

Phylogenetic and systematic position of *Sesarma rubripes* Rathbun, 1897 (Brachyura: Grapsidae)

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The American grapsid crab *Sesarma rubripes*, classified as *Metasesarma rubripes* by Rathbun (1918), was compared with *M. rousseauxi*, the type species of *Metasesarma*, and was found to be different in a number of characters. On the other hand, *S. rubripes* is very close to those species of American *Sesarma* that are considered to be members of the subgenus *Chiromantes*. The characters common to *S. rubripes* and the American *Chiromantes* can be interpreted as synapomorphies by means of an out-group comparison. *Aratus pisonii* and the West African *Sesarma elegans* are further members of the group in question and both share special derived characters with *S. rubripes*. As a consequence, *S. rubripes* should be returned to the genus *Sesarma*. It is recommended, however, to maintain the generic status of the monotypic genus *Aratus*.

Die systematische Stellung der westatlantischen Krabbenart *Metasesarma rubripes* wurde überprüft. Die bisherige systematische Einordnung dieser Art erscheint zweifelhaft, denn *M. rubripes* zeigt größere Abweichungen im morphologischen Vergleich mit *M. rousseauxi*, der Typusart der Gattung *Metasesarma*. Andererseits gibt es Argumente für einen gemeinsamen phylogenetischen Weg von *M. rubripes* mit denjenigen amerikanischen Arten der Gattung *Sesarma*, die als Vertreter der Untergattung *Chiromantes* angesehen werden. Die ermittelten morphologischen Übereinstimmungen können anhand eines Außengruppenvergleichs als Synapomorphien interpretiert werden. Weitere Abkömmlinge der amerikanischen *Chiromantes* sind *Aratus pisonii* und die westafrikanische *Sesarma elegans*. Beide Arten bilden wahrscheinlich eine Abstammungsgemeinschaft mit *M. rubripes*. Während für *M. rubripes* eine Rückführung in die Gattung *Sesarma* am sinnvollsten erscheint, wird empfohlen, die monotypische Gattung *Aratus* beizubehalten.

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Introduction

The mangrove crab *Metasesarma rubripes* (Rathbun, 1897), belonging to the subfamily Sesarminae, is distributed on the east coast of America from Nicaragua to Argentina. The genus *Metasesarma* was established by H. Milne Edwards (1853) for the Indo-Pacific species *M. rousseauxi* H. Milne Edwards, 1853. A second representative in the Indo-Pacific area is *M. aubryi* (A. Milne Edwards, 1869), so that the genus comprises three species at present.

As originally defined by H. Milne Edwards (1853, 1855), the genus *Metasesarma* is separated from *Sesarma* by having the antenna completely excluded from the orbit by the contact of the infra-orbital lobe with the ventral margin of the front (fig. 1). The discovery of this character in *Sesarma rubripes* caused Rathbun (1918) to place this species in the genus *Metasesarma* subsequently.

An investigation of the phylogeny of the American Sesarminae (Niem, 1992) led to the conclusion that *M. rubripes* is not related to the Indo-Pacific species of *Metasesarma*,

