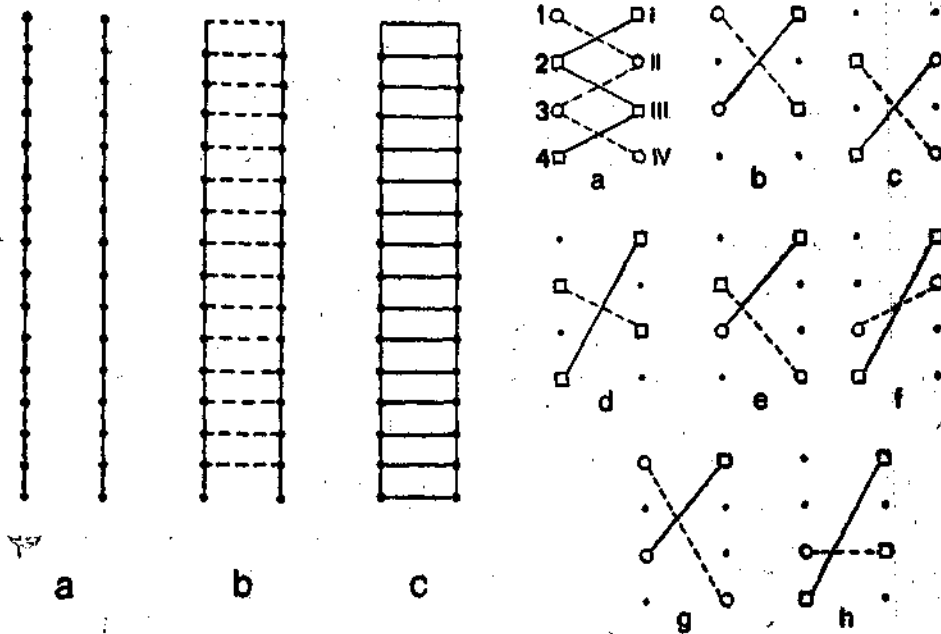


Fig. 1. Transition from Annelid type of locomotory innervation to primitive Arthropod type. a. *Geophilus*. b. *Cryptops*. c. *Lithobius*, Dots : ambulatories, Fullline : strong neural and Broken line : weak neural connection (after Von Holst, 1934).

Fig. 2. Mixture of longitudinal and transversal locomotory innervation in Arachnida, leading to the crosswise walking type as in a. Arabian numbers denote animal's right, Latin numbers its left legs. b-h : leg coordination after amputation (after Von Holst, 1935).

From this mixture of longitudinal and transversal innervation one can easily trace the evolution of the typical crosswise activation of ambulatories which is seen in Arachnida (Von Holst, 1935), and which persists even after severe amputations of several walking legs (Fig. 2). The general type of activating the ambulatories, then, is synchronous innervation of diagonally arranged legs, and alternately activating antero-posteriorly neighbouring legs.

This neural principle applies also to Hexapods (Graber, 1877, and later authors) and Crustacea. From these, *Palinurus* (*Macrura Reptantia*) deserves special mention : having not yet evolved any chelipeds, its first pair of legs still serves locomotion proper (Bethe, 1930) and one sees a crosswise activation of walking legs, i.e. alternately moving the legs of each pair and synchronous activation of legs in a diagonal position (sometimes allowing for certain phase differences ; phase difference 0=synchronous movement, phase difference 1/2=alternating leg movements).

In the rather primitive crab *Eriochelr sinensis*, the chelipeds are sometimes used in walking (Kühl, 1931 ; Herter 1932 ; see also Manton, 1952). Hence, a

theoretic diagram of such a 'general crab' with chelipeds still used in locomotion would look like that in Fig. 3. In the higher Crustaceans, however, the chelipeds are no longer used in locomotion. In systematic amputation experiments on *Carcinus maenas* (Bethe, 1930), in which all ambulatories were removed except one pair, the animal uses again the chelipeds in locomotion (Von Holst, 1935, Fig. 4).

This means that in such deplorable cases of emergency these animals take again to the phylogenetically older type of locomotion. This same fact shows up in an intricate detail: Normally, Brachyura go sideways, proceed laterally, which is easily observed in any Brachyuran. If one disconnects the supra-oesophageal ganglion from the rest of the central nervous system, the Brachyuran will proceed frontally, i.e. rely on the locomotory type of its ancestors, the Macrura Reptantia.

