

CARDISOMA CARNIFEX (BRACHYURA):
WHERE HAVE ALL THE BABIES GONE?

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A B S T R A C T

Young *Cardisoma carnifex* were found living within burrows of conspecific adults, in diverticula starting from the main branch of the burrow. Their gill chamber structure is much less adapted for air-breathing than that of the adult. The young spend at least three years in this environment, probably feeding on leaves remaining from the adult meals. Nothing is known about when they start to dig their own burrows or how they avoid being cannibalised within the adult burrows.

The Gecarcinidae, together with the Coenobitidae, are the best land colonisers among Decapoda, who are able to settle as far as 5 km from the sea (*Cardisoma guanhumi* Latreille; see Gifford, 1962). However, they are also obliged to perform periodic seaward migrations in order to spawn, because their larvae are strictly marine pelagic (Hartnoll, 1988).

When the megalopae return to the shore (after 30–40 days in *C. guanhumi*, Costlow and Bookhout, 1968; 27 days in *Gecarcoidea natalis* (Pocock), Hicks, 1985), they promptly moult, and a catadromic migration takes place, allowing the young to reach suitable habitat. After this, the young land decapods “are seldom seen, and little is known about their habitat or ecology” (Wolcott, 1988). Moreover, the destiny of these young, once they reach their suitable habitat, has rarely been studied.

Among the Coenobitidae, with a single exception (Reese, 1968), nobody has observed specimens of *Birgus latro* (L.), the terrestrial coconut crab found in many Indo-Pacific atolls whose adults reach about 35 cm in length, smaller than about 8 cm (2–3 cm thoracic length). Fletcher and Amos (1994) reported that estimates of recruitment for this species are virtually nonexistent. Held (1963) and Fletcher (1991) have shown that the smallest stages of the coconut crab are buried most of the time and only forage infrequently and for short periods. Juvenile *G. natalis* smaller than 35 mm (at least 3 years old) are seldom seen on the surface;

larger specimens (9 cm carapace width) may be 20 years old (Wolcott, 1988).

In some cases, the young are said to occupy a different habitat from the adults, such as forest litter (Wolcott, 1988). The young of *Gecarcinus lateralis* (Freminville), *G. ruricola* (L.), and *G. lagostoma* H. Milne Edwards (see Fimpel, 1975; Bliss *et al.*, 1978; Britton *et al.*, 1982) may not dig holes but live in crevices or under cobbles and supratidal stones. Young specimens of *G. lateralis* and *C. guanhumi* have been found in large burrows, presumably belonging to conspecific adults (Feliciano, 1962; Henning, 1975; Klaassen, 1975).

If a certain size class cannot be observed in a population, the possible explanations are that 1) recruitment may occur irregularly in time, and one or more generations may be completely missing (as in *G. natalis*, P. Greenaway, personal communication); 2) the young occupy a different environment from adults; 3) the young occupy the same environment as the adults but remain concealed in refuges.

During twelve years of research on several mangrove decapods of the Kenyan coast, including *Cardisoma carnifex* (Herbst) (Micheli *et al.*, 1991), a species about the same size as *G. natalis* (see Wolcott, 1988), we have never observed an individual smaller than 5.0 cm carapace length (thus, presumably at least 3 years old).

Since 1988, Mida Creek, Kenya, has been intensively explored in all conditions of light,

Table 1. Measurements (in mm) of five young *Cardisoma carnifex* found in adult holes.

Year	Sex	Carapace width	Carapace length	Posterior margin	Frontal margin	Third pereiopod total length	Major claw length
1999	M	14.0	12.5	6.1	4.0	26.1	8.7
1999	F	15.5	13.0	6.4	5.1	28.0	9.5
1999	M	16.0	14.0	6.5	5.1	30.5	10.3
1999	F	23.6	20.2	9.7	7.2	40.3	16.2
1998	M	44.4	35.6	15.7	11.2	69.8	35.5

tide, and season, and most microhabitats have been searched for any sort of taxa. Adult *C. carnifex* are very common, and their average density in the study area has been estimated at 0.25/m² (Micheli *et al.*, 1991). It was thus apparent that the evident lack of small *C. carnifex* was a constant pattern (hence rejecting hypothesis of sporadic recruitment) and that the young did not occupy some unexplored habitat (rejecting hypothesis 2). Where could the young conceal themselves (hypothesis 3)? The only apparent refuges were burrows of the same or different species as recently had been shown in S. Africa, for *Neosarmatium meinerti* (De Man) (see Emmerson, 2001).