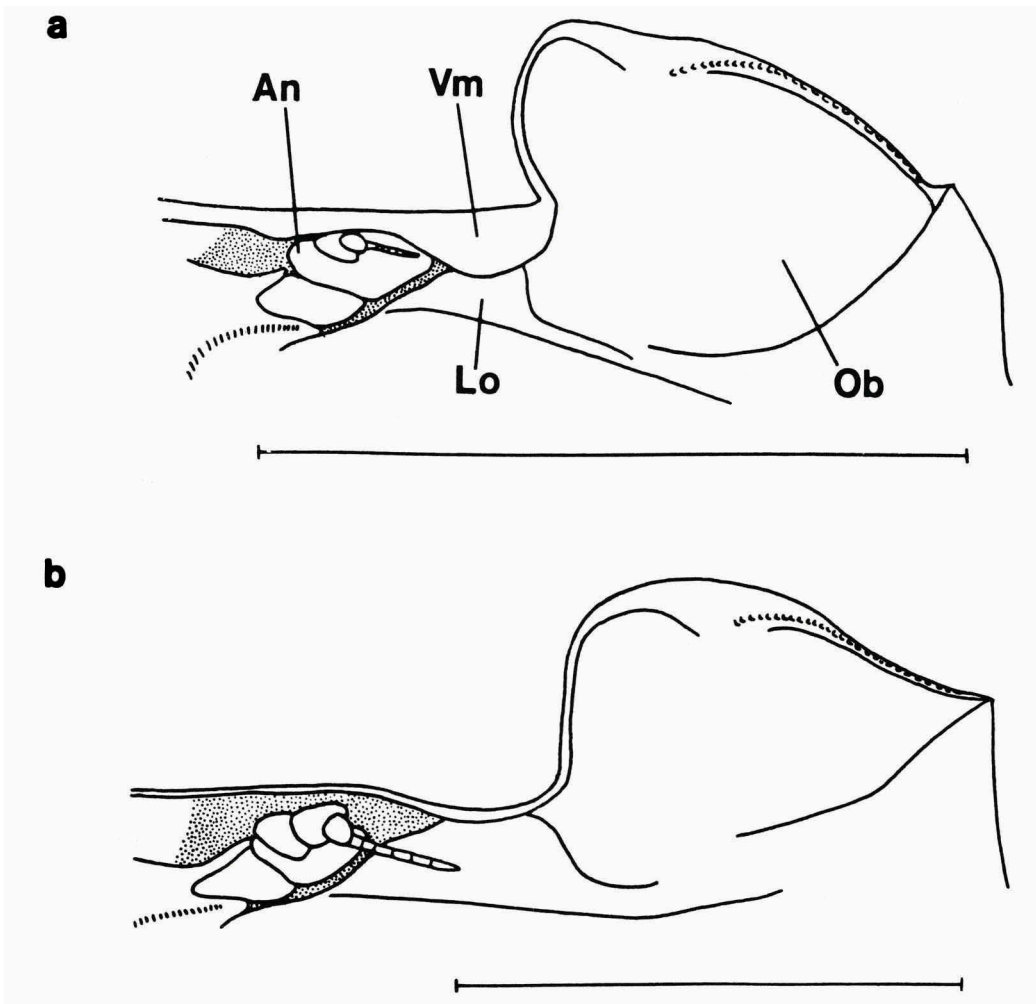


Fig. 1. Left orbit in frontal view, with position of left antenna. a, *Metasesarma rousseauxi* H. Milne Edwards; b, *Sesarma* (= *Metasesarma*) *rubripes* Rathbun. An = antenna. Ob = orbit. Lo = infra-orbital lobe. Vm = ventral margin of front. Scales 5 mm.

but shows affinities to several American species of *Sesarma*, and is especially close to *Aratus pisonii* and to the West African *Sesarma elegans*. To elucidate the true systematic position of *M. rubripes*, the present paper discusses some of its morphological features and compares them with those of *M. rousseauxi*, *A. pisonii* and *S. elegans*.

Material examined

The following abbreviations are used: cb refers to maximum carapace breadth; RMNH to the Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden; VH to the collection von Hagen, Marburg.

(1) *Aratus pisonii* (H. Milne Edwards, 1837): Trinidad, 1965-66, H.-O. von Hagen, VH; 15 ♂♂, cb 16.0-24.5 mm; 10 ♀♀, cb 9.9-19.6 mm.— Trinidad, viii.1977, H.-O. von Hagen, VH; 3 ♂♂, cb 11.0-21.0 mm; 7 ♀♀, cb 10.1-19.6 mm.— Puerto Pizarro, Peru, iv.1966, H.-O. von Hagen, VH; 1 ♀, cb 19.0 mm.

(2) *Metasesarma aubryi* (A. Milne Edwards, 1869): locality unknown, xii.1910, P.J. Buitendijk, RMNH D 1986; 5 ♂♂, cb 13.4-16.6 mm; 4 ♀♀, cb 13.8-17.3 mm.

(3) *Metasesarma rousseauxi* H. Milne Edwards, 1853: locality unknown, 1910, P.J. Buitendijk, RMNH D 1983; 1 ♂, cb 13.5 mm; 2 ♀♀, cb 11.7-12.9 mm.

(4) *Metasesarma rubripes* (Rathbun, 1897): Trinidad, 1965-66, H.-O. von Hagen, VH; 6 ♂♂, cb 11.0-22.5 mm; 12 ♀♀, cb 10.2-19.9 mm.— Trinidad, 23.vii.1977, H.-O. von Hagen, VH; 2 ♂♂, cb 15.2 and 15.7 mm; 3 ♀♀, cb 13.3-16.2 mm.— Venezuela, 1979, N. Sinclair, VH; 1 ♀, cb 17.4 mm.

(5) *Sesarma elegans* Herklots, 1851: Tico, Cameroon Estuary, Cameroon, 9.i.1984, C.H. Otto, VH; 7 ♂♂, cb 4.5-12.5 mm; 4 ♀♀, cb 6.9-12.5 mm.

The following list of species refers to the composition of the "outgroups" chosen for the phylogenetic considerations below:

Sesarmiinae: *Chasmagnathus convexus* de Haan; *Chasmagnathus granulata* Dana; *Clistocoeloma merguense* de Man; *Cyclograpsus cinereus* Dana; *Helice tridens* de Haan; *Metagrapsus curvatus* (H. Milne Edwards); *Metaplax crenulata* (Gerstaecker); *Metopaulias depressus* Rathbun; *Sarmatium crassum* Dana; *Sesarma aequatoriale* Ortmann; *S. alberti* Rathbun; *S. angolense* de Brito Capello; *S. buettikoferi* de Man; *S. erythrodactyla* Hess; *S. haematocheir* (de Haan); *S. huzardi* (Desmarest); *S. mederi* H. Milne Edwards; *S. rectum* Randall; *S. reticulatum* (Say).

