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THE TREE-CLIMBING CRABS OF TRINIDAD

by

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INTRODUCTION

The remoteness of crab and tree in the scheme of nature (referred to by DARWIN, 1839) is as much taken for granted in our opinion as the lack of relations between fish and tree. Observations that such relations nevertheless exist somewhere (mostly in the tropics) must therefore create the idea of reporting something peculiar ("Who says, fish can't climb trees?", POLUNIN, 1972). This may be the reason why the robber crab (*Birgus*) climbing coconut trees was probably mentioned as early as the 9th century (SOLEYMAN, see REYNE, 1939: 284–285).

Since the days of the Arab merchant SOLEYMAN many accounts on tree-climbing crabs have been published. Even a shrimp (*Merguia rhizophorae*, Natantia: Hippolytidae) was observed ascending mangrove roots (ABELE, 1970; cf. HOLTHUIS, 1959a). However, until now little comparative work has been done. The symposium on "Terrestrial Adaptations in Crustacea" (*Amer. Zoologist* 9, 3, 1969) hardly mentioned tree-climbing at all, though species climbing up into the atmosphere normally should be regarded as "more terrestrial" than ground-living forms.

The general affinity of terrestrial groups of crabs to tree-climbing habits does not mean, however, that these habits always imply need of terrestrial adaptations. Some climbing species keep close to the ground or stay on mangrove roots that are rather constantly submerged. Others live in *phytotelmata*, i.e. micro-pools within or upon plants (see THIENEMANN, 1935, and WESENBERG-LUND, 1943, for general remarks on phytotelmic animals). On the other hand, several species of terrestrial crabs progressing very far inland or high up into the mountains were never observed scaling trees. Typical inland forms of this kind seem to be *Sesarma foxi* Kemp (TWEEDIE, 1940), *S. trapezoideum* H. Milne Edwards (DE MAN, 1902; FOREST & GUINOT, 1961), *Geograpsus grayi* (H. Milne Edwards) (GIBSON-HILL, 1947) and *Coenobita rubescens* Greeff (GREEFF, 1882, 1884).

It is the purpose of the present paper to present a first review on the habit of tree-climbing in brachyuran and anomuran crabs and thus to provide a certain basis for future research.

This review was induced by observations in Trinidad (West Indies), where several tree-climbing crabs occur.

I am greatly indebted to Prof. J. S. KENNY (University of the West Indies, Trinidad) for his many-sided assistance and to Prof. L. B. HOLTHUIS (Leiden, Netherlands) for identifying the crab material collected (except *Uca*), for drawing my attention to several papers that mention tree-climbing crabs, for correcting the nomenclature used in Table 2 and for reading and criticizing the manuscript.

The visit to Trinidad (1965/66) was made possible by financial support of the Stiftung Volkswagenwerk, the Deutsche Ibero-Amerika-Stiftung and the Deutsche Forschungsgemeinschaft.

LOCALITIES, HABITATS AND SYSTEMATICS

General remarks on topography, climate, vegetation and tidal pattern of the island of Trinidad are omitted here (short introductions are given by KENNY, 1969, VON HAGEN, 1970b and STONLEY, 1975). The data reported in this paper were collected in the course of a year mainly devoted to the study of fiddler crabs (genus *Uca*).

A systematic synopsis of the tree-climbing crab species of Trinidad is given in Table 1. Five species (*Pachygrapsus gracilis*, *Sesarma angustipes*, *Cardisoma guanhumi*, *Hexapanopeus caribbaeus*, *Coenobita clypeatus*) that occur in Trinidad but were not seen climbing by the author, were nevertheless included in the table and in the text, because they are known as tree-climbing or at least phytotelmic from literature. The maximum carapace width listed in each case is meant to give a certain idea of the crabs' sizes.

The numeration of the localities of observation is taken from VON HAGEN (1970b). Identification figures *Tr 5*–*Tr 17* refer to the east coast, the following ones to the north-western coasts adjacent to the Gulf of Paria. Details on pertinent regions are given by BACON (1970) and STONLEY (1975).

List of localities:

Tr 5	Mouth of Salybia River (east of Toco).
Tr 6	Mouth of Balandra River.
Tr 9	Mouth of L'Ebranche River.
Tr 10	L'Ebranche River Bridge of Eastern Main Road near Lower Manzanilla.
Tr 13	Nariva River from Nariva Bridge to the mouth.
Tr 17	Mouth of Lawai River, Guayaguayare Bay.
Tr 23	Entrance Canal (East-West Trench no. 9) between Princess Margaret Highway and Blue River, Caroni Swamp.

Tr 24	Blue River, Caroni Swamp.
Tr 26	El Socorro Entrance, Caroni Swamp.
Tr 27	Main waste-water ditch, Laventille Swamp.
Tr 31	Cocorite Swamp, east of Diego Martin River.
Tr 32	Mouth of Diego Martin River.

Figure 8 outlines the upstream distribution of the crabs mentioned and their main habitats. Species occurring in different zones and habitats are listed only once (indicating their main occurrence).

GRAPSIDAE

The seven species of grapsids to be dealt with fall into three categories:

a) Species known as tree-climbing or phytotelmic from literature only (*Pachygrapsus gracilis, Sesarma angustipes*).

b) Species known as tree-climbing or tree-living from literature and frequently seen on trees at many places in Trinidad by the author (*Aratus pisonii, Goniopsis cruentata, Metasesarma rubripes*).

c) Species not known as tree-climbing from literature and found climbing in Trinidad at restricted localities only (*Sesarma roberti, S. ricordi*).

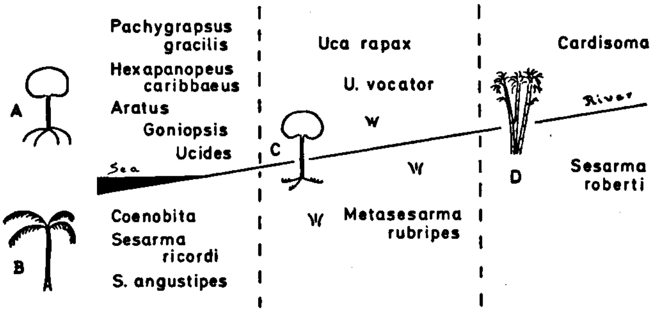

Fig. 8. Upstream distribution and habitats of the crab species mentioned in the text (schematically).

A Mangrove swamp with *Rhizophora mangle,*
B Supralittoral zone of sandy beach,
C *Laguncularia racemosa* mangroves and grassy outskirts,
D Bamboo wood.

The following GENERAL REMARKS (preceding the annotated species list) refer only to the five species mentioned under (*b*) and (*c*). All of them were kept in terraria in the laboratory in order to obtain a closer view of their climbing behaviour.

DIET

In addition to observations of feeding crabs in the field and in captivity, the stomach contents of 9–13 freshly killed adult specimens of each species (except *Goniopsis cruentata*) were examined. All species examined were found to be mainly herbivorous. In captivity, they eagerly feed on dead crabs or fish. In the field, however, these additions seem to be obtained rather rarely as all stomachs contained only or mostly macerated plant material together with grains of fine sand and indefinable detritus. Only one stomach out of 13 in *Metasesarma rubripes*, and 3 out of 9 in *Sesarma roberti* yielded some insect remains. The plant material consisted of a variety of angiosperm tissue and algae. In two species the remains were rather uniform: The stomachs of *Aratus pisonii* yielded mainly algae and black or brown opaque pieces of decayed mangrove wood, those of *Metasesarma rubripes* contained mainly very small roots and various leaves.

