Hypercarcinisation: an evolutionary novelty in the commensal porcellanid *Allopetrolisthes spinifrons* (Crustacea: Decapoda: Porcellanidae)

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Abstract

Porcellanids are, after brachyuran crabs, the most successful decapod group to achieve a crab-like body form through carcinisation. Unlike brachyurans, porcellanids retained the ability to swim by flapping their abdomen, armed with a well developed tail fan. Here, we present an exceptional case of carcinisation, with the temperate South-American porcellanid *Allopetrolisthes spinifrons,* an obligatory commensal of the sea-anemone species *Phymactis papillosa* and *Phymanthea pluvia.* As a consequence of this association, *A. spinifrons* evolved morphological adaptations most noticeable in the shape of the abdomen in a process we here call hypercarcinisation. The abdomen in *A. spinifrons* males resembles the one typically shown by brachyuran males, as it is significantly narrower, and its uropods, normally well developed in porcellanid males and females, are degenerated to vestiges. These adaptations led to the loss of the swimming ability. In females of *A. spinifrons* the abdomen, telson and uropods form a hood that completely covers the egg mass. A further distinctive morphological adaptation observed in both males and females regards the spination of the walking legs. Spines, typically present on different segments of the walking legs in porcellanids, are completely absent or notoriously reduced. Hypercarcinisation in *A. spinifrons* is further discussed within an evolutionary context regarding morphological and ecological adaptations in other commensal and free-living porcellanids.

Key words: Porcellanidae, Actinia, carcinisation, commensalism, temperate South America.

Introduction

Porcellanidae Haworth comprises a diverse family of marine, crab-like, filter-feeder decapods, which constitutes the most abundant crustacean group in many coralline and rocky habitats. Many of the 276 species are distributed throughout the tropical regions of all oceans, and some occur in temperate and sub-temperate waters (Haig, 1960; Viviani, 1969; Werding *et al.,* 2003; Werding and Hiller, 2007). Porcellanidae is a well-defined taxon classified in the anomuran Superfamily Galatheoidea together with the Galatheidae and Chirostylidae (*see* McLaughlin *et al.,* 2007). Compared to these and all other families contained in the Infraorder Anomura, porcellanids represent the group with the major tendency towards carcinisation, the process of becoming a crab (McLaughlin and Lemaitre, 1997). Their evident crab-like body form makes this family an ideal group for evolutionary studies on carcinisation processes in anomurans and brachyurans (true crabs).

Carcinisation is treated here as the reduction and folding of the abdomen beneath the sternum (ventral surface of the crab's body), accompanied by the shortening of the body length-axis in reptant

decapods (*see* McLaughlin and Lemaitre, 1997). In brachyuran crabs, the most extreme case of carcinisation, the ability to swim with the aid of the abdomen was lost. Also, in most brachyuran groups there is an evident sexual dimorphism regarding the abdomen, narrow in males and broad in females, modified into a brood pouch that covers the egg mass. The telson (terminal nonmetameric segment in arthropods) is usually small relative to the rest of the abdomen, and the uropods (flattened, lateral appendages of the last abdominal segment) are reduced or lacking in both sexes (Figure 1; for further details on carcinisation in brachyurans see Guinot and Bouchard, 1998 and Ng *et al.,* 2008). In contrast, porcellanid crabs show a ventrally folded abdomen that ends in a fully-developed terminal flap consisting of an extended telson and flattened biramous uropods. There is no obvious sexual dimorphism regarding this character, and therefore, females as well as males are able to swim by rapidly flapping the abdomen (Figure 2). Most species [*e.g.* genus *Petrolisthes* Stimpson, 1858], the largest genus in the family with over 100 species use this capability for seeking refuge if detached from their substrate. The abdomen also supports agile mobility on smooth surfaces (*e.g.* intertidal boulders), as rapid and short flapping creates a temporary vacuum between the crab's sternum and the substrate (unpubl. data). Other species [*e.g.* genus *Pachycheles* (Stimpson, 1858)] that inhabit closed spaces formed in fouling systems or within sponges, sabellarid-worm formations and other types of biogenic systems also show a well developed abdomen, though swimming ability is scarcely used, as detachment from and movement within these habitats is more difficult. Another important function of the abdomen in most porcellanids is to aid the crab in righting itself if flipped over. In this position, the crab is completely vulnerable, and the relatively heavy chelipeds, which in many species outweigh the body (unpubl. data), make it difficult moving back to its natural posture. As in most