Grapsinae: *Geograpsus lividus* (H. Milne Edwards); *Goniopsis cruentata* (Latreille); *Metopograpsus frontalis* Miers; *Pachygrapsus gracilis* (de Saussure); *Planes minutus* (Linnaeus).

Varuninae: *Eriocheir sinensis* H. Milne Edwards.

Results

The characters depicted in figs. 2 to 5 are suitable to point out the systematic position of *M. rubripes*. The semi-schematic drawings are brought to about equal size each time.

In a first step, only *M. rousseauxi* ((a) in each drawing) and *M. rubripes* (b) will be compared. Similarities of (b) with *S. elegans* (c) and *A. pisonii* (d) will be considered later.

Dorsal view of carapace (fig. 2).

In (a) the lateral margins of the carapace are subparallel and the carapace is more or less quadratic. The interregional grooves on the surface are almost wanting, only the cervical groove (Cg) and those bordering the mesogastric region (Mg) are represented by shallow depressions. There are many short and only weakly developed striae (St) on the branchial regions.

In (b) the lateral margins of the carapace converge posteriorly, so that the carapace becomes trapezoidal. The regions of the carapace are distinct. The oblique striae on the lateral parts of the branchial regions consist of long, elevated lines.

Frontal view of carapace (fig. 3).

In (a) the front shows, at both lateral corners, a conspicuous thickened projection

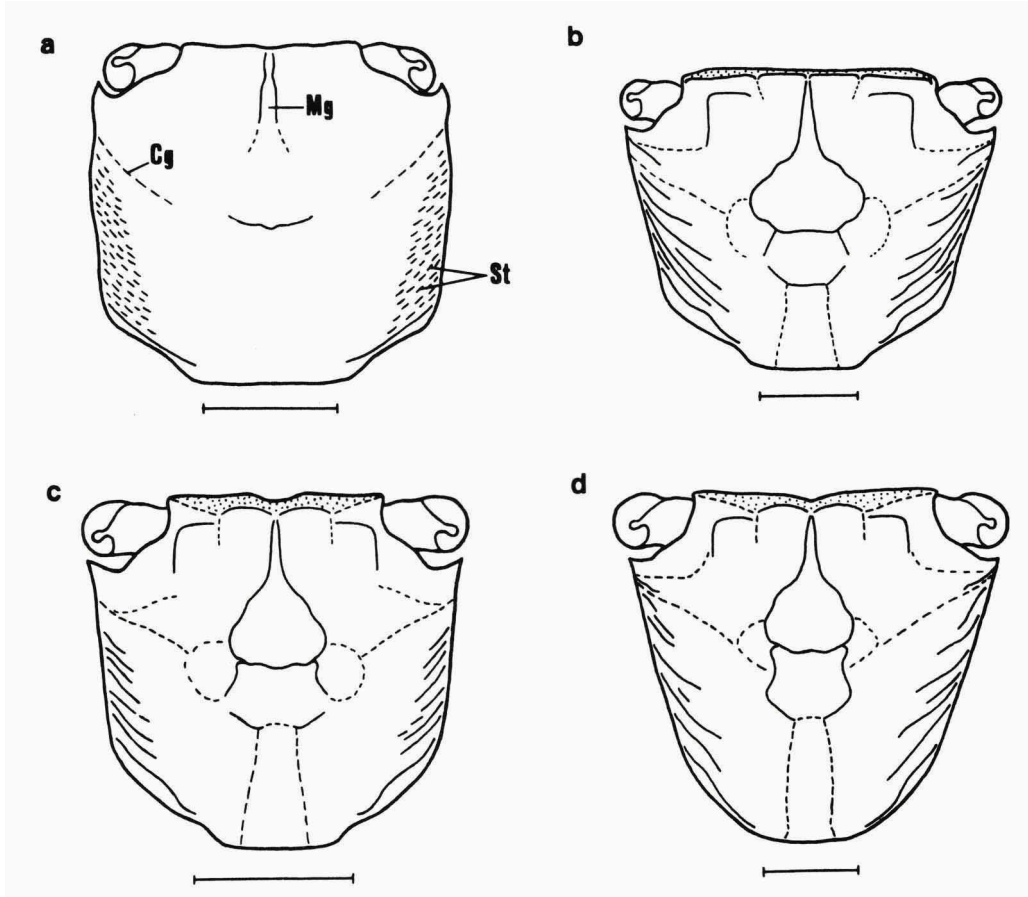


Fig. 2. Dorsal view of carapace. a, *Metasesarma rousseauxi* H. Milne Edwards; b, *Sesarma* (= *Metasesarma*) *rubripes* Rathbun; c, *Sesarma elegans* Herklots; d, *Aratus pisonii* (H. Milne Edwards). Cg = cervical groove. Mg = mesogastric region. St = striae. Scales 5 mm.