Hogue and Bright (1971) studied the burrows of six *C. carnifex* in Kenya (Kilifi Creek) and found some small diverticula inhabited by *Uca* and Sesarminae crabs.

In order to verify if these diverticula were a constant feature and if they might be inhabited by young conspecifics, we excavated several burrows of *C. carnifex* and of other species living in the same environment. Small *C. carnifex* that were found were studied by analysing their growth pattern as well as their gill-chamber structure in order to evaluate whether or not the "lung" was already developed, enabling them to conduct a fully aerial life.

MATERIALS AND METHODS

The study site was Mida Creek (Kenya, 80 km north of Mombasa). The greatest concentration of *C. carnifex* adults (5–9 cm carapace width, CW) was recorded within the upper *Avicennia marina* (Forsk.) Vierh. zone and the neighbouring meadows and bush. A commonly associated large species (4–5 cm CW) in the *A. marina* area is *Neosarmatium meinerti* (Grapsidae Sesarminae). Holes of smaller Ocypodidae species, such as *Uca inversa* (Hoffmann) (2 cm CW) and *U. annulipes* (H. Milne Edwards) (2 cm CW), were commonly found, depending on the substratum and canopy density. Another member of the Grapsidae, *Sesarma ortmanni* Crosnier (3 cm CW), was also very common but it has never been seen digging its own holes (Martin Skov, personal communication).

In October 1999, casts of eight *C. carnifex* and twenty-one *N. meinerti* burrows were taken by pouring pure liquid

concrete into the largest holes. The solid cast was excavated a few days later, measured, and broken into small pieces to identify any animals trapped within the concrete. Moreover, in both October 1998 and October 1999, we hand-excavated 25 burrows of the above species as well as about 20 of the two common *Uca* species (*U. inversa* and *U. annulipes*).

Collected crabs were sexed and measured by recording maximum carapace width (CW) and length (CL), front width (measured at the bases of the eyestalks) and posterior margin width (measured at the bases of the fifth pereiopods).

We also performed an SEM investigation of fragments of the median region of the gill chamber lateral walls, following a standard procedure for preserved crustaceans. The pieces were first desiccated through passages in 70, 80, 90 and 100% alcohol, then metallized with a gold layer (Felgenhauer, 1987).

RESULTS

The large *C. carnifex* burrows appeared to be occupied by adults, and in two cases their bodies remained trapped in the concrete. Eight *C. carnifex* burrows that we measured had a diameter of 9.1 cm (SE = 0.9 cm) just below the entrance. They reached the water table 49 cm below the soil (SE = 5.3 cm), being steeply inclined for a length of 117 cm (SE = 14.5 cm). In seven cases, there were one or two accessory branches, 10–35 cm long, of the same diameter as the main branch. The two captured crabs were 6.2 and 6.9 cm CW, and their entrance hole diameters were 7.3 and 8.6 cm, respectively; thus, the crab-CW/burrow-diameter ratios were 85% and 80%, respectively. The whole structure strongly resembled the one illustrated by Hogue and Bright (1971); by simple excavation (without any casting), these authors had found burrows that were about 135 cm long and 8 cm wide, with occasional short accessory branches.

We observed smaller diverticula than those found by Hogue and Bright (1971), but the density of the concrete, the orientation of the diverticula and their diameter (1–2 cm) did not allow good casting.

In one case, after we excavated the cast, we found a small *C. carnifex* in a cavity in the soil. At the same time, after exploring the diverticula by hand 20–40 cm below the surface as well as

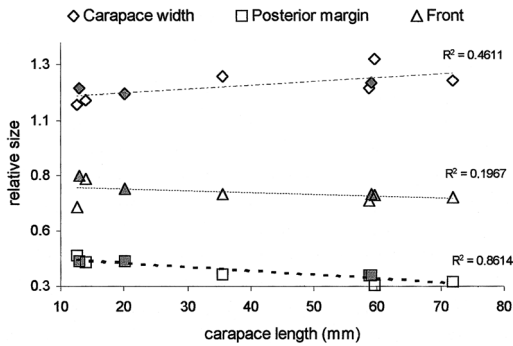


Fig. 1. *Cardisoma carnifex*. Growth pattern of carapace width, posterior margin length, and anterior margin (front) length relative to carapace length. Females, filled symbols.

digging from the top trying to follow the direction of the diverticulum, we were able to collect five more small *C. carnifex*, from five distinct burrows.

Thus, a total of six small *C. carnifex* were collected. Table 1 shows measurements of five of them, because one was lost.

By comparing these measurements with those of other specimens preserved in the Museum of Zoology "La Specola," University of Florence, collected in the same locality during 1990–1997 expeditions, we could study the allometric growth pattern of some of the parameters.