Figure 1. Ventral view of a male (a) and a female (b) of the brachyuran crab *Plagusia inmaculata* Lamarck. Scale = 10 mm.

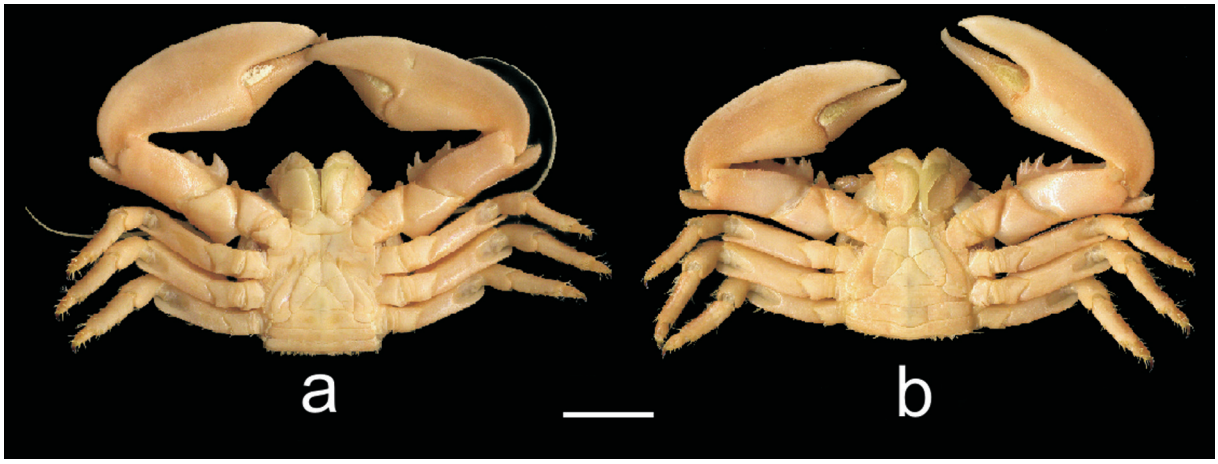

Figure 2. Ventral view of a male (a) and a female (b) of the porcellanid crab *Petrolisthes tuberculosus* (H. Milne-Edwards). Scale = 10 mm.

decapod groups, porcellanid females cement their eggs to the pleopods (abdominal limbs), and aerate them by flapping the abdomen and tail fan.

In her monograph on the Porcellanidae of the eastern Pacific, Haig (1960) created the genus *Allopetrolisthes* Haig, 1960 to receive three southern temperate species formerly contained in *Petrolisthes: Allopetrolisthes angulosus* (Guérin), *A. punctatus* (Guérin) and *A. spinifrons* (H. Milne Edwards, 1837). While the first two species are free living, *A. spinifrons* (Figure 3) is an obligatory commensal of the sea anemones *Phymactis papillosa* (Lesson) and *Phymanthea pluvia* (Drayton). Haig (1955) reported four young specimens of *A. spinifrons* on sea stars in Montemar, Chile, emphasizing that this finding represented the first known instance of commensalism for the species, and assuming that probably only young specimens lived in this association. Haig (1960) described the species as "taken under stones in the littoral" but referred to one specimen from Peru as "associated with anemone".