(arrow in fig. 3a) that meets the infra-orbital lobe (see fig. 1a). The frontal region clearly widens ventrally. The branchial regions (Br) are unusually swollen.

In (b) the front does not markedly increase in width ventrally and is not provided with thickened projections. The branchial regions are not swollen.

Lateral margin of carapace and coxae of walking legs (fig. 4).

In (a) the meeting point of the ventral (Vm) and lateral margin (Lm) of the carapace is dorsal to the emargination between the second and third walking leg (arrow in fig. 4a). None of the walking legs shows a coxal process as depicted in (b).

In (b) the two margins of the carapace are meeting ventrally to the emargination between the second and third walking leg. The upper part of the coxae of the last three walking legs is produced anteriorly to form a hairy process (Cp), which extends into the intercoxal gap.

Merus and ischium of the third maxillipeds (fig. 5).

An oblong area (Oa), located at the inner margin of the merus, is delimited from the remaining surface of the merus by a row of hairs, which is extending toward the

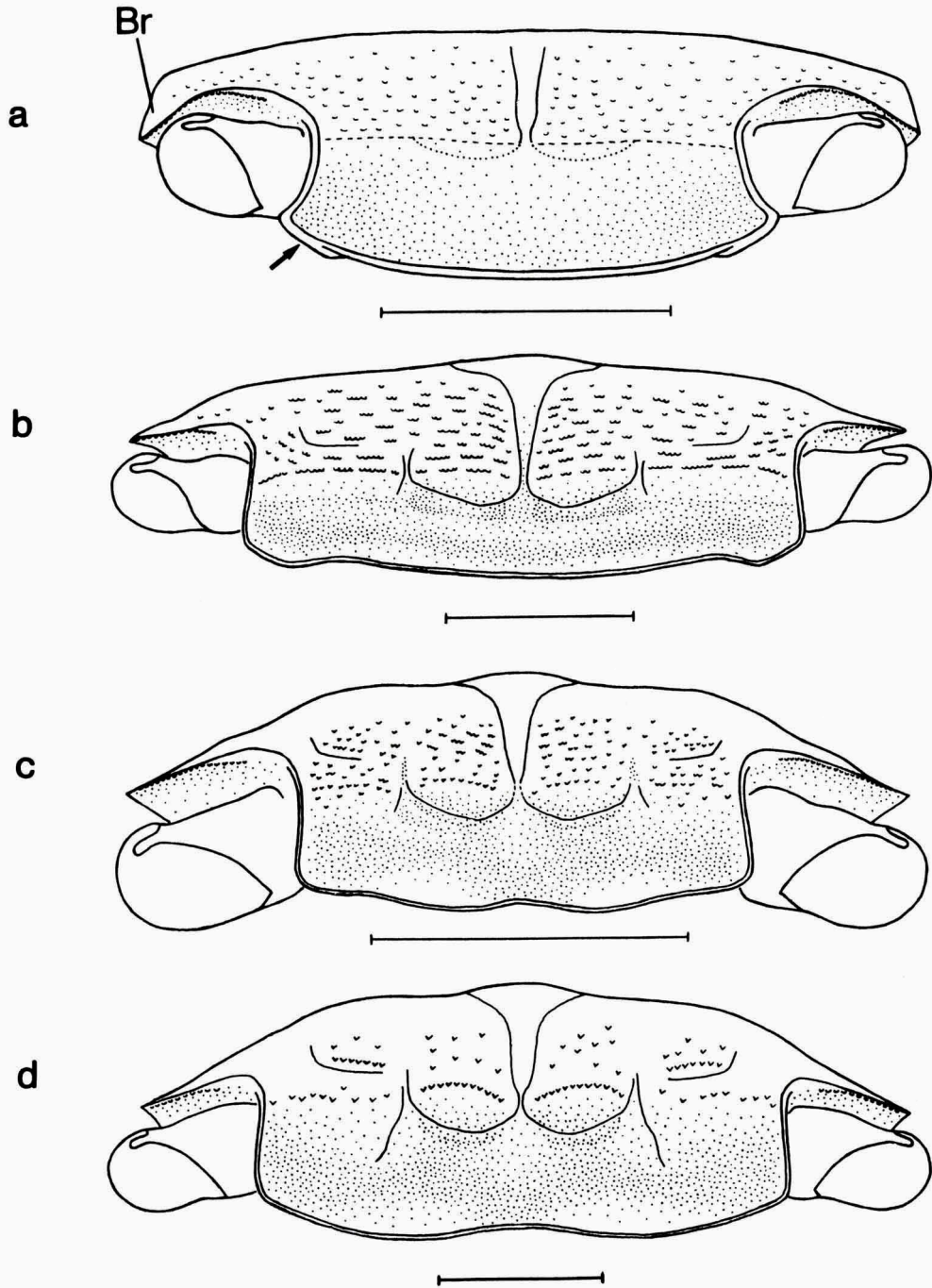


Fig. 3. Frontal view of carapace. a, *Metasesarma rousseauxi* H. Milne Edwards; b, *Sesarma* (= *Metasesarma*) *rubripes* Rathbun; c, *Sesarma elegans* Herklots; d, *Aratus pisonii* (H. Milne Edwards). Arrow in (a) points on thickened projection at the ventral margin of front; Br = branchial region. Scales 5 mm.