Brachyura, then, show the typical crosswise activation of ambulatories when walking at normal speed and if undisturbed by agonistic rivals, sexual conspecifics and the like (Fig. 5). Explained more clearly, the animal in Fig. 5 would start walking by first moving its first right leg, than its first left, than its second right, and so on (these legs, moved first in each respective pair, are drawn in full black in the graphs). Let us denote the ambulatories of the animal's right side with Latin numerals (I-IV), and those of its left side with Arabian (1-4). From motion picture analyses one finds a certain time lag—phase difference—between activating the legs I and III (and 1 and 3) and II and IV (and 2 and 4) which according to the type of surface and the arousal level of the animal amounts to 0,45 bis 0,6 s. This time lag extends in a postero-anterior direction which means that locomotion starts with activating the hindmost legs (IV and 4) first so that, neurologically, the crab moves 'from tail to head'.

Apart from the ambulatories considered so far, *Uca* and other waving fiddler crabs have those well-known large chelipeds, one on the left or the right side in a 50 : 50 distribution. How do these former walking legs fit into the locomotory pattern described above? There are some *Uca* species which—at a high level of sexual arousal—wave the large and the small claws synchronously. This denotes that there is no longer any alternate innervation of the limbs. As regards the claws, evolution seems to have proceeded beyond the elementary locomotion type of crosswise innervation.

To get a clear idea of those neurophysiological correlations between claw movement and locomotion, my collaborator H. Kinne analysed our motion pictures of *U. stylifera* (Fig. 6). In 22 out of 24 display wavings (at highest excitation level = stage 3, according to Von Hagen's scale; 1962) there was a strict correlation of waving the large claw and moving the ambulatories in the manner shown in Fig. 7. The correlation of marching and waving in *U. stylifera* is 92%. This crab (in the male) can wave its claw only while marching. *U. stylifera* males at rest cannot display. The reverse is of course not true and cannot mean that locomotion must be accompanied by waving. Correspondingly, the correlation of waving and marching decreases with decreasing excitation level and sexual arousal. A crab in stage 1 and 2 is under a less rigid command to wave its claw and march (Fig. 8).

Another interesting feature emerged from the frame-to-frame analyses and the correlation calculations: Raising the large claw is homologous to the forward stride of an ambulatory, lowering the major cheliped is the homologon to the resting phase in the walking movement, i.e. keeping the leg in contact with the ground. This finding is of explanatory importance for the understanding of the rotation type of

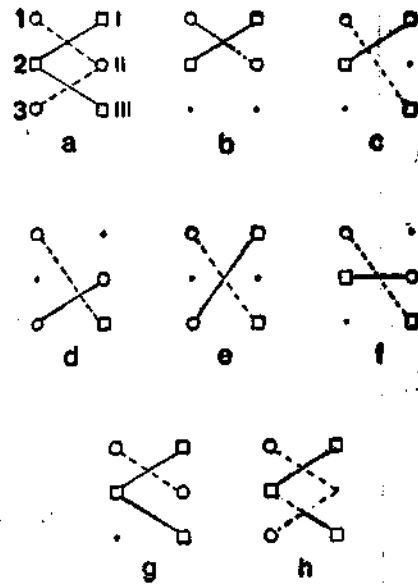
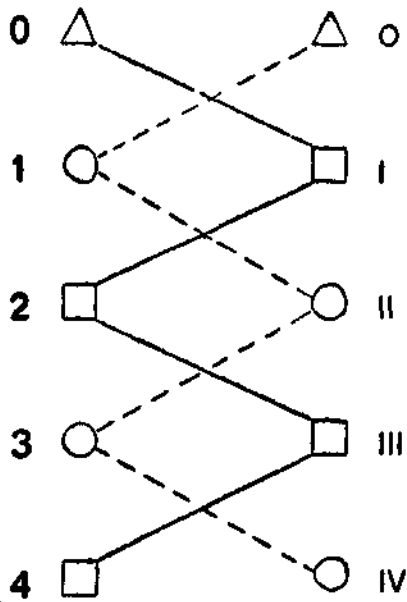


Fig. 3. Schematized locomotion of a primitive crab in which the chelicerae (Δ) are still used in walking.
 Fig. 4. Ambulatory innervation pattern (a) of a crab and persistence of crosswise walking after systematic amputation experiments (b-h). After Von Holst, 1935.