The first to recognize a close relationship of *A. spinifrons* with the anemone *Phymactis papillosa* (= *Phymactis clematis*) was Viviani (1969) who described this association in some detail. With few exceptions the crab was found on *Phymactis* climbing on the trunk. Usually, only one individual occupies an anemone. Other associations were found only casually with a sea star and with limpets. Baeza and Stotz (2001) showed that only small juveniles inhabit hosts other than anemones, and Baeza *et al.* (2001) confirmed that a single adult crab, either male or female, usually inhabits one anemone. Thiel *et al.* (2003) studied the occupation of the two host species by the crab, concluding that host density determines the crab's behavior regarding its fidelity to an anemone individual. At low host densities the crab prefers not to move from its anemone, basically due to predation pressure. Häussermann (2004) confirmed that the crab is usually attached to the column of the anemone, and moves rapidly among its tentacles and oral disc without disturbing it.

Figure 3. Dorsal view of *Allopetrolisthes spinifrons* (H. Milne Edwards). Scale = 15 mm.

In the present study, we report and interpret morphological, ecological and ethological observations of the temperate East Pacific porcellanid *Allopetrolisthes spinifrons.* We introduce the concept of hypercarcinisation, and compare this evolutionary novelty to typical carcinisation in other commensal and free-living species within Porcellanidae.

Material and Methods

Morphological examination of 20 males and 20 females of *Allopetrolisthes spinifrons* and other porcellanid species, including the two other congeneric ones, *A. angulosus* and *A. punctatus,* was carried out using material collected in the region of Coquimbo, Chile. Ecological and ethological observations of *A. spinifrons* were made in this region during 10 field trips carried out between January and June of 2007. In order to confirm our field observations a total of 10 males and 10 females of this species, and 8 individuals of the anemone *Phymactis papillosa* were collected using snorkel gear, and kept alive in two 300 l aquaria for a period of one month. Aquaria were filled with natural sea water, and every 3 days about half of the water volume was replaced by fresh sea water. Anemones were fed with pieces of shrimp, and the crabs with commercial food for sea water fish. Besides standard aeration, we used two powerheads (AquaClear 70, Hagen) per aquarium to generate turbulence and thus a proper filtering atmosphere for the crabs. Observations were recorded several times a day. Crabs used for morphological purposes were preserved in 70% ethanol and will be deposited in different museums.

Results

Allopetrolisthes spinifrons lives on the stem of its host anemone, and if disturbed it moves to the opposite side of a potential threat. If further disturbed, the crab retreats to the oral disc hiding among tentacles or even inside the coelenteron of

the host. The anemones frequently occur on steep walls of rocky-channel systems, where wave oscillation is strong. Since *Phymactis papillosa* usually lives in neighboring aggregations (average distance 10 ± 3 cm, Thiel *et al.,* 2003), the crabs casually move among hosts scrambling over the rocky surface.

We observed a striking sexual dimorphism regarding the abdomen of *Allopetrolisthes spinifrons.* The male abdomen (Figure 4A) is rather similar to that in Brachyura, as it is conspicuously reduced to a small triangle that covers the sternum only partially. The telson comprises the central plate, a pair of elongated, lateral plates, and a pair of sub-triangular terminal plates (Figure 5A). The uropods are reduced to small vestiges consisting of the basipodite and two small fragments of the branches (Figure 5B). The reduction of the abdomen can be observed in males of all sizes. While the largest specimens may reach a carapace length of over 20 mm, the smallest male in our samples has a carapace length of 3 mm and exhibits, besides a pair of fully developed pleopods (male sexual organs), the same reduction of the abdomen as large males. The female abdomen (Figures 4B and 6A) is broad, and forms a hood that covers the entire egg mass. The whole structure has the shape of a semicircular plate, with quite enlarged telson plates, and amplified by the uropods. The uropod's endopod is significantly larger than the exopod, and together, both branches exhibit an outer fringe of dense setae that borders the entire flap (Figure 6B).