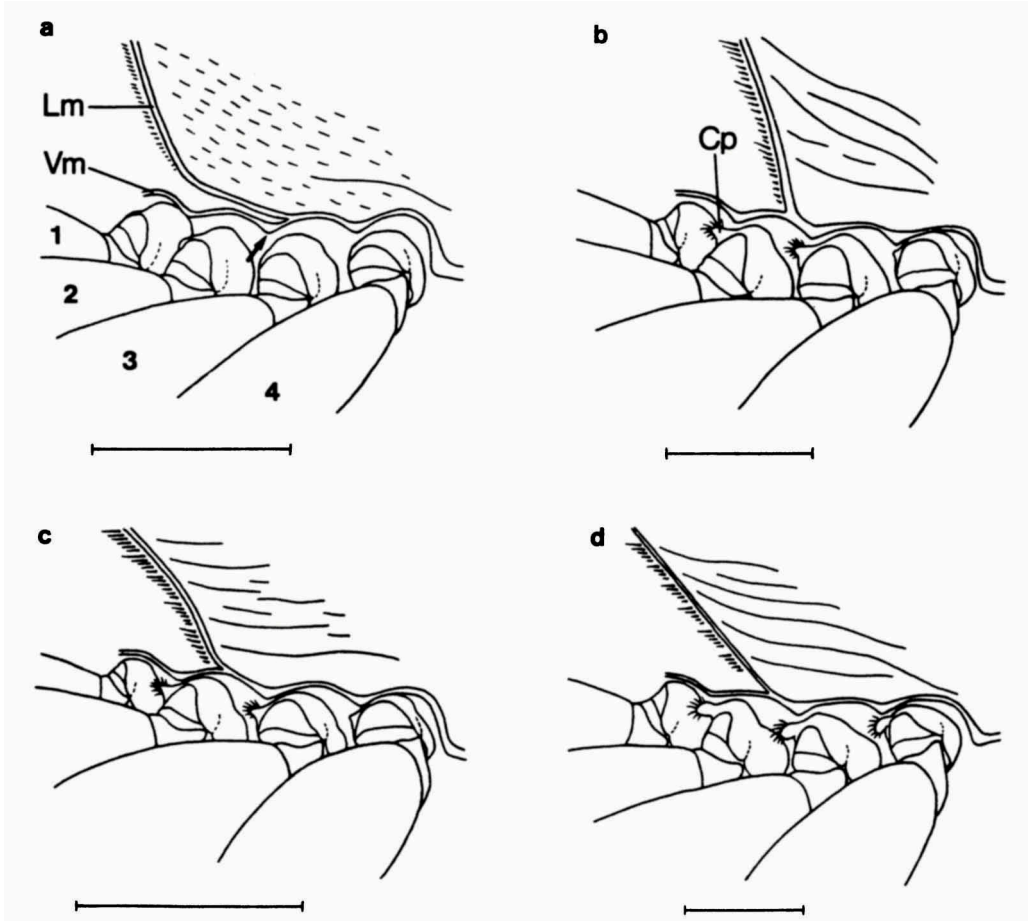


Fig. 4. Lateral margin of carapace, with bases of left walking legs. a, *Metasesarma rousseauxi* H. Milne Edwards; b, *Sesarma* (= *Metasesarma*) *rubripes* Rathbun; c, *Sesarma elegans* Herklots; d, *Aratus pisonii* (H. Milne Edwards). 1-4 meri of walking legs; arrow in (a) points on emargination between walking leg no. 2 and 3; Cp = coxal process. Lm = lateral margin of carapace. Vm = ventral margin of carapace. Scales 5 mm.

outer margin of the ischium.

In (a) the oblong area is relatively broad and not narrowed in its distal half. The ischium is bulgy produced at its inner margin.

In (b) the oblong area of the merus is narrow in its whole extension, especially in its distal half. The ischium is not produced at its inner margin.

From the comparison of the characters described above, it is obvious that there are fundamental differences in the morphology of *M. rubripes* and *M. rousseauxi*. At the same time, the exclusion of the antenna from the orbit (fig. 1) proves to be the only special derived feature that both species have in common. On the other hand, *M. rousseauxi* closely resembles *M. aubryi*, the third member of the genus *Metasesarma*. This similarity refers to the swollen branchial regions, the short striae and the thickened projections of the front, which is widening ventrally in both species.

