

## A REVIEW OF THE CARRYING BEHAVIOUR IN BRACHYURAN CRABS, WITH ADDITIONAL INFORMATION ON THE SYMBIOSES WITH SEA ANEMONES