A further distinctive feature in *A. spinifrons* is the complete lack of spines on the flexor margin of the propodus of the walking legs, and reduction of those on the inner side of the dactylus to tiny, blunt relicts (Figure 7A). This contrasts with the typical porcellanid walking leg, including that of the other two *Allopetrolisthes* species, which live on hard substrates, and which generally bear three or more accessory movable spinules on the dactylus, and a set of similar spines forming a terminal triplet and some additional spines on the flexor margin of the propodus (Figure 7B).

Discussion

In the present study we introduce the term hypercarcinisation as an evolutionary novelty, mainly consisting of morphological adaptations of the pleon (abdomen), driven by the commensal association with sea anemones. Most porcellanid species are free-living, shallow-water and hard-substrate inhabitants. The special adaptations observed in all species of this family, *i.e.,* carcinisation with retained swimming ability, and filter-feeding capacity, reflect the main selective pressures associated to living in densely crowded habitats occupied by many other non-sessile and sessile organisms. In terms of competition for resources the specialized filter-feeding habit of porcellanids allows the assumption that the main resource limitation is not food but available substrate, which

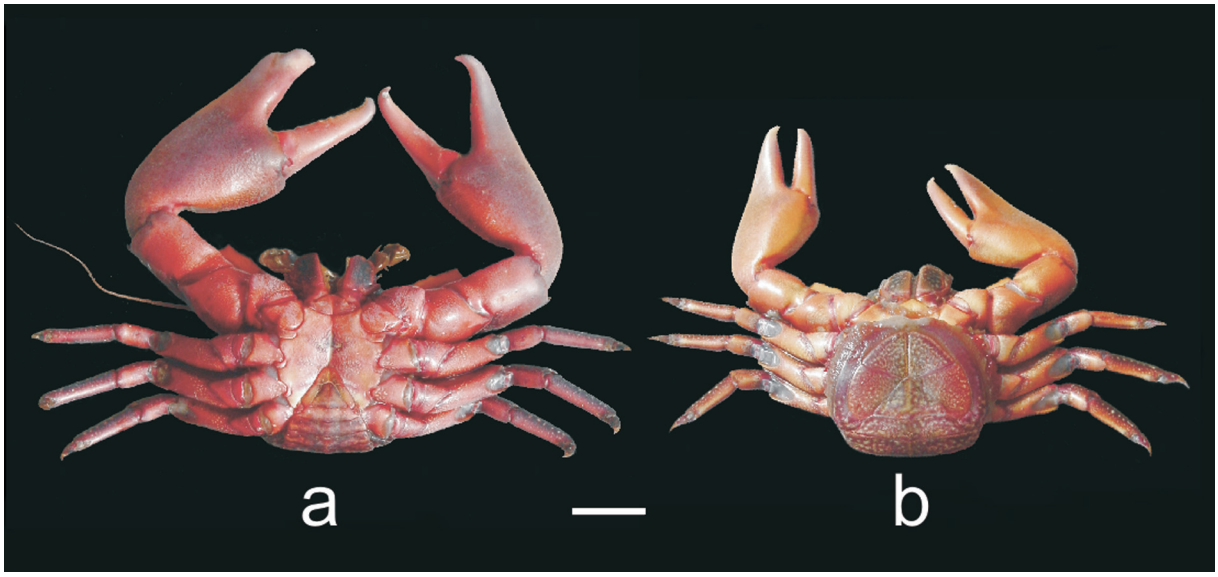

Figure 4. *Allopetrolisthes spinifrons.* Ventral view of (a) male and (b) ovigerous female. Scale = 10 mm.