In the case of *M. rubripes* several morphological characters indicate close affinity

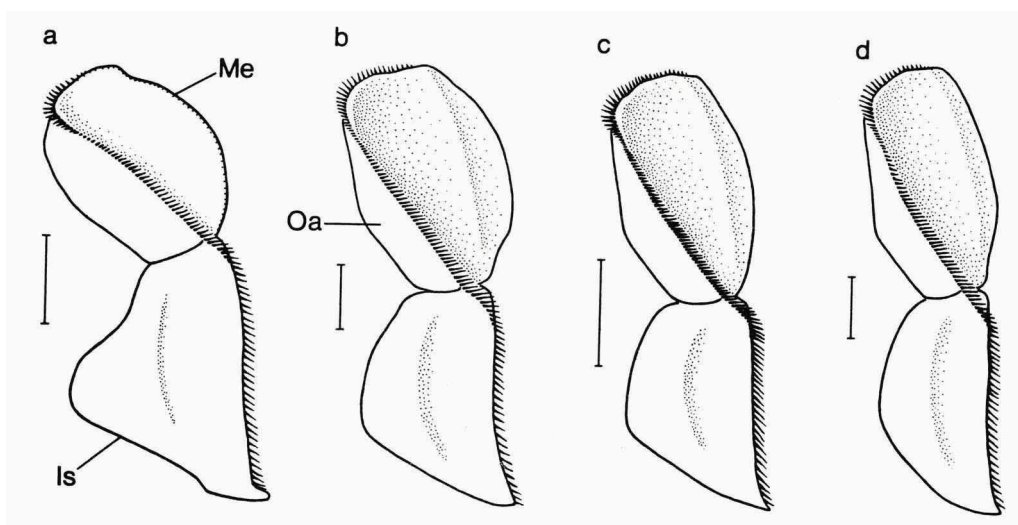


Fig. 5. Merus and ischium of left third maxilliped. a, *Metasesarma rousseauxi* H. Milne Edwards; b, *Sesarma* (= *Metasesarma*) *rubripes* Rathbun; c, *Sesarma elegans* Herklots; d, *Aratus pisonii* (H. Milne Edwards). Is = ischium. Me = merus. Oa = oblong area of merus. Scales 1 mm.

to the American representatives of the genus *Sesarma*, which are included in the subgenus *Chiromantes*. The following American species belong to this subgenus:

S. americanum Saussure; *S. angustipes* Dana; *S. angustum* Smith; *S. cinereum* (Bosc); *S. gorei* Abele; *S. magdalenense* Rathbun; *S. miersii* Rathbun; *S. occidentale* Smith; *S. ricordi* H. Milne Edwards; *S. roberti* H. Milne Edwards.

To verify, however, that the determined morphological correspondences are due to a close relationship of the species mentioned, a cladistic weighting of the characters is necessary.

For the distinction of plesiomorphic and apomorphic characters a comparison with related systematic groups (representatives of the Grapsidae, mainly of the subfamily Sesarminae) was carried out. As a result of this outgroup comparison the characters of *M. rubripes* and the American *Chiromantes* listed below are considered synapomorphic. Apomorphies 1 to 4 were originally depicted and described by von Hagen (1978) only with respect to the American species previously called *Holometopus* (now *Chiromantes*). Except for no. 2 the characters are not illustrated here. For further informations see Niem (1992) and Niem (in prep.). All numbers explained in the following lists of characters are finally used in the phylogenetic tree of fig. 6.

1. Ventral margins of propodus and dactylus of the first and second walking leg of male provided with a brush of short dense hair. This hair pattern, confined to the male, seems to be a common derived character of the American *Chiromantes*.

2. Lateral margin of carapace meets the ventral margin ventrally to the emargination between the second and third walking leg (fig. 4b-d). In other grapsids, the meeting point of the carapace margins is dorsal to the emargination, or mostly, the two margins do not meet at all.

3. Relative position of the male pleon to the sternum: separating line between pleonal segment 3 and 4 is posterior to the suture between sternite 4 and episternite 5. In all other species of *Sesarma* examined, as well as in other Sesarminae, the sepa-