Only *Goniopsis cruentata* seems to be truly omnivorous. It has been recorded to feed on young mangrove shots (SCHÖNE & SCHÖNE, 1963 and HARTNOLL, 1965) as well as on sponges growing on mangrove roots (STONLEY, 1975) and to prey on living *Aratus pisonii* fallen to the ground (WARNER, 1967) though, apparently, it never attempts to catch *A. pisonii* when being on a tree (Pl. I, below). In *Tr 31* *G. cruentata* was observed to prey on *Uca maracoani*. Furthermore, it was seen killing and eating lesser individuals of its own species in captivity (cf. frequent cannibalism in the related *Grapsus grapsus*; KRAMER, 1967).

BODY ORIENTATION DURING LOCOMOTION

The main activity of all species mentioned (except *Aratus pisonii*) is performed on the ground. When being there, the crabs normally run with the typical brachyuran orientation of their body, i.e. sideways. Like all brachyurans (LOCHHEAD, 1961: 330), they are, however, able to walk temporarily forward or diagonally, especially at low speed. Only *A. pisonii* clearly prefers walking forward on any substratum and in any speed though still being able to walk sideways.

In climbing, body orientation is chosen according to the degree of inclination of the tree etc. and according to its diameter. Apart from *Aratus*, walking sideways is retained on big inclined and sometimes even vertical trees and on horizontal branches (Pl. I, above) and those with numerous secondary twigs. Normally this orientation of the body is abandoned on vertical trunks and as soon as the crab is forced to embrace the root, trunk or branch because of their small diameter.

In ascending, *Goniopsis cruentata* always climbs backward (Fig. 9a). When starting from the ground, it turns after very few steps taken forward or sideways.

The four remaining species prefer to go up head first (Fig. 9b). When climbing up a stick in experiment, they will turn (i.e. reorientate their body) when the stick is turned. But they are able to

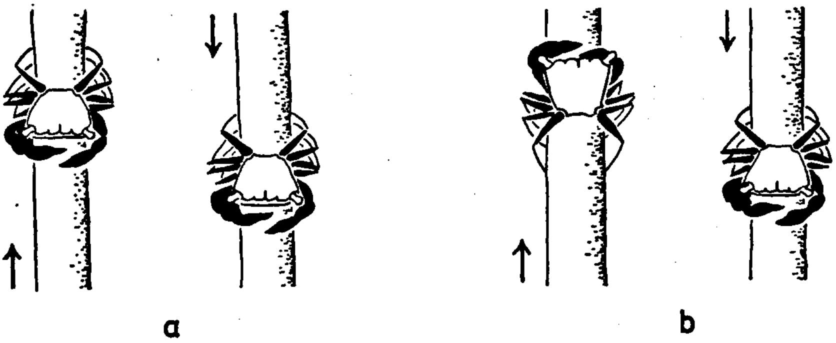

Fig. 9. Body orientation of tree-climbing grapsids. Ascending (left) and descending (right) in (a) *Goniopsis cruentata*, (b) the 4 species of the subfamily Sesarminae.

ascend backward when chased after the turning of the stick. Dexterity in performance, however, decreases in the following order: *Aratus pisonii, Metasesarma rubripes, Sesarma ricordi, S. roberti.*

None of the species is able to descend with great speed. The normal escape response therefore consists in hiding behind a trunk or fleeing up the tree. On close approach the crabs nearly always loosen their hold and jump or fall to the ground or into the water trying to hide there – a very common escape response of tree-climbing crabs (see below). The effect of these responses remains ambiguous, however. Crabs normally do not get hurt when they fall on soft ground but may become exposed to ground-living predators (e.g. *Goniopsis cruentata* preying on *Aratus pisonii* as mentioned above).

At high tide, chasing tree crabs into the water can mean to provide food for fish (e.g. *Colomesus psittacus*) – as was experienced in *Tr 31*. When being unmolested, all species are able to climb down

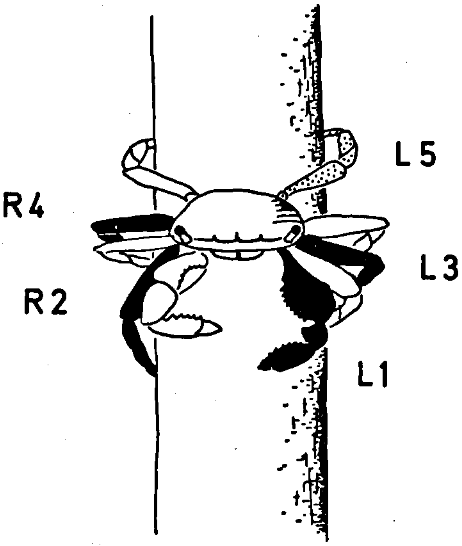

Fig. 10. *Goniopsis cruentata* ascending a *Laguncularia* tree. During movement of one set of legs (left white and not lettered) the crab is supported by the other set (drawn in black and lettered) which will move next. L 5 (stippled), instead of joining the black set, behaves independently. (Drawn from a photograph).

for considerable distance. This is always done head first (drawings on the right in Fig. 9a b). Only *Sesarma roberti* was observed once to descend backward for a few centimeters. Coming down backward seems to be the normal way of descending in *Birgus* (HOLTHUIS, 1959b: 309; cf. REYNE, 1939: 300, for a discussion of different opinions).

When perched on a tree, all species prefer to sit head down. *Aratus pisonii* and *Metasesarma rubripes* were found hanging underneath branches. Both are able to walk in this position without the aid of their chelipeds.

USE OF CHELIPEDS AND HINDMOST AMBULATORIES

Use of chelipeds as support during ascending and descending seems compulsory for all species except *Aratus pisonii* and *Metasesarma rubripes*, which can even perform arboreal display rotations of their chelipeds. In *A. pisonii* the chelipeds are held close to the carapace during forward ascent. They are, however, normally used as an additional pair of legs as soon as the crab moves in inverted body orientation (with its head down).

When ascending head first all species tend to stretch at least their hindmost pair of ambulatories posteriorly ("froglike", see Fig. 9b). These hindmost walking legs as well as the chelipeds are more independent of the normal stepping order than the other peraeopods (Fig. 10).

STEPPING ORDER

The general type of *gait* known for crabs (LOCHHEAD, 1961: 331) is retained through the change of walking direction from sideways to forward or backward. But as the chelipeds can participate in climbing locomotion there are normally two alternating quintets (instead of quartets) of legs, namely R1 – L2 – R3 – L4 – R5 and L1 – R2 – L3 – R4 – L5. In Figure 10 (ascending *Goniopsis cruentata*) the latter set (drawn in black and lettered) is giving walking support, whilst the former set (left white and not lettered) is moving.

Crabs climbing up and down with the same orientation of their body are, of course, used to change the *stepping direction*. It is interesting to note that, in addition, the *stepping sequence* of the legs can alter during climbing. An analysis of a few 8 mm motion pictures of *G. cruentata* ascending and descending vertically on a *Laguncularia* trunk shows that on the way up the stepping order can be changed from 1 – 3 – 5 – 2 – 4 to 4 – 2 – 5 – 3 – 1 (when taking in account one side only). As *G. cruentata* ascends backward (i.e. head down) it thus can either push itself "upstairs" with the front legs stepping first or pull itself up with the hind legs leading. It is not known whether one of the two sequences is preferred. In descending (likewise head down) all species seem to use only the sequence 1–3–5–2–4 pulling themselves down cautiously. It may be more dangerous to push oneself the way down.

Goniopsis cruentata (Latreille, 1802/3) "Mangrove Crab"

Like the two other species of this genus (Table 2) *G. cruentata* is well known as tree-climbing in literature (RATHBUN, 1918: 238; DANSEREAU, 1947: 466; GERLACH, 1958: 673; RODRIGUEZ, 1959: 266; SCHÖNE & SCHÖNE, 1963: 643; WARNER, 1967: 322; STONLEY, 1975: 325).

G. cruentata was seen on prop roots and trunks of *Rhizophora* and on trunks and (rarely) even on branches of *Laguncularia* (Pl. I, above), usually less than 2 m but sometimes up to 4 m above the ground. On two occasions these crabs were observed climbing on and hiding within stone walls in the mangrove area (cf. LANG in RATHBUN, 1921: 444, for *G. pelii*).