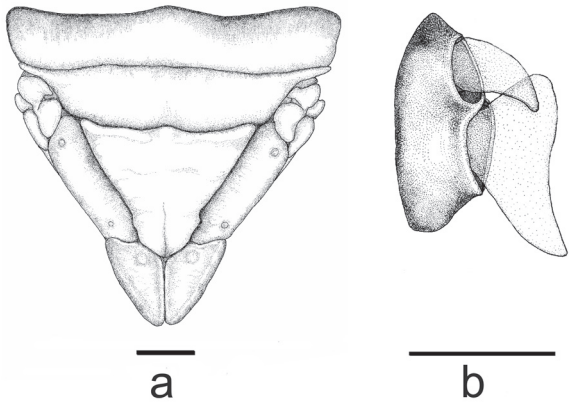

Figure 5. *Allopetrolisthes spinifrons,* male. (a) Dorsal view of last abdominal segment showing the telson and vestigial uropods. (b) Ventral view of left vestigial uropods. Scale = 1 mm.

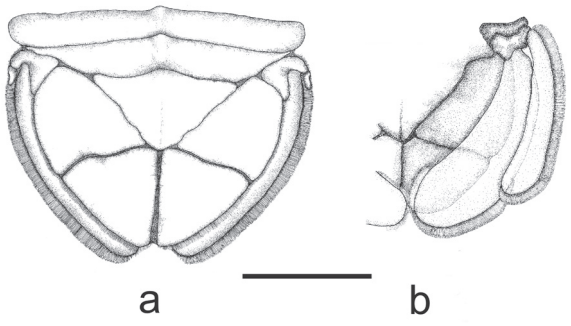

Figure 6. *Allopetrolisthes spinifrons,* female. (a) Dorsal view of last abdominal segments showing uropods and telson. (b) Ventral view of left uropods slightly folded up. Scale = 5 mm.

must meet the conditions of being hard, optimally exposed regarding water movement, and offering the crabs protection from predators (Hiller *et al.,* 2006). Considering this, we interpret the development of a commensal association in porcellanids as an alternative to finding an adequate habitat for filtering and mating.

We interpret the evolutionary advantages of carcinisation as (1) energy economization resulting from reducing the abdominal muscle mass, and (2) acquiring a body plan that allows rapid and easy movement. The fact that carcinisation evolved independently in several decapod groups (McLaughlin and Lemaitre, 1997; Morrison *et al.,* 2002), suggests that there is a high selective pressure against a long-stretched body, as it invests large amounts of energy in building abdominal muscle-mass, but displays a relatively inefficient locomotion, restricted to brusque contractions of the abdomen, and clumsy movements of the thin walking legs. The evolutionary success of acquiring a short pleon, short body axis and agile walking legs is reflected in the marked difference in species diversity between the Infraorders Macrura (decapods with a developed pleon), with some 900 species, and Brachyura (true crabs), with over 5,000 species. The Anomura Infraorder occupies an intermediate position with about 2,450 species (*see* Gruner, 1993; Martin and Davis, 2001; Ng *et al.,* 2008; De Grave *et al.,* 2009). The evolutionary path that led to Brachyura or Anomura remains uncertain, as there is no consensus on the sister taxon relationship between these infraorders, nor on the systematic relationship between them and other decapod taxa (*see* Porter *et al.,* 2005; Tsang *et al.,* 2008). Even though the evolutionary relationships within Anomura remain uncertain, there is general agreement that the sister family of Porcellanidae is Galatheidae (squat lobsters) based on evidence from adult somatic and spermatozoal morphology (Haig, 1960; Martin and Abele,