Compared to carapace length, the anterior margin (front) showed a slight, nonsignificant, negative allometry ($r = -0.444$, $d.f. = 7$, ns), the posterior margin showed a significant negative allometry ($r = -0.928$, $d.f. = 7$; $P < 0.001$), whereas the maximum carapace width, as measured across the branchial region, showed a significant positive allometry ($r = 0.679$, $d.f. = 7$, $P < 0.05$) (Fig. 1). These results were compared with the growth pattern of the same parameters in a member of a closely related family (Sternberg and Cumberlidge, 2001), *Ocypode ryderi* Kingsley (Ocypodidae). In the latter species, all the measures (Fig. 2) showed a significant negative allometry when compared to carapace length for relative carapace, relative front, and relative posterior margin widths, respectively ($r = -0.872$, $r = -0.917$, $r = -0.964$, $d.f. = 14$, $P < 0.001$ in all cases). In *C. carnifex*, both relative front and relative posterior margin width (Fig. 2B, 2C) showed a negative allometry (only the former being significant: $r = -0.868$ and $r = -0.600$; $d.f. = 7$, $P < 0.01$ and ns, respectively). Relative carapace width of *C. carnifex*, on the

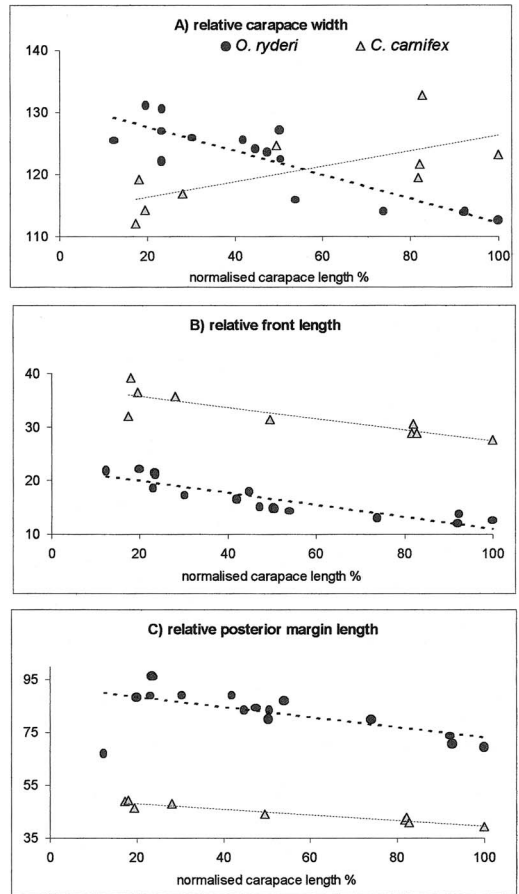


Fig. 2. Relationship between A) relative carapace width (carapace width/100/carapace length), B) relative anterior margin (front) length, C) relative posterior margin width, and the normalized carapace length in *Cardisoma carnifex* (Gecarcinidae) and *Ocypode ryderi* (Ocypodidae). Such a measure, for each species, consisted in the carapace length of each specimen-100/carapace length of the longest specimen (in both species, a fully grown adult male).

contrary, showed a distinct positive allometry (Fig. 2A), significantly different ($r = 0.679$, $d.f. = 7$, $P < 0.05$) from the *O. ryderi* one (comparing the two regression coefficients: $t = 6.02$; $d.f. = 21$, $P < 0.001$). The carapace widths of the two species have, thus, a clearly opposite growth pattern.

Samples of the "lung", i.e., of the lateral walls of the gill chambers, were taken for SEM examination from a young specimen of 14.0 mm CW, and it was compared with a sample from an adult of 71 mm CW (Fig. 3).

The vascularized tissue layer was thinner and the vascularization less pronounced in the young than in the adult. The surface of the