Tree-climbing of *G. cruentata* occurred periodically during every (day and night) flooding of the mangrove forest at high tide. The greatest number of perched individuals was always seen within about 100 m from the seaward fringe to the interior of the mangrove swamp. This corresponds to the pattern of occurrence found by counting the individuals on the floor during low tide in Jamaica (WARNER, 1969). Frequently the crabs "wait" until the tide is actually coming in. They may crowd the last patches of the floor of the swamp not yet submerged, until they finally rush to the roots of the trees. They ascend gradually ahead of the rising tide, sitting motionless and head down during the intervals (Pl. I, below) and keeping well away from each other.

When escaping from a human observer or an aggressive neighbour the crabs jump into the water and hide in the burrows of *Ucides cordatus*. Normally they return into the open rather soon, but some individuals do not reappear until the tide has receded. Juveniles were found to spend the periods of high water always hidden on the ground, e.g. under the bark of dead recumbent trees. Individuals from open areas clear of trees stay under overhanging portions of steep river banks during high tide.

During low tide most individuals keep to the ground, but there is a considerable up and down climbing activity of crabs of different sizes. At least some of these vertical excursions seem to be motivated by search of food (see above). Feeding from the algae coat of the *Rhizophora* roots (cf. *A. pisonii*) was, however, observed in younger individuals only.

Unlike *A. pisonii* and *M. rubripes*, *G. cruentata* was never seen courting females when being on a tree.

Aratus pisonii (H. Milne Edwards, 1837) "Tree Crab"

A. pisonii is the best known of all tree-climbing crabs. F. MÜLLER (1864: 20) already mentioned its special abilities when speaking of an "allerliebsten, lebhaften Krabbe, die auf die Manglebüsche (*Rhizophora*) steigt und deren Blätter benagt". It is not only a tree-climbing but a truly tree-living species – at least when adult. Unlike in the fully phytotelmic *Metopaulias depressus* the larval period is spent in the sea, and juvenile individuals keep to the lowest portions of the mangrove trees and hide under the bark or on the ground. The adults, however, spend most of their time on mangrove trees (occasionally on others in the vicinity of mangroves). There seems to be no fully corresponding form in the Indo-West Pacific mangrove faunas.

We are well informed on breeding, larval development, growth, maturity and sexual dimorphism (HARTNOLL, 1965; WARNER, 1967, 1968), but there has been little attempt to understand some outstanding morphological features in respect to tree-climbing or to consider the specialized locomotion habits of *A. pisonii* in more detail than on p. 30.

There should be no doubt that *A. pisonii* is able to feed on mangrove leaves as reported by MÜLLER (1864) and HARTNOLL (1965). But considering the stomach contents of the specimens from Trinidad (see above), it becomes dubious whether leaves always "form its principal food" (HARTNOLL, 1965: 116). The examination of stomach contents fitted well into observations in the field. When continuously recording the activities of the *Aratus* population (about 20 adult crabs and some young ones) of one *Rhizophora* tree (diameter of root system about 5 m) in *Tr 24* for nearly a day, not a single individual was found to feed on leaves. A continuous feeding activity was observed only when the tide receded from the lower portions of the prop roots (those extending from the trunk) and the aerial roots (those dropping from branches). Feeding individuals of various sizes crowded the moist roots (Pl. IV, centre), which the tide had just uncovered, the "bare" ones as well as those grown with epizoans (oysters, barnacles, sponges etc.; see BACON, 1970, for scientific names and zonation data). This behaviour was also noted by HARTNOLL (1965: 117), but ascribed to smaller crabs (less than 5 mm) only. All roots are encrusted with a coat of detritus-covered algae ("bostrychietum", see GERLACH, 1958: 699, and BACON, 1970: 47, for species names), which apparently forms the main food of *A. pisonii* during the low tide period.

Between two feeding periods of this kind at least half of the crabs rested perched on the shaded trunk (Pl. I, bottom) or hanging underneath the roots and branches within 2 m above the ground, though there was always a certain climbing activity between the bottom and the top of the tree (about 6 m high). Among these climbers occasional feeding occurred in taking up portions of decayed tissue from wounded mangrove roots and in picking up the faeces of other *Aratus* specimens from the bark of the tree.

Components of intraspecific behaviour in *A. pisonii* are described by WARNER (1967, 1970). Display and copulation take place on the mangrove trees.

Metasesarma rubripes (Rathbun, 1897)

The tree-climbing of *M. rubripes*, already mentioned briefly by RODRIGUEZ (1963: 201) and probably by PEARSE (see below, under *S. roberti*) was observed frequently in all localities mentioned in Table 1, especially in *Tr 26*. In daytime as well as at night, crabs of both sexes and of different sizes ascended the grass *Paspalum serpentinum*, the stems and branches of *Laguncularia* trees and the lower trunk region of *Bactris* and coconut trees (Pl. IV, left), mostly up to 3 m, rarely as far as 6 m above the ground.

Climbing activity frequently occurred during periods of high water though not regularly. Apparently, the crabs are able to endure submersion within their self-dug burrows with oval-shaped entrances in or near the banks of rivers or hidden under recumbent trees and other plant material on the ground. Climbing was seen during normal high tides though the largest numbers of arboreal individuals were counted during periods of prolonged inundation of river banks after heavy rains (cf. *Uca rapax*). Many of the climbers were found sitting motionless head down (cf. *G. cruentata* and *A. pisonii*), others remained active. Some males were seen courting females on *Laguncularia* branches.

Periods of flooding are, however, not the only situations causing this species to climb trees. As in *G. cruentata*, there was a considerable climbing activity at low tide.

From all grapsids mentioned, *M. rubripes* comes closest to the climbing dexterity of *A. pisonii*.

Sesarma roberti H. Milne Edwards, 1853

S. roberti usually hides under logs and stones on the ground or within galleries dug into steep clayey banks of rivers and ditches, the entrance of the burrows being oval-shaped. To reach the entrance the crab often has to climb up vertically. *S. roberti* was seen by CHACE & HOBBS (1969: 186) scaling the wall of a cliff and the almost vertical surface of the cement wall of a bridge.[1]

In the two main localities of observation in Trinidad (*Tr 10, 31*) *S. roberti* lived within or close to a bamboo forest, but only in *Tr 10* these crabs were found to climb up and to hide within the stems. This local behaviour may have been induced by the fact that some of the bamboo had been cut a considerable time ago. A maze of loose smaller canes lay about (Pl. II, above) facilitating access to the stumps of the bigger stems. Several stumps were open on top (Pl. II, below) and had partly filled with rain water thus forming phytotelmae. Six individuals were taken out of these stumps up to 2 m above the lowest roots, a seventh from a lateral slit in an internode. Several others were seen climbing among the loose smaller canes and upon roots exposed by the action of the stream.

As mentioned above, examination of stomach contents yielded insect fragments in one third of the 9 specimens opened (all from *Tr 10*). One male contained fragments of no less than 8–10 different insect specimens. It can be concluded, therefore, that the bamboo provided moist hiding places and food at the same time.[2]

Sesarma ricordi H. Milne Edwards, 1853 "Beach Crab"

During daytime, this relatively small and cryptic-coloured crab keeps usually hidden on the beach along and somewhat above high water mark, among driftwood, leaf litter, stones and coconut husks. *S. ricordi* moves far from cover at night only. This may be the reason why relatively little is known of the behaviour of this species.

At night the crabs were seen foraging in the tidal zone in *Tr 32*

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[1] PEARSE (1915: 553) reported that in Colombia *S. roberti* "walked about over the roots or climbed in the trees". But as he remarks that these crabs "had burrows among the mangroves" it seems dubious whether his notes actually refer to *S. roberti*. Furthermore, the carapace measurements given by PEARSE do not fit those of the subquadrate *S. roberti*. They excellently fit the proportions of *M. rubripes* instead.