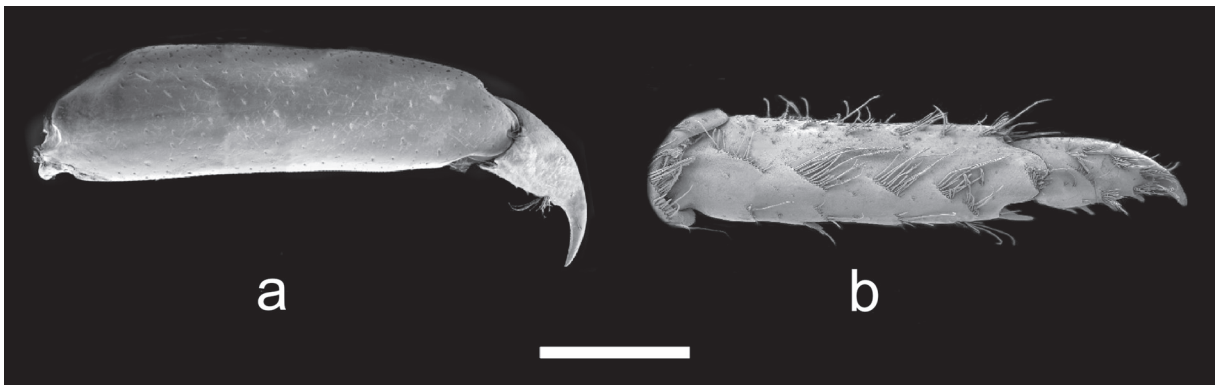

Figure 7. SEM images of propodus and dactylus of walking leg in (a) *Allopetrolisthes spiniforns,* showing absence and reduction of spines in each of these segments, respectively, and (b) *Petrolisthes tuberculosus,* representing a typical porcellanid walking leg with setae and conspicuous spines on flexor margin of propodus and dactylus. Scale = 2 mm.

1986; McLaughlin and Lemaitre, 1997; Tudge, 1997; Schram, 2001) and genetic data (Morrison *et al.,* 2002). The porcellanid habitus can be deduced from the squat lobster bauplan, which is relatively elongated and with a robust abdomen bent towards the crab's ventral side. Galatheids use the abdomen in a similar way lobsters do, *i.e.,* swimming backwards with brusque, strong and rapid movements of the abdomen, mainly in situations when their safety is in jeopardy. Moreover, they have forwardly directed chelipeds (first pair of legs bearing chelae or pincers), what makes backward-swimming more efficient. Galatheids use many different food resources using their pincer-shaped fingers of the chelipeds to select, tear and transport food to the maxillipeds (legs modified into mouth appendages; Garm and Høeg, 2000; Hudson and Wigham, 2003).

In contrast, porcellanids achieved a crab-like form, a narrower and thinner abdomen that allows swimming and also aids the crab attaching to the substrate while moving with their walking legs by creating a temporal vacuum between the crab's sternum and the substrate. The chelipeds are directed sideward, more like in a true crab, and besides being used for defense against predators, and aggressively protecting their filtering territory, they give the crab stability in the backward and sideward movement performed by the walking legs. This highly efficient form of motility may be interpreted as a balanced energy investment in swimming and walking in systems of hard-substrate crevices and boulders typical of rocky shores and reef ecosystems.

Besides swimming, the abdomen in female porcellanids is also used for egg grooming, like in most decapod crustaceans. Eggs are attached to the pleopods (abdominal limbs), and are protected with the aid of the relatively large telson and developed uropods, which form a tail fan that covers most of the female's sternum. Females ventilate the eggs by flapping their abdomen in a swim-like motion, while remaining attached to the substrate with the aid of motile spines on the flexor margin of propodus and dactylus of the walking legs (penultimate and last segments, respectively). This constitutes a further efficient morphological adaptation to movement on hard-substrate surfaces. Most porcellanid species show a terminal triplet of motile, conical spines on the ventral surface of the propodus, and 3 to 5 movable, claw-like spines on the ventral surface of the dactylus, providing the crab with a most efficient attachment device. Werding and Hiller (2004) presented some cases of modifications of the walking-leg dactylus in mangrove dwelling species of *Petrolisthes.* Such modifications can be interpreted as adaptations for locomotion on surfaces different from hard bottoms. Therefore, the almost complete lack of spines and setae on the inner side of the walking legs in *Allopetrolisthes spinifrons* can be interpreted as an adaptation to climbing and laterally moving on the host.