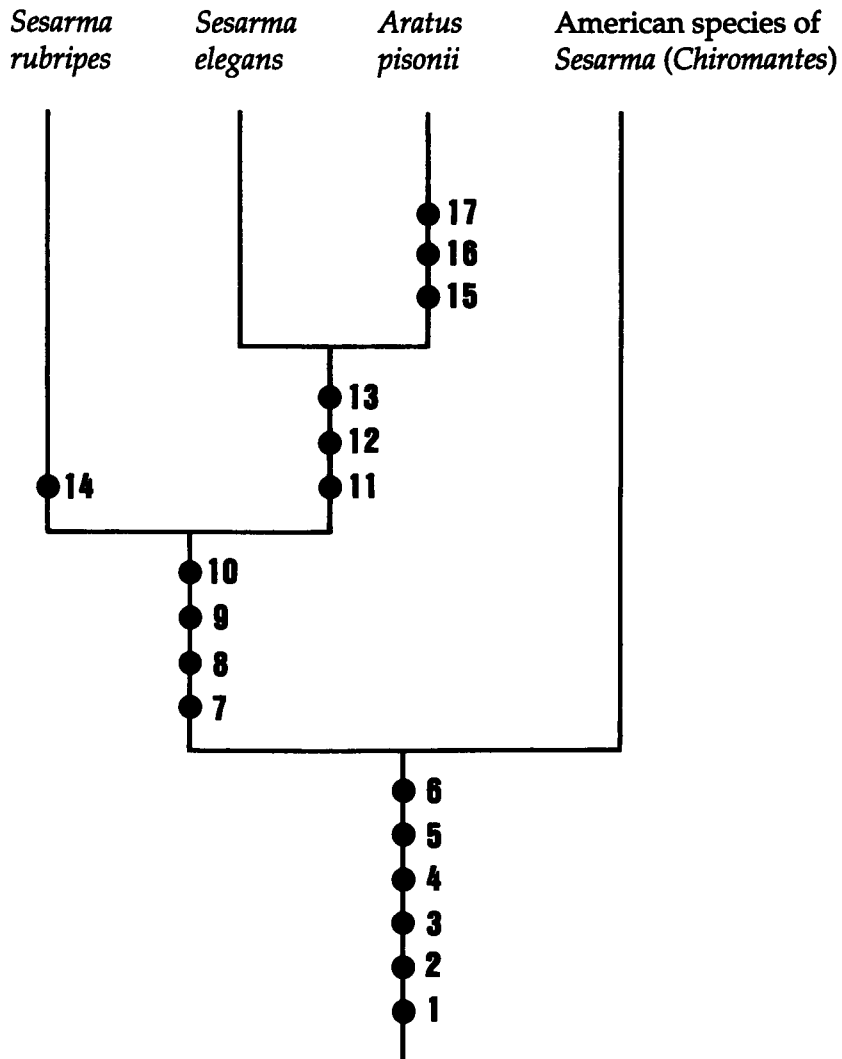


Fig. 6. Phylogenetic tree. Figures refer to the apomorphies listed and discussed in the text.

rating line is anterior to the suture mentioned.

4. A diagonal groove of the epistome, named "Verwey's groove", is delimited by a lower row of hairs only. In most species of *Sesarma* and in the genera *Clistocoeloma*, *Metagrapsus* and *Sarmatium*, Verwey's groove is delimited by an upper hairy row in addition to the lower one.

5. The granular crest, which separates the epistome from the endostome, does not traverse the lower part of Verwey's groove. In all other species of *Sesarma* and of genera supplied with Verwey's groove (see apomorphy 4) the granular crest traverses the lower part of the groove.

6. Third segment of male pleon distally wider than proximally. In most Sesarminae the third segment is proximally as wide as distally or wider.

There are two more sesarmids which share the six listed synapomorphies with the American *Chiromantes*, namely the American species *Aratus pisonii* and the West African species *Sesarma elegans*. The close affinity between *S. elegans* and the American *Chiromantes* was already stated by Zölzer (1987).

As can be seen from figs. 2 to 5, the characters that separate *M. rubripes* (b) from *M. rousseauxi* (a) also apply to *S. elegans* (c) and *A. pisonii* (d). According to an out-group comparison (using the grapsid species listed above), the presence of long striae and of distinct carapace regions (fig. 2b-d) as well as the non-swollen branchial regions and the non-diverging front (fig. 3b-d) must be considered plesiomorphic. Nevertheless, there still remain some distinct synapomorphies to identify *S. elegans* and *A. pisonii* as nearest relatives of *M. rubripes*. These synapomorphies (numbered 7-10, cf. fig. 6) are as follows:

7. Coxae of last three walking legs with hairy process antero-dorsally (fig. 4b-d). Coxal processes of this kind are apparently limited to *M. rubripes*, *S. elegans* and *A. pisonii* and were found to be largest in *Aratus*.

8. Elevated oblong area of merus of third maxilliped tapering in its distal half (fig. 5b-d). In the remaining Sesarminae examined the oblong area is variously formed, but always in a different manner (when compared with fig. 5b-d).

The following synapomorphies are not illustrated:

9. Carpus of cheliped distinctly longer than wide. In the Grapsidae the carpus is usually about as long as wide.

10. Ventral longitudinal row of setae on the anterior meral surface of cheliped is partitioned in groups of setae. These setae appear to be present in the Sesarminae only, but are usually arranged in an unbroken row.

The presumptive relation of *S. elegans* and *A. pisonii* as sister species depicted in fig. 6 is based on the following synapomorphies:

11. Merus of walking legs dorsally with a terminal and a subterminal spine. In other grapsids only a subterminal spine could be found.

12. Dactylus length of walking legs clearly less than half propodus length. The usual length of dactyli in Sesarminae amounts to more than half propodus length.

13. Median tooth of gastric mill with increased number of transverse ridges. In *S. elegans* there are five ridges, whereas in *Aratus* six ridges are present. The usual number of ridges in Sesarminae is presumably three (as in *M. rubripes*).