[2] It is interesting to note that in Malaya the internodal space of intact bamboo canes is utilized by roosting bats (two species of *Tylonycteris*) and nesting tree-mice (*Chiropodomys gliroides* and *Hapalomys longicaudatus*). The two latter, however, gnaw their entrance holes themselves (MEDWAY, 1969).

and climbing (1–2 m above ground) in large numbers the branches of dead trees and shrubs washed ashore (cf. *Metopograpsus latifrons* and *Sesarma guttatum*, Table 2). They fed on small particles from the surface of the stems and branches. Though sometimes found on sandy ridges within the mangrove area, *S. ricordi* was never seen nocturnally ascending living mangrove trees.

In captivity these crabs always hid during daytime and climbed on twigs and the walls of the terrarium at night.

Sesarma angustipes Dana, 1852

S. angustipes was not seen ascending trees in Trinidad, but is nevertheless taken into account here, because this species recently was found to live in the tanks of bromeliads in Brazil. From this phytotelmic habitat it was reported as "*Sesarma ricordi*" by SATTLER & SATTLER (1965), as "*Sesarma miersii*" by MCWILLIAMS (1969; for synonymy see ABELE, 1972b) and finally as "nickel-size marine crab (genus *Sesarma*)" by ZAHL (1975). The Brazilian bromeliads (*Neoregalia cruenta* and others) were growing on boulders in each of the cases mentioned.[1])

Prof. J. S. KENNY (personal communication) found crabs in the tanks of bromeliads in Trinidad (Cocos Bay) and, apparently, in those growing on trees. The crabs he collected possibly belonged to this species. But, unfortunately, they got lost on their way to Germany so that confirmation is still wanting.

Until now we can only be sure that in Trinidad *S. angustipes* occurs under coconut husks and palm leaves near the mouth of rivers.[2]) A single specimen was collected from inside the walls of a deep abandoned well in *Tr 31* (together with *S. roberti*).

[1]) A single male from Rio Parahyba do Norte, Cabedello, Brazil (USNM 25712) mentioned by RATHBUN (1918: 304) as "*Sesarma miersii*" and later identified as *S. angustipes* by ABELE (1972 a, b) was found "on mangroves". But obviously this male was only afterwards isolated from 9 specimens of *Aratus pisonii* with the same collecting data (USNM 25713, RATHBUN, 1918: 324) so that the remark "on mangroves" may be only a description of the typical habitat of this latter species.

[2]) The conformity of crabs collected at these sites with those living in Brazilian bromeliads was stated by ABELE (1972 a, b) who finally cleared up the taxonomic status of *S. angustipes* Dana (ABELE, 1972a) and examined part of my material from Trinidad,

Though apparently able to live in the tanks of bromeliads, *S. angustipes* is very far from the state of adaptation reached by the true bromeliad crab, *Metopaulias depressus* Rathbun, which is endemic to Jamaica and restricted to large saxicolous and epiphytic bromeliads in the limestone hill area above 250 m (LAESSLE, 1961; HARTNOLL, 1964). *M. depressus* is phytotelmic throughout its whole life cycle, the zoeal stages being condensed into a non-feeding phase lasting only 3 days (HARTNOLL, 1964).

The most striking adaptations of *S. angustipes*, however, are adaptations to water uptake from the ground, i.e. tufts of hair between the coxae of the second and third and the third and fourth ambulatories. These hairs are nearly as long and dense as in the closely related *S. ricordi*, where maximum development of the tufts is reached. *S. angustipes* is even able to dig. When kept in a terrarium an individual of *S. angustipes* excavated the ground under a hiding log thus digging a shallow pit.

It should be mentioned that there is at least a third species of Sesarminae occurring in bromeliads. Like *Metopaulias depressus*, it was found in Jamaica. However, the only specimen known so far could not be identified with certainty until now (*Sesarma jarvisi* Rathbun or *S. cookei* Hartnoll; cf. HARTNOLL, 1964: 164, and 1971: 259).

Pachygrapsus gracilis (De Saussure, 1858)

P. gracilis was collected by the author in *Tr 31* only. It was found among a local aggregation of stones at the seaward fringe of the mangrove area, associated with *Petrolisthes armatus* (Gibbes). This species is included here, because HARTNOLL (1965: 114) saw *P. gracilis* in Jamaica "among the algae and sponges covering the mangrove roots which hang into the water".

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sent to Washington by Miss J. M. STONLEY (ABELE, 1972a: 168; 1972b: 123). Another part of the material (now in Leiden Museum) was already identified as *S. angustipes* Dana by Prof. L. B. HOLTHUIS (Leiden) in 1966 and mentioned under this name by VON HAGEN (1968).

OCYPODIDAE

The two species of *Uca* (*vocator* and *rapax*) to be mentioned here are rather closely related. They both belong to the "jerker group" of New World fiddler crabs. A third member of this group, *U. brevifrons*, was found perched on a tree by CRANE (see Table 2). A fourth species, *U. thayeri* Rathbun, ascended branches in captivity only (VON HAGEN, 1970b: 390) and is omitted here.

Ucides cordatus, briefly mentioned below, was transferred from the Gecarcinidae to the Ocypodidae by CHACE & HOBBS (1969), a view also adopted by TÜRKAY (1970). Incorporation into one of the subfamilies is still wanted.

Uca vocator (Herbst, 1804)

U. vocator is one of the *Uca* species that invade the freshwater area. In contrast to most other species, possession of a burrow is not compulsory. Males can be found displaying among herds of feeding crabs on driftwood floating on ditches (VON HAGEN, 1970b: fig. 9). They were likewise seen waving on the stump of a tree, which they ascended up to 20 cm above the ground. When molested, these males hid in slits and holes of the wood or underneath the bark.

Ovigerous females from stagnant pools periodically (especially around full and new moon) gather in large numbers on the banks of nearby canals with tidal influence until the hatching of their larvae. The females are normally joined by a few males. As these females are alternately molested by egg-stealing poeciliid fishes and grackles in *Tr 23* and *26* (VON HAGEN, 1969), they keep close to the water's edge and ascend *Laguncularia* and *Rhizophora* mangroves, when the tide rises (Pl. III).

A few individuals of *U. vocator* that were observed on the stems of *Laguncularia* in *Tr 31* are mentioned together with *U. rapax* below.

Uca rapax (Smith, 1870)

Displaying males of this and other species of *Uca* tend to select small elevations of the ground or heaps of mud pellets near the entrance of their burrows as special courting places. In two instances males of *U. rapax* were observed to use shrubs instead. However, they ascended the branches (which had been washed ashore in *Tr 32*) not higher than about 5 cm above the ground.

More impressive heights were achieved by the inhabitants of an inland *Laguncularia* grove in *Tr 31*, which was continuously flooded by fresh water from the river during and after a period of heavy rain in June. Numerous individuals of *U. rapax* and a few *U. vocator* were found up to 40–50 cm above water level (Pl. IV, right). As the water covered the ground 50–60 cm high the total climbing height was more than 1 m. On higher ground *U. rapax* ascended tall grass.

The "arboreal period" lasted for only two days. Some of the crabs fed on moist bark, but most of the perched individuals sat motionless, some with the eyestalks laid down in their sockets (i.e. in the so-called "sleeping condition"). Crabs still moving ascended head first or (more rarely) backward. One male came slowly down with its head first. When molested, the perched fiddlers behaved just as the grapsids mentioned above. They tried to dodge around the trunk and, on closer approach, leaped down into the water. In the males a threat display of the big claw usually preceded this retreat. Some individuals reappeared after a while. On the third day the number of perched crabs had drastically decreased though the water was still high.

Ucides cordatus (Linnaeus, 1763)

Some medium-sized individuals of *U. cordatus* ascended trees within the flooded mangrove area together with *U. rapax* (see above). All crabs seen kept a few centimeters above water level.