As a consequence of its association with Actinians, *Allopetrolisthes spinifrons* gave up the swimming ability, and optimized the shape of the abdomen for its particular mode of life, in a process that we call hypercarcinisation. This species usually moves around the stem of *Phymactis* searching for protection at the opposite side of where the threat comes from. If heavily disturbed, the crab hides in the tentacle area and even inside the gastrocoel of the anemone. The crab monopolizes its anemone but may change among different anemones occurring at close range. This behavior is not only conditioned by the large size of the crab in relation to the host (which restricts an optimal filtering surface only for one individual crab) but also by the easy accessibility of various host individuals. The protection the anemone provides the crab with is so effective, that swimming does not seem to be necessary. Moreover, the anemones frequently live on vertical walls in rocky channels where swimming would be of high risk due to heavy wave-oscillation. Considering that one individual crab, independent of being male or female, tends to monopolize one host individual, the only reason to temporally leave the anemone is to search for a mating partner, or eventually move to another host individual to find a better filtering position. In these cases the crab has to move scrambling on the rocky surface until reaching the next uninhabited host, or one inhabited by an individual of the opposite sex. Since *Phymactis papillosa* normally lives in aggregations of dozens of specimens occurring at close range (Thiel *et al.,* 2003), it appears easier and safer to move from one host to another scrambling on the rocky surface.

The special modifications of the female's abdomen may be interpreted as protection of the developing eggs against nematocysts. The large telson and the uropods, laterally as well as ventrally extended towards the sternum, forming a hood-like structure that efficiently protects the egg

mass by enclosing it completely. The dense fringe of setae on the uropod branches and the external ring provide mechanical protection allowing water exchange without exposing the eggs to nematocysts or other external stress. The female abdomen, similar to brachyurans, is optimized for egg protection. In males it is extremely reduced and has lost its function as a swimming organ. Surprisingly, *A. spinifrons* seems to be the only porcellanid species exhibiting this type of adaptation, which may be interpreted as an enhancement of the normal porcellanid carcinisation, leading to a similar abdominal shape as in brachyurans.

Some other porcellanid genera, (*e.g. Megalobrachium* Stimpson, 1858 and *Enosteoides* Johnson, 1970) have an escape strategy that does not involve swimming, but camouflaging themselves with the substrate, and if detached from it, passively and rapidly sinking to a deeper surface, resembling a falling stone. Two *Megalobrachium* species show reduction of male uropods, *M. soriatum* (Say, 1818) from the Western Atlantic (Lira *et al.,* 2001), and its transisthmian sister species *M. tuberculipes* (Lockington, 1878). However, the male abdomen isn't significantly reduced in size, and that of the female shows no enlarged telson.

Species of a further genus, the Indo-West Pacific *Neopetrolisthes* Miyake, 1937, also live in close association with Actinians. Nevertheless, the relationship between host and symbiont is of a different nature. The host anemones belong mainly to the Family Stichodactylidae, and live frequently isolated in coral systems. They are generally very large in comparison with the crab symbiont, which usually lives among the tentacles or on a spot protected by the large, overhanging tentacles. In case of a potential threat the crab retreats among the tentacles but never flees. The crabs have to live in pairs since the distance between available anemones is usually relatively large, making it too risky to abandon it in search of a mating partner. In contrast to *Allopetrolisthes spinifrons,* the species of *Neopetrolisthes* have no similar adaptations in the abdomen, and males and females have a normal porcellanid pleon. The walking legs, however, exhibit a conspicuous reduction in the spines on propodus and dactylus.

The case of *Allopetrolisthes spinifrons* provides a new insight into porcellanid carcinisation, as it shows that a further reduction of the abdomen is possible in porcellanids, if positively selected. We interpret the porcellanid bauplan as an alternative, independent way to achieve a crab-like form, different from that in Brachyura, but very successful in littoral, hard-substrate environments. The retention of the abdomen for swimming purposes should not be viewed as a less advanced stage of carcinisation regarding brachyurans, but as a highly efficient strategy for locomotion without investing too much energy in its construction. The abdomen enables not only efficient swimming in hazardous situations but also supports rapid movement upon hard substrates in situations where gravity cannot secure an adequate contact with the surface.

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