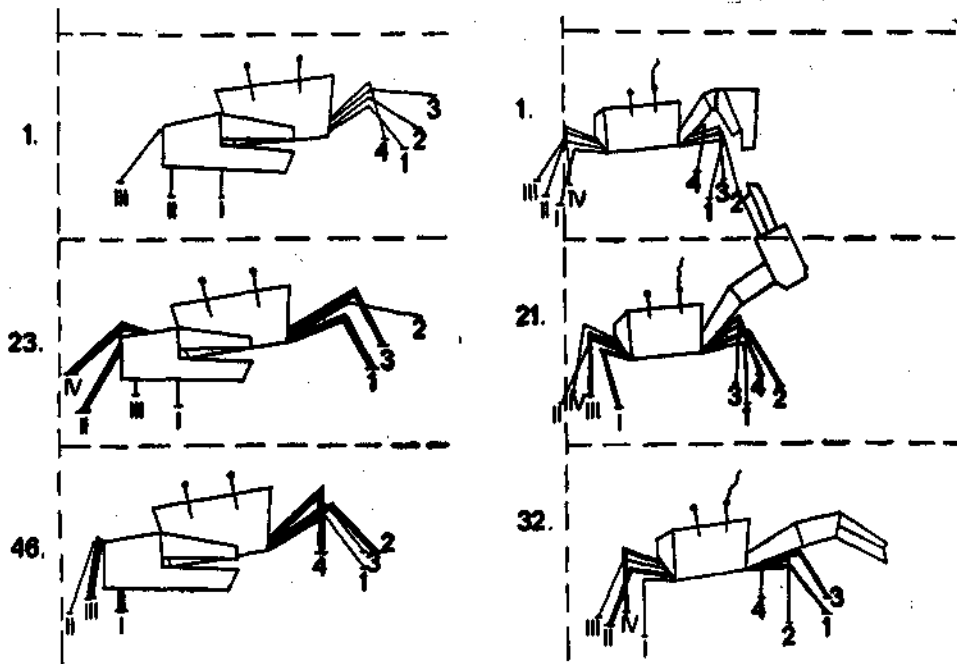


Fig. 5. Locomotion in the crab, *Uca tangeri*. Legs of each pair moved first are drawn full black. From motion pictures (24 frames per second), frame number on left.
 Fig. 6. Movements of claw and ambulatories in waving-cum-locomotion in *U. stylifera* (from motion pictures, 24 f/s).

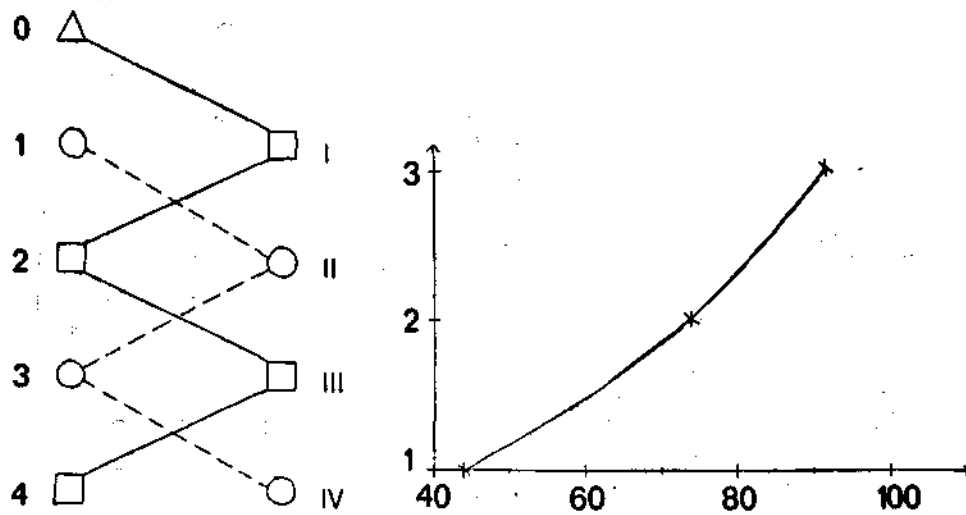


Fig. 7. Schematic correlation of claw (Δ) and ambulatory movement in *U. stylifera*.