GECARCINIDAE, XANTHIDAE AND COENOBITIDAE

The brachyurans *Cardisoma guanhumi* and *Hexapanopeus caribbaeus* as well as the anomuran crab *Coenobita clypeatus* are mentioned together here, because all information on their climbing behaviour was obtained from second hand.

Cardisoma guanhumi Latreille, 1825

Tree-climbing of *C. guanhumi* was observed by PEARSE (1915: 553) in Colombia and by GIFFORD (1962: 219) and STEPHENS (1965: 201) in Florida. CHACE & HOBBS (1969: 197) found this species perched on the braces of a temporary bridge in Dominica. A more detailed account has recently been given by HENNING (1975: 284, fig. 20–22) who reported males and females to climb regularly up to 3 m on reed, palm trunks and *Prosopis juliflora* feeding on leaves and insect remains.

Hexapanopeus caribbaeus (Stimpson, 1871)

This small xanthid crab, usually collected from under driftwood and stones in the tidal zone, was found in Trinidad "in the encrustations on the mangrove roots" by STONLEY (1975: 38).

Coenobita clypeatus (Herbst, 1791)

This species occurs in the coastal area of north-eastern Trinidad only, where it hides during the day and is active at night. Local people reported to have seen these "Soldier Crabs" perched on trees. This corresponds to similar observations on the same species in Florida (PHILLIPS, 1964: 5, HAZLETT, in litt.). While PHILLIPS simply speaks of trees, HAZLETT writes of "mangrove rootlets and other small plants near the shore".

DISCUSSION AND CONCLUSIONS

In order to get an impression whether the observations on climbing crabs in Trinidad are typical, pertinent data from literature (including climbing on vegetation other than trees) were compiled in Table 2. To achieve a certain synopsis, the Trinidad species were included, though without repetition of relevant references. Most of the earlier reports on *Birgus* (reviewed by REYNE, 1939) were omitted intentionally. Other accounts on tree-climbing crabs (e.g. BERRY, 1963: 94, on "grapsoids", and many remarks of HARMS, 1929) could not be included for lack of species names. Certainly many further references escaped the author's attention.

It can be read from Table 2, that all crabs which were observed climbing trees in Trinidad belong to systematic groups containing other climbing members. Typically (see introduction) these are mostly groups that contain many or only terrestrial forms. The prevalence of Sesarminae (15 species) is impressive. All these groups could share certain *motives* and *predispositions* to tree-climbing. In addition, the accumulation of names of observers in certain species reveals different *grades* of affinity to trees. Some of these species (especially *Aratus pisonii*, *Sesarma rotundatum* and *Goniopsis cruentata*) were named "tree crabs" by various authors. The term "trees", however, appears to be a collective noun for rather different kinds of vegetation (though the word "mangroves" is, of course, prevailing). Therefore some considerations on different *phyletic routes* to climbing habits are necessary. Finally some *consequences* to the animals involved should be discussed.

MOTIVES

It will not be discussed here why animals emigrate from the sea at all (see PEARSE, 1950) and that intertidal and coastal vegetation in general favour this evolution. We shall restrict ourselves to certain motives apparent from the behaviour of the crabs observed in Trinidad and elsewhere.

1) ESCAPE FROM FLOODING OF THE GROUND. Crabs inhabiting the tidal zone and being active in air during low tide, either hide in burrows or climb upwards into the vegetation when the ground is flooded. The latter crabs behave much like certain species of Indo-West Pacific mud-skippers, especially *Periophthalmus chrysospilos* (MACNAE, 1968: 186, POLUNIN, 1972). Some crab species (*Metasesarma rubripes, Goniopsis*) take advantage of the two possibilities though the burrows used by *Goniopsis* are those of other species. As many of the climbing forms can survive submersion in sea water for long periods under experimental conditions (e.g. *Sesarma mederi* for 190 hours; VERWEY, 1930: 242) climbing as well as hiding is probably mainly induced by predators (fishes, portunid crabs) that come in with the rising tide ("Flutgäste", GERLACH, 1958: 718). Crabs like *Goniopsis, Aratus, Sesarma mederi* and others, climbing trees instead of hiding in burrows, expose themselves to predators from the air (see *Uca vocator*). On the other hand, they are not trapped within their own burrows by prolonged inundations. *Cardisoma guanhumi* endures aperiodic freshwater floods within its burrow (HENNING, 1975: 284). *Uca rapax* and *Ucides cordatus*, however, start climbing in this (and only in this) case. Escape from low salinities may be the main reason.

2) ESCAPE FROM LOW TIDE PREDATORS (observed in *Cardisoma guanhumi*; HENNING, 1975: 284) or conspecifics (observed in *Goniopsis cruentata*; WARNER, 1967: 332).

3) SEARCH OF FOOD. The food frequently consists of material of the vegetation itself: leaves, fruits, decayed wood, bark. Even blossoms (of *Pandanus* and a tall lily) have been reported as food of climbing hermit crabs, probably *Coenobita*, of the Marshall Islands (SCHNEE, 1902). Other species feed on epiphytic or epizoic encrustations. Several individuals of *Sesarma rotundatum* were taken from "green patches of moss or lichens" on bread fruit trees (HOLTHUIS, 1953: 33). *Aratus* feeds on the algae cover (the bostrychietum) on the roots and stems of mangroves, *Goniopsis* at least locally on sponges growing on *Rhizophora* roots. *Pachygrapsus gracilis* and the xanthids mentioned may eat parts of still other encrustations on these

roots. Capture of agile prey is reported more rarely. Examination of stomach contents in *Metopaulias* yielded arthropod remains (HARTNOLL, 1964; 147), probably insects as in *Sesama roberti* and *Metasesarma rubripes*. PHILLIPS (1964: 4) figured a tree-climbing "*Sesarma* crab" (possibly *Aratus*) preying on a live 17-year cicada in Florida. HARMS (1929: 261) mentioned a crab (not identified) perched on a flooded mangrove thicket and eating a tree frog.

4) SEARCH OF SHELTER IN TREE HOLES AND UNDER TREE BARK. Typically, several species collected from trees were (like *Sesarma roberti*) found in tree holes: *Geograpsus crinipes* (HOLTHUIS, 1953: 29), *Sesarma rotundatum* (LAIRD, 1956: 67), *Coenobita clypeatus* (PHILLIPS, 1964: 5). *Uca vocator* and juvenile *Aratus* and *Goniopsis* were found to hide under the bark of trees. Of course, phytotelmata (see 5) have a shelter function, too.

5) SEARCH OF WATER IN PHYTOTELMATA. Water supply by phytotelmata is not only important for inhabitants of these micro-pools (*Metopaulias, Sesarma angustipes, S. roberti*), but also for land crabs in dry habitats. The earliest reference to the climbing habits of *Birgus* (SOLEYMAN, see introduction) is perhaps a correct statement on a main motive (MCNEILL, 1961), because it says that the "fish" climbs the coconut trees to drink something (whether sap or water is not quite clear). *Birgus* prefers fresh water to sea water in captivity (HARMS, 1932, GROSS, 1955) and has the lowest blood concentration when compared to two species of the closely related genus *Coenobita* (GROSS, 1964).

6) USE OF LOW BRANCHES AND TREE STUMPS AS A SORT OF LOOKOUT by displaying *Uca* males.

GRADES

With respect to time spent on the tree (compared to periods on the ground) most of the species can be placed into the following categories:

a) temporary and sporadical, e.g. *Callinectes, Uca, Ucides, Ocypode, Sesarma ricordi*;
b) temporary and frequent, but not rhythmic, e.g. *Birgus, Coenobita, Cardisoma, Sesarma rotundatum*;
c) temporary and frequent and mostly periodical (corresponding to the tidal rhythm), e.g. *Goniopsis, Metopograpsus latifrons, Metasesarma rubripes, Sesarma elegans, S. mederi*;
d) permanent except larvae and juveniles, *Aratus*;
e) permanent including larvae and juveniles, *Metopaulias*.