For the sake of completeness some autapomorphies of the species are to be mentioned (see fig. 6):

14. The gap between the fingers of the chelae bears a tuft of hairs proximally. This is a peculiarity of *M. rubripes*.

15. Outer surface of chelae covered with tufts of black bristles. Only found in *A. pisonii*.

16. Outer surface of chelae covered with blunt tubercles. Although occasionally present in other Sesarminae, this is a constant characteristic of *A. pisonii*.

17. Pleon of male extraordinary widening from segment 3 to segment 6, so that the pleon becomes subcircular. This is a very conspicuous feature of *Aratus*. In most other brachyurans the width of the male pleon decreases from segment 3 to segment 6 and the pleon is very far from circular.

In the case of *S. elegans* no definable autapomorphies could be detected.

Discussion

Zoologists of the last century often gave their confidence in the taxonomic value of single characters, when separating taxa. For example, two of the subgenera of *Sesarma*, *Sesarma* s. str. and *Chiromantes*, were differentiated for a long time by the presence or absence of an antero-lateral tooth posterior to the external orbital angle. The uncertainty of this character was stated by von Hagen (1978), who provided new data to distinguish between the two American subgenera of *Sesarma*.

A similar example apparently exists in the exclusion of the antenna from the orbit. Although in the previous and recent literature this character has been used to define the genus *Metasesarma*, the presence of the character is not very constant. According to de Man (1895: 195) and Tesch (1917: 257), in small specimens of *M. rousseauxi*, there may remain a more or less wide gap between the infra-orbital lobe and the front (as in *Sesarma*), so that the antenna is not excluded from the orbit. Furthermore, a convergent development seems not unlikely, since the exclusion of the antenna from the orbit is not only a characteristic of *Metasesarma*, but also present in other grapsids, namely *A. pisonii*, the genera *Clistocoeloma* (Tesch, 1917: 234, 235), *Goniopsis* (Rathbun, 1918: 236) and several species of *Metopograpsus* (Tesch, 1918: 78; Edmondson, 1959: 166, 167).

On account of the insufficiency of this character and with regard to the morphological divergences described above, *M. rubripes* should not be considered congeneric with *M. rousseauxi* any longer. A future new definition of the genus *Metasesarma* may be established by comparison with Indo-Pacific species of *Sesarma* from which *M. rousseauxi* and *M. aubryi* probably arose. The non-*Metasesarma* status of *M. rubripes* can be confirmed in regarding its phylogenetic position among the American Sesarminae. Most probably, *M. rubripes* has a common origin with *S. elegans*, *A. pisonii* and the American members of *Sesarma* (*Chiromantes*), a phylogenetic reconstruction of which will be given in a special publication (Niem, in prep.).

Some doubts might be put forward with respect to the exact phylogenetic position of *M. rubripes* and its nearest relatives. *M. rubripes* and *A. pisonii* are well known to climb trees in mangrove swamps (see photographs in von Hagen, 1977) and *S. elegans* also appears to be "naturally arboreal" (Powell, quoted in Manning & Holthuis, 1981: 244). Because of similar life-styles, a convergent character development, caused by functional adaptation, is surely thinkable (e.g. in respect to the short dactyli of *S. elegans* and *Aratus*). However, the preference for a theory of close relationship as shown in fig. 6 results from the extent of commonly derived characters found in these species. Especially apomorphy 7 is unique in the Sesarminae and therefore a weighty argument for the monophyly of the three species *M. rubripes*, *S. elegans* and *A. pisonii*.

Finally, some nomenclatural considerations seem to be warranted. Since the phylogenetic position of *M. rubripes* and *A. pisonii* is located between the members of the subgenus *Chiromantes* (fig. 6), this subgenus has to be regarded as paraphyletic. To avoid the state of paraphyly, a splitting of the American *Chiromantes* in several systematic groups may come into question, but would be most unpractical. In comparison with this, a shifting of *M. rubripes* and *A. pisonii* to the genus *Sesarma* seems to be a more suitable solution. Nevertheless, in spite of paraphyly the status of a separate genus should be affirmed in *Aratus pisonii*, for this species possesses enough special

derived characters to distinguish it from *Sesarma*. Furthermore, an equivalent example exists in the bromeliad-inhabiting *Metopaulias depressus* Rathbun, 1896 from Jamaica, a grapsid crab which probably arose from Jamaican members of *Sesarma* (*Sesarma*). The exceptional systematic position of monotypic genera like *Metopaulias* and *Aratus* is well established by their drastic modifications, caused by high specialized life-style, and should therefore remain untouched.

Although *M. rubripes* without doubt is somewhat deviating from the American *Chiromantes* in its general appearance, it shows in contrast to *Aratus* no sufficient morphological features that would justify the creation of a separate genus. In consequence, the name of the species should be determined again as *Sesarma rubripes* Rathbun, 1897.

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