Fig. 8. Correlation (in %, on abscissa) of waving and locomotion in relation to excitation level (1-3, on ordinate) in *U. stylifera* (from Kinne, 1970).

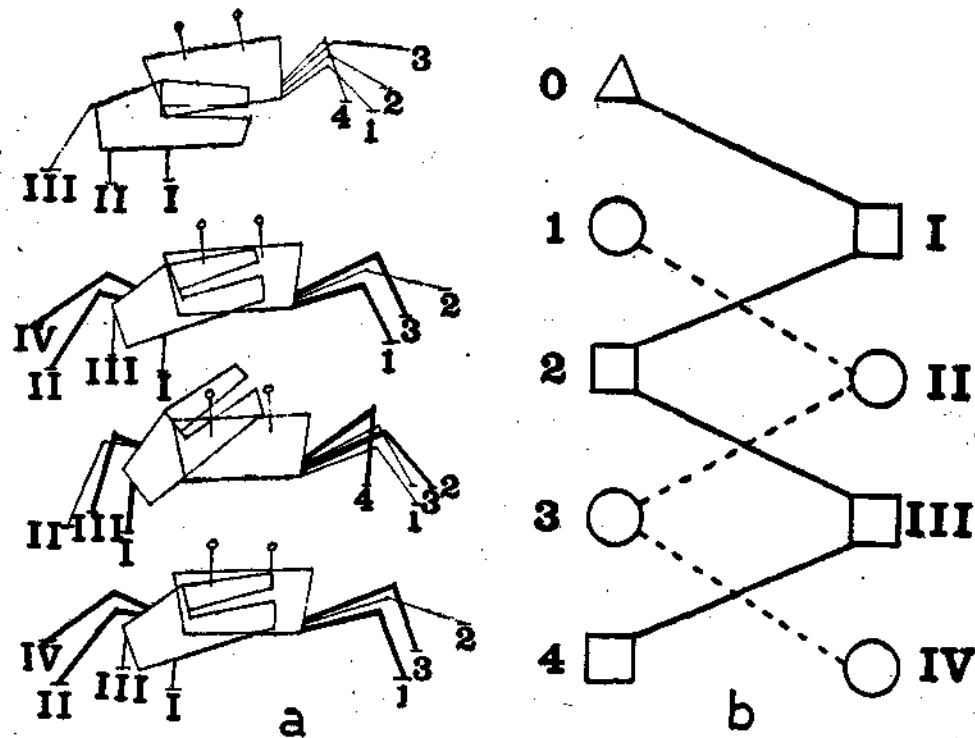


Fig. 9. *Uca vocans* (=marionis). a. waving and locomotion, from motion pictures, and b. Diagram showing ancestral correlation of waving (large claw : Δ) and locomotion.

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cheliped waving (as in *U. insignis*, Altevogt, 1970 ; Altevogt and Altevogt, 1968a). The retro-dorsal semi-circle of the 'wave' represents the homologon of the forward stride, the forward half circle of the rotation movement 'is' the surface contact phase of the large claw. In arousal level 3 all this is done without any locomotion : The crab stands on its tiptoes and rotates its claws. In excitation levels 1 and 2 there is some locomotion and some waving of an intermediate and inefficient type.

Other species, like *U. princeps* and the Indian *U. vocans* (= *marionis*, see re-naming this species to *U. vocans* : Holthuis, 1959) confirmed the statement, that in some species there is a strong neurophysiological correlation of waving and locomotion proving that the old crosswise activation of ambulatories is still very pronounced and that the chelipeds are still rather rigidly a functional part of locomotion. (Fig. 9a, b). Such species, then, can only be regarded as rather poorly evolved on the phyletic scale. A tentative quantitative statement on this degree of correlation based on frame-analyzed waving-cum-locomotion scenes would read as follows: 92% in *U. stylifera*, and about 60% in *U. princeps*.