It is interesting to note that grapsid crabs of the subfamily Sesarminae are represented in each category.

Superimposed on this rough basic scale, there are several other gradients, characterized by the following extremes (examples given in parenthesis): aquatic (*Callinectes*) to almost completely terrestrial (*Birgus*), marine (*Ocypode*) to freshwater-adapted (*Sesarma roberti, Metopaulias*), seaward fringe (*Goniopsis*) to inland forest (*Potamonautes*), grass and reed (*Callinectes*) to huge trees (*Potamonautes*), roots (*Pachygrapsus*) to topmost branches (*Aratus*)

These different scales do not coincide in every case. *Metopaulias* e.g., is more permanently living on trees than *Aratus*. The latter is nevertheless more terrestrial than the former, which normally hides in the tanks of large bromeliads. Such discrepancies can be explained by different phyletic routes.

PHYLETIC ROUTES

At least the first two phyletic routes from sea to tree are quite apparent:

1) Estuary – freshwater – tanks of saxicolous bromeliads growing near the sea – epiphytic bromeliads growing on trees and high up in the hills. The last two stages are represented by *Sesarma angustipes* and *Metopaulias*, respectively. The former species, however, is not as clearly phytotelmic as the latter. A third species, *S. roberti*, is even less phytotelmic and inhabits a somewhat different niche.

In the Indo-West Pacific *S. rotundatum*, only young individuals were found between the leaves of *Crinum asiaticum.*

2) Ground of intertidal zone – mangrove roots – trunks and branches of mangrove trees – (inland trees). This is another phyletic route of the Sesarminae but, obviously, of other groups too: mangrove vegetation is mentioned in more than half of the examples listed in Table 2. In the mangrove belt of Trinidad, there are typical ground-living, burrowing species of the subgenus *Sesarma* s. str. (*curacaoense* and *rectum*; see VON HAGEN, 1977) that never ascend vegetation. *Metasesarma rubripes* is a skilful climber though still digging holes. *Aratus* represents a final evolutionary stage never digging burrows in the ground. Typically, this stage is reached within the shaded and humid mangrove thicket; taller trees growing beyond the terrestrial fringe of the mangrove area are ascended only occasionally. The same seems to hold true for the Indo-West Pacific *Sesarma mederi* and others.

3) It is possible, however, that some species of *Sesarma* (e.g. *S. rotundatum*) progressed via sandy beaches, which may have been also the route of the Coenobitidae culminating in *Birgus*. However, at least some of the tree-climbing Coenobitidae were also recorded from mangroves (Table 2) and cliffs (*Coenobita clypeatus* according to CHACE & HOBBS, 1969: 126).

4) A fourth phyletic route could have begun on rocky shores. This seems to be the route of some grapsid crabs of the subfamily Grapsini and of at least one of the xanthids mentioned. *Pachygrapsus gracilis*, occurring among stones at the seaward fringe of the mangroves and on encrustations (algae and sponges) covering mangrove roots, seems to be displaced from the rocky marine environment where the closely related *P. transversus* still lives on similar encrustations.[1] The xanthid *Hexapanopeus caribbaeus* could be another displaced rock crab. Both these crabs live on the lower portions of the roots that are submerged during most of the tidal

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[1] On the confusion of habitat data of these two species of *Pachygrapsus* by RATHBUN (1918, following JARVIS, 1897) see HARTNOLL (1965).

cycle. But even the "air-climber" *Goniopsis* with its tendency to hide in occasional stone walls within the mangrove vegetation, is likely to have evolved directly from rock-living ancestors of the *Grapsus* type. This would explain the lack of digging abilities in *Goniopsis.*

Affinities of rock climbers to tree climbing lead to the idea of predisposition discussed in the following section.

PREDISPOSITION

When shifting its habitat from encrustations on rock to those on mangrove roots, *Pachygrapsus gracilis* had mainly to adapt to lower salinities. Its locomotion and feeding habits could remain similar.

Predisposition to tree climbing can therefore firstly be given by the nature of the original habitat. Trees may possess characteristics similar to this habitat so that the animal is scarcely "aware" of being displaced. Further examples of this kind are provided by species (*Uca vocator, Sesarma roberti*) that locally take tree holes as equivalents of their burrows. Likewise, the individual of *Potamonautes* sp. observed by DIETERLEN in Irangi forest (eastern Congo, see Table 2) may have taken the huge Parinari tree for the steep bank of a river.

Secondly, predisposition to tree climbing can be given by certain preadaptations of the crabs themselves, e.g. specializations for air breathing and water economy (see VERWEY, 1930, EDNEY, 1960, BLISS, 1968 and MACNAE, 1968) which are typical for most groups living in semi-terrestrial environments (Ocypodidae, Sesarminae, Gecarcinidae, Coenobitidae). The shell of hermit crabs, though reducing the dangers of desiccation and predation in any terrestrial situation (REESE, 1969), is nevertheless a handicap for a climber. *Birgus* not possessing a shell is superior to the species of *Coenobita* with respect to climbing.

Preadaptations can, of course, include behavioural components. Is is possible that not only the ability of scaling rocks (see above) is preadaptive to tree climbing, but also the habit of climbing up and down within the more vertical portions of a burrow. Burrowing is common in the Ocypodidae and Gecarcinidae and also in the more ancestral Sesarminae from which the expert climbers as *Metasesarma rubripes* and *Aratus* must have evolved.

CONSEQUENCES TO THE ANIMALS

The book by PEARSE (1950) contains a long chapter on "how the animals have changed". Until now, very little can be said on special adaptations to arboreal life in crabs. Some characters like bent dactyli with spines in *Coenobita* (referred to by BALSS, 1955: 1314) could be classified as preadaptations (see above) as well. All authors dealing with *Metopaulias*, stress that it has a very flat carapace fitting easily into the narrow spaces between the leaves of bromeliads. The specialized ontogeny of *Metopaulias* (see above, under *S. angustipes*) should be mentioned here, too.

Dodging behind the trunk of a tree and finally leaping to the ground or into the water in presence of a close observer or predator, seems to be a common behavioural trait of different (unrelated) species of climbers. This escape response is known from *Birgus* and *Coenobita* (HARMS, 1932: 176). In Trinidad, it was observed in grapsids as well as in ocypodids. The splashing noise of falling crabs seems to be a characteristic noise of any flooded mangrove swamp (see LANG in RATHBUN, 1921: 453, and VERWEY, 1930: 183, concerning *Sesarma elegans* and *S. mederi*, respectively; cf. PETERS e.a., 1933: 84, on *Eriocheir*).

The locomotion patterns are generally not clearly specialized. The common tendency to use the chelipeds as additional walking legs can be interpreted as an activation of a locomotor pattern still present thus indicating that the first pair of peraeopods is not as remote from its original locomotor function as one might believe. A parallel is found in the praying mantis (*Mantis religiosa*), which normally uses only the two posterior pairs of legs during walking. The specialized prothoracic legs join these posterior legs in their locomotor action when the insect is climbing a vertical surface (ROEDER, 1937: 363).

Most of the species listed in Table 2 are still mainly ground-living and even burrowing. Their morphology and behaviour should be expected to turn out at best a compromise between needs of climbing and other activities. The specializations of *Aratus*, however, are worth a closer examination.

SUMMARY

An annotated list of the brachyuran (12) and anomuran (1) tree-climbing crabs of Trinidad (West Indies) is presented (see Table 1 for species names). Some of the species mentioned (e.g. *Aratus pisonii, Goniopsis cruentata*) are well-known tree-climbers, in others (e.g. *Sesarma roberti, S. ricordi*) this peculiar behaviour is recorded for the first time. Some data on the diet and the locomotion of climbing Grapsidae are given. *Aratus* was found to feed mainly on algae and decayed wood, not on mangrove leaves. A synopsis of pertinent data from literature (Table 2) yielded 30 further species names of tree-climbing crabs. Like in Trinidad, most of these belong to systematic groups comprising many or only semiterrestrial species. The trees ascended are mangroves in about half of all cases. Motives, grades, phyletic routes, predispositions and consequences of the habit of tree-climbing are discussed.