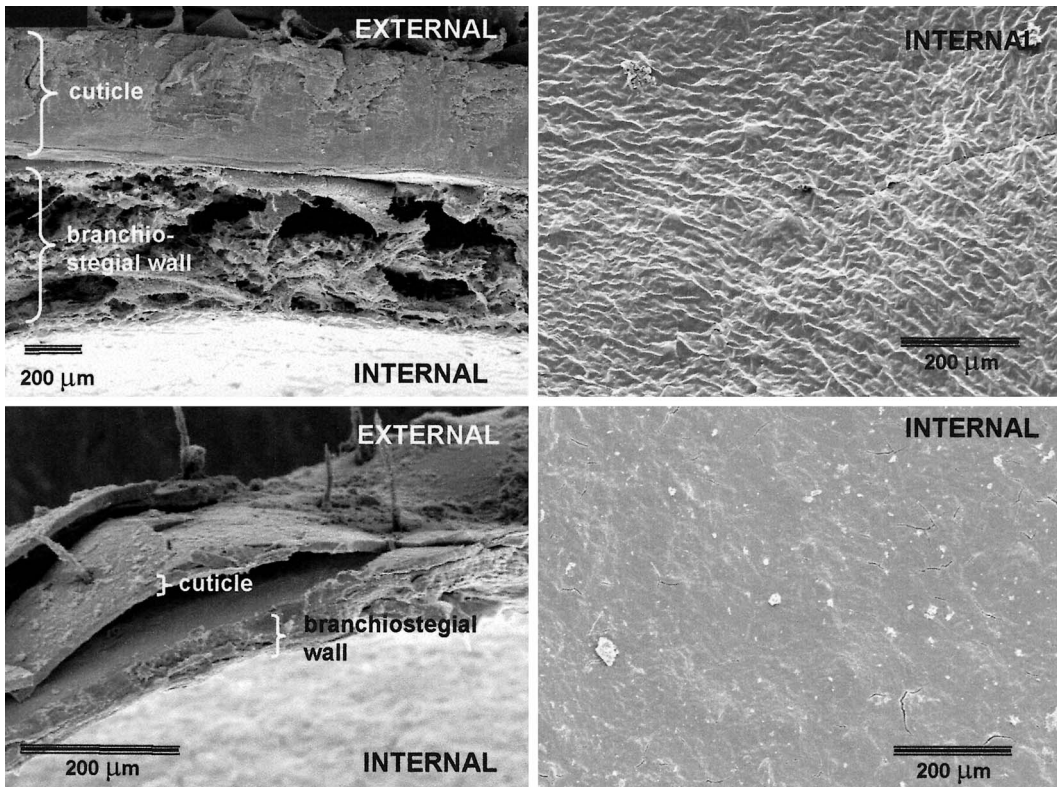


Fig. 3. *Cardisoma carnifex*. Section and internal surface of the lateral side of the gill chamber of an adult (female 71 mm carapace width, upper images) and a young (male, 15 mm carapace width, lower images).

internal wall was smooth and flat in the young crabs, whereas it was strongly corrugated in the adult, thus increasing the total surface area for gaseous exchange.

DISCUSSION

We confirmed that small *C. carnifex* live in burrows of conspecific adults for at least three years. However, several questions arose. Why do the young remain for so long in the adult burrows? Where exactly do they stay within the hole? What do they feed on? How do they avoid being cannibalised?

Cardisoma carnifex probably carries into its burrow an amount of leaves in excess of its requirements (Micheli *et al.*, 1991). Thus, for the young crabs, feeding may not be a problem as has been suggested for the young of *Neosarmatium meinerti* (Emmerson, 2001), which inhabit adult burrows and probably depend on leaf accumulation by the adult. Instead, defending themselves from adult conspecifics could be a problem.

In the laboratory, *G. lateralis* and *C.*

guanhumii capture and eat conspecifics (Wolcott and Wolcott, 1984; Wolcott, 1988), as does *B. latro* (see Helfman, 1979). There are many reports of cannibalism in the wild (*B. latro*, Helfman, 1979; *G. lateralis*, Bliss *et al.*, 1978; *G. planatus*, Erhardt and Niassaut, 1970; *G. natalis*, Hicks *et al.*, 1984), although active predation has only been observed by Gibson-Hill (1947) in *G. natalis*, whose adults feed on the young during the latter's inland migration.

Comparison of the general carapace pattern of *C. carnifex* with that of *O. ryderi* (family Ocypodidae, strictly related to Gecarcinidae), an intertidal species whose young share the same habitat and habits of the adults, shows that the growth pattern of *C. carnifex* is characterised by rapid "inflation" of the branchial region, the branchial chamber becoming a sort of expanded "lung" (Bliss, 1968; Powers and Bliss, 1983). The process involves not only the relative volume of the branchial chamber but also the corrugation of its internal surface, the thickness of the vascularized tissue, and the level of vascularization (Farrelly and Greenaway, 1993). This trans-

formation accompanies the change in life-style from young to adult: the former is probably unable to abandon the wet adult burrow, where water is always available at the bottom (from our findings, this seems a constant pattern for *Cardisoma carnifex* burrows), before its aerial respiratory system is sufficiently developed.

The biology and anatomy of young land crabs needs to be studied in detail, because they form crucial and underestimated elements of the complex system of their terrestrial adaptation.

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