This is not so in the other Indian species *U. annulipes*, *triangularis*, the Neotropical broadfronts *rapax*, *beebel*, *festae*, *terpsichores*, *stenodactylus*, and the Afro-European *U. tangeri*. In these species there is only a slight correlation of waving and locomotion proper or none at all. This means that the males of these species can wave while remaining in place, can display at a fixed spot : can attract the female to the male's hole better than the males of the abovementioned less highly evolved species can do which must march while displaying.

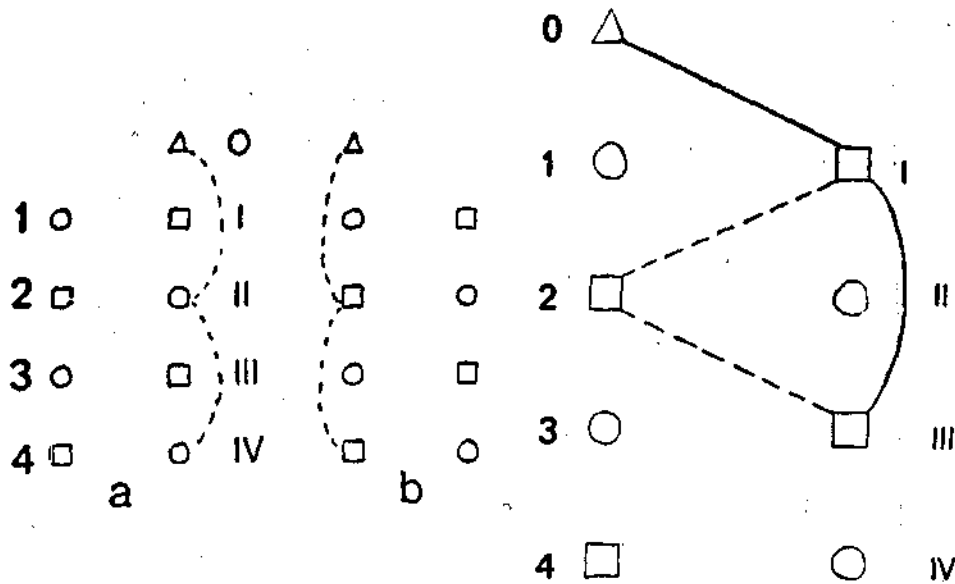


Fig. 10. Poor correlation of waving [large claw Δ on right side of animal in (a), on left side in (b)] and moving ambulatories in *U. mertensi*.

Fig. 11. *Uca rapax* : Mixture of ancestral (crosswise) and modern type of claw (Δ) and leg movements.

Clearly, then, locomotion innervation has been left behind, and the impulse to wave the cheliped(s) has proceeded separately so that the large claw can be moved without moving the ambulatories. The higher the excitation level of the male and the more intense the waving movement, the more will one or more ambulatories become part of the display gesture. But this taking part in the display by walking legs is in no way comparable to the actual walking movements of the legs in *U. vocans*, *stylifera* and the like, but has become more or less or even fully independent from the ancestral type of locomotion.

This can be seen in *U. mertensi* for instance, a small species from the Eastern Pacific (Altevogt and Altevogt, 1968b). In 92 display movements analyzed cinematographically, one finds a 'perturbating variety of ambulatorial participation' in the display gestures (Kinne, 1970, p. 25) and the legs II and IV of the large claw-side are sometimes activated metachroneously with the movement of the major cheliped. This is certainly not favourable with regard to body balance and shows the phyletic remoteness of this type of limb movement (Fig. 10).

In *U. rapax* (Atlantic, Central and South America), the situation is similar though sometimes a reminiscence of the ancestral crosswise innervation type can still be traced (dotted line in Fig. 11).

From this and similar species one can infer that raising the ambulatories at the higher stages of display is ritualized locomotion more or less remote from the ancestral neurological pattern.

This is especially clear also in the Indian *U. annulipes* (Figs. 12 and 13) in which at peak display with major claw extremely stretched sideways the opposite ambulatories 2 and 3 are raised syn-vor slightly metachroneously with the upward-outward and then inward-downward movement of the large claw. At peak display, the body of an *annulipes* male balances on its minor claw side only on legs 1 and 4 (Fig. 13).