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TABLE 1

SYSTEMATIC SYNOPSIS OF TRINIDADIAN SPECIES MENTIONED

(including measurements and observation localities)

group		species	maximum cb[1]) in mm	main localities (observations of climbing behaviour)[3])
BRACHYURA				
GRAPSIDAE,	Grapsinae	*Goniopsis cruentata*	(56)	*Tr 9, 13, 31*
		Pachygrapsus gracilis	(15. 9)	(*Tr 31*)
	Sesarminae	*Aratus pisonii*	(26)	*Tr 13, 24, 31*
		Metasesarma rubripes	22. 3	*Tr 23, 26, 31*
		Sesarma angustipes	24. 6	(*Tr 5, 6, 9, 17, 31*)
		Sesarma ricordi	23. 4	*Tr 32*
		Sesarma roberti	(27)	*Tr 10*
OCYPODIDAE,	Ocypodinae	*Uca rapax*	(34)	*Tr 31, 32*
		Uca vocator	36. 1	*Tr 23, 26, 31*
	incertae sedis	*Ucides cordatus*	91. 8	*Tr 31*
GECARCINIDAE		*Cardisoma guanhumi*	(113)	(*Tr 26, 31*)
XANTHIDAE		*Hexapanopeus caribbaeus*	(11. 5)	(*Tr 32*)
ANOMURA				
COENOBITIDAE		*Coenobita clypeatus*	(26. 8)[2])	(*Tr 5*)

[1]) cb = width of carapace, figures in parenthesis from literature.

[2]) Length of carapace (used for *Coenobita* only).

[3]) Identification figures refer to list of localities given below, those in parenthesis are merely collecting sites and refer to crab species known from literature to ascend trees, but not observed climbing by the author.

TABLE 2

SYNOPSIS OF BRACHYURAN AND ANOMURAN CRAB SPECIES THAT ARE KNOWN TO CLIMB TREES

species	author(s)	geographic region, vegetation ascended (climbing height above ground)
BRACHYURA		
GRAPSIDAE		
Geograpsus crinipes Dana	HOLTHUIS (1953: 29)	Marshall Islands: *Pisonia* trunk
Goniopsis cruentata (Latreille)	see text	Eastern Neotropics: mangroves (4 m)
Goniopsis pelii (Herklots)[1]	LANG in RATHBUN (1921: 443)	Congo Estuary: mangroves (1.5 m)
Goniopsis pulchra (Lockington)	RATHBUN (1918: 240), ? WEYL (1953: 126), VON HAGEN (unpubl.)	Western Neotropics: mangroves
Metopograpsus latifrons (White)	HARMS (1929: 305), MACNAE (1967: 436)	Java: mangroves North Queensland: mangroves
Metopograpsus thukuhar (Owen)	LEWINSOHN (in litt.)	Ethiopia: dead recumbent mangroves
Pachygrapsus gracilis (De Saussure)	see text	Jamaica: *Rhizophora* roots
Eriocheir sinensis H. Milne Edwards	PETERS et al. (1933: 84, 92)	Germany: bushes and tree trunks
Aratus pisonii (H. Milne Edwards)	see text	Neotropics: mangroves and other trees (6 m)
Metasesarma rousseauxi H. M. Edwards	HOLTHUIS (1953: 33)	Marshall Islands: trunk of *Messerschmidia argentea* (2 m)
Metasesarma rubripes (Rathbun)	see text	Venezuela and Trinidad: mangroves and other trees, grass (6 m)
Metopaulias depressus Rathbun	ANDREWS (1892) and others (e.g. HARTNOLL, 1964; cf. READ, 1969)	Jamaica: epiphytic bromeliads on boulders and trees
Nanosesarma minutum (De Man)	MACNAE (1968: 167)	South East Asia: *Rhizophora* roots
Sesarma angustipes Dana	see text	Brazil: bromeliads growing on boulders
Sesarma angustum Smith	ABELE (in litt.)	Cocos Island (Costa Rica): tree (2 m)

[1]) mentioned as "*Goniopsis cruentata* (Latreille)", for synonymy see HOLTHUIS (in prep.).

Table 2 (continued 1)

species	author(s)	geographic region, vegetation ascended (climbing height above ground)
Sesarma elegans Herklots	Lang in Rathbun (1921: 453)	Congo Estuary: mangrove roots
Sesarma eumolpe De Man	Verwey (1930: 245)	Java: mangroves
Sesarma guttatum A. Milne Edwards	Lewinsohn (in litt.)	Etiopia: branches of dead recumbent mangroves
Sesarma mederi H. Milne Edwards[2])	Harms (1929: 306), Verwey (1930: 180, 183)	Java: coconut tree Java: mangroves and ferns
Sesarma meinerti De Man	Verwey (1930: 180)	Java: mangroves and ferns
Sesarma ricordi H. Milne Edwards	see text	Trinidad: branches of dead recumbent mangroves (1.5 m)
Sesarma roberti H. Milne Edwards	see text	Trinidad: bamboo (2 m)
Sesarma rotundatum Hess[3])	Borradaile (1900: 594), Schnee (1904: 406), Holthuis (1953: 33, 63–65) Laird (1956: 67)	Ellice and Marshall Islands: breadfruit and other trees (4.5 m, Holth.), young individuals on *Crinum asiaticum* (Schnee)
Ocypodidae		
Ocypode ceratophthalmus (Pallas)	Altevogt (1959: 131)	Bombay: mangrove bushes
Uca brevifrons (Stimpson)	Crane (1941: 177)	Costa Rica: tree trunk (1.5 m)
Uca rapax (Smith)	see text	Trinidad: *Laguncularia* trees and grass (1m)
Uca vocator (Herbst)	see text	Trinidad: mangroves (20 cm)
Uca sp.	Thesing (1912: 103, fig.)	Indo-West Pacific: mangrove roots
Ucides cordatus (L.)	see text	Trinidad: mangroves
Gecarcinidae		
Cardisoma guanhumi Latreille	see text	Colombia: trees and reed (3 m), Florida: mangroves

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[2]) mentioned as "*Sesarma taeniolata* White", for synonymy see Tweedie (1940).

[3]) mentioned as "*S. gardineri* Borradaile" (Borr.) or "*S. oceanica* De Man" (Schnee), for synonymy see Tesch (1917).

TABLE 2 (continued 2)

species	author(s)	geographic region, vegetation ascended (climbing height above ground)
Gecarcinus weileri (Sendler)[4]	GREEFF (1882: 26)	S. Thomé and Rolas (West Africa): trees and buildings
XANTHIDAE		
Hexapanopeus caribbaeus (Stimpson)	see text	Trinidad: mangrove roots
Rhithropanopeus harrissii (Gould)	RODRIGUEZ (1963: 201),	Venezuela: *Rhizophora* mangroves
	McCOSCER & DAWSON (1975: 347)	Panama: *Rhizophora* mangroves
POTAMIDAE		
Potamonautes sp.	DIETERLEN (in litt.)	Eastern Congo: *Parinari* trunk (20 m)
PORTUNIDAE		
Callinectes sapidus Rathbun	ABBOTT (1967: 128)	Gulf Coast (USA): *Spartina* grass (40 cm)
ANOMURA		
DIOGENIDAE		
Clibanarius longitarsus (De Haan)	MACNAE (1968: 167)	South East Asia: *Rhizophora* mangroves
COENOBITIDAE		
Birgus latro (L.)	RUMPHIUS (1705: 7) and many others (e.g. HARMS, 1932, HOLTHUIS, 1959b, figs, ALTEVOGT & DAVIS, 1975)	Indo-West Pacific: trees on islands (20 m)
Coenobita cavipes Stimpson	? HARMS (1929: 252, 307–308, 327), VERWEY (1930: 180, 184)	Java: mangroves and other trees (6 m)
Coenobita clypeatus (Herbst)	see text	Florida and Trinidad: trees and mangrove roots (80 cm)

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[4]) mentioned as "*G. ruricola* (L.) (GREEFF) or "*G. lagostoma* H. Milne Edwards" (RATHBUN, 1918), for synonymy see TÜRKAY (1973).

TABLE 2 (continued 3)

species	author(s)	geographic region, vegetation ascended (climbing height above ground)
Coenobita compressus H. Milne Edwards	BALL (1972: 271)	Western Neotropics: trees and bushes
Coenobita longitarsis De Man	HOLTHUIS (in litt.)	New Guinea: trees
Coenobita perlatus H. Milne Edwards	? BORRADAILE (1901: 92)[5]	Minikoi (Maldive Islands): *Pandanus* bushes and *Hernandea peltata* (6 m)
	SEURAT (1904: 238–239)	Mangareva (Tuamotu Islands): *Hibiscus tiliaceus* and coconut trees
Coenobita scaevola (Forskal)[6]	WERNER in PESTA (1927: 72)	Port Sudan: bushes

[5] When speaking of the tree-climbing habits of *Coenobita*, BORRADAILE gives no species name. The list of *Coenobita* spp. he found (p. 68) comprises *C. perlatus* H. Milne Edwards, *C. rugosus* H. Milne Edwards and *C. brevimanus* Dana (mentioned as "*C. clypeatus* Latr.").

[6] mentioned as "*Clibanarius signatus* Heller" (for explanation see LEWINSOHN, 1969).

PLATE I

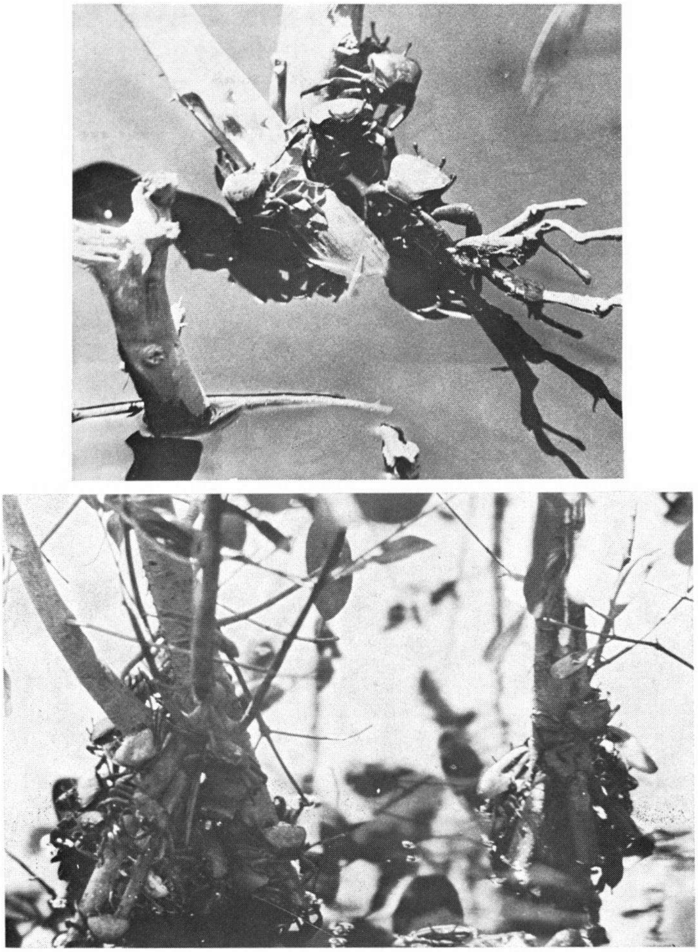
Above. – *Goniopsis cruentata* perched on a branch of a *Laguncularia* tree, about 3 m above ground (*Tr 31*).

Below. – *G. cruentata* (right) and *Aratus pisonii* (left) on a *Rhizophora* trunk at low tide. Both species prefer to rest head down.

PLATE II

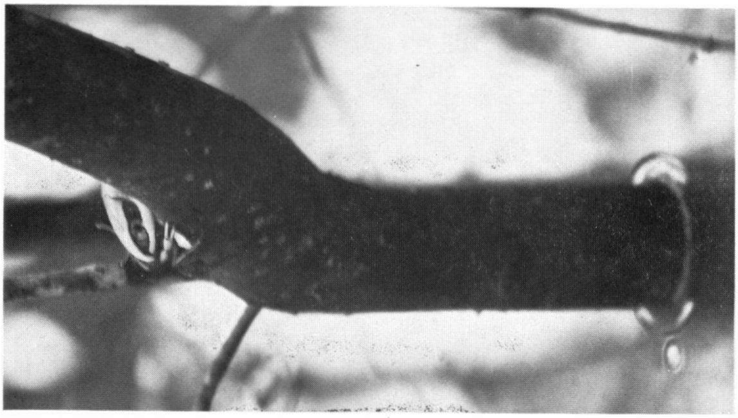
Above. – *Sesarma roberti* (arrow) climbing within a maze of loose bamboo canes (*Tr 10*).
Below. – The legs of *S. roberti* are visible within a bamboo stump partly filled with rain water (thus forming a phytotelma).

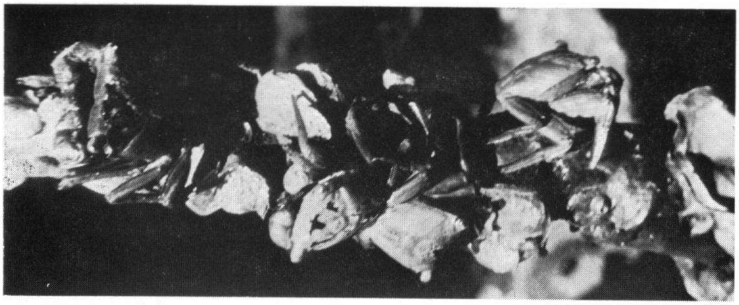
PLATE III

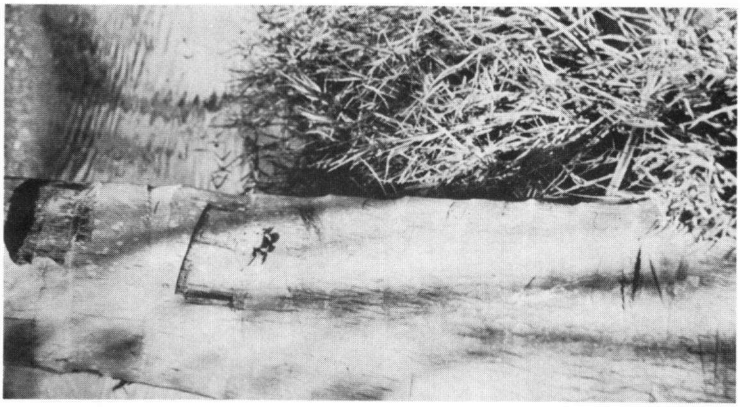


Above and below. – Ovigerous females and a few males (below right) of *Uca vocator* ascending the lower portions of *Laguncularia* trees ahead of the rising tide (*Tr 27*).

PLATE IV


right


centre


left

Left. – *Metasesarma rubripes* on the trunk of a coconut tree, 1.5 m above the flooded grass *Paspalum serpentinum* (*Tr 26*).
Centre. – Four individuals of *Aratus pisonii* feeding, at low tide, among oysters (*Crassostrea rhizophorae*) on *Rhizophora* roots (*Tr 24*).
Right. – A male of *Uca rapax* perched on a *Laguncularia* tree in an area (*Tr 31*) flooded after heavy rains. (From VON HAGEN, 1970b).