In the Pacific *U. beebel*, it is the ambulatories 3 and 4 or III and IV that are raised off the ground in maximum display making body balance even more difficult than in *annulipes*.

We cannot yet go into more quantitative details regarding the percentage of correlation of display and (actual or ritualised) locomotion as more analyses from our motion picture material are under way, but suffice it to say that the aspects and methods presented in this paper have yielded the following findings :

1. Evaluating the correlation of claw display and locomotion in *Uca* species gives an index for grading them on a phylogenetic scale.
2. Waving the large claw is derived from locomotion, and in the most primitive species, it is still an integral part of the innervation pattern of locomotion.
3. Primitive *Uca* species can fully wave (stage 3) only while marching. In the more highly evolved species the display movements have become more or less independent from locomotion.

4. Raising the large claw in the (various types of) waving movements is homologous to the forward stride of locomotion, lowering the major cheliped is the homologue to the resting (surface contact) phase.

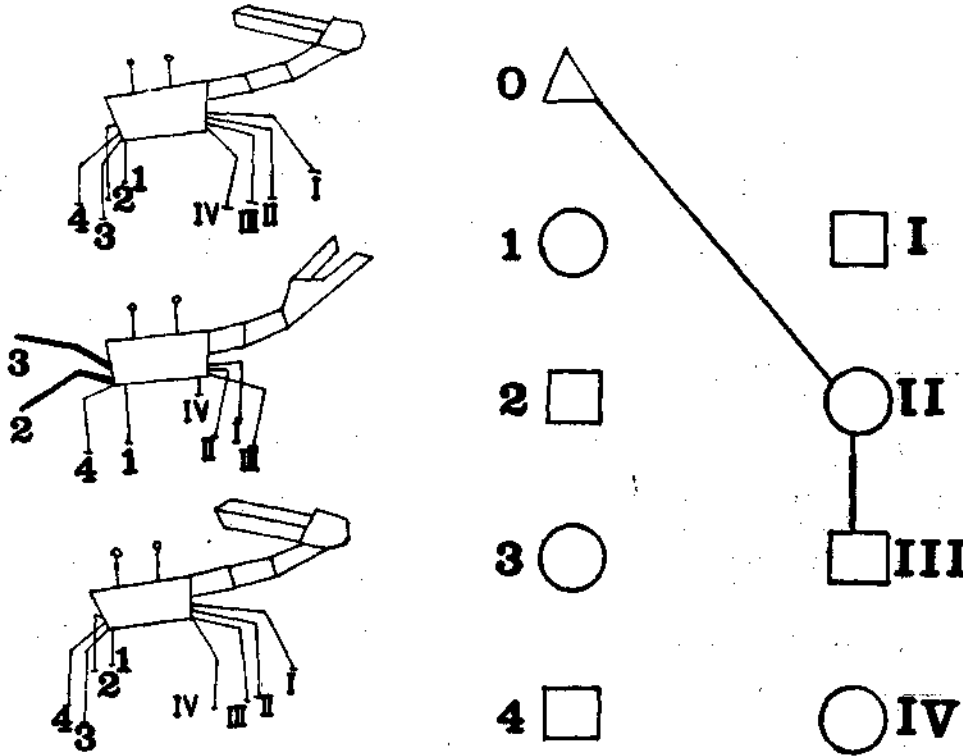


Fig. 12. Ritualised locomotion in legs 2 and 3 in the waving gesture of *U. annulipes* (from motion scenes).

Fig. 13. Highly evolved activation pattern in claw (Δ) and leg (II, III) movement in a displaying *U. annulipes*.

5. In species showing the rotation type of waving (*U. insignis*), moving the claw(s) outward-backward corresponds and is homologous to the forward stride, while the inward-forward movement 'is' the resting phase.
6. The more remote from the old Arthropod type of locomotion innervation a *Uca* species is, the more is it apt and likely to have also evolved some sort of vibrational signalling with the large claw as using the large claw in knocking at the substratum, its own body (appendages) etc. requires that the claw movement must be independent from the old locomotory pattern.
7. The correlation calculations based on motion picture analyses do not lend support to the assumption that the narrow-fronted *Uca* species are—as a group—less highly evolved than the broad-fronted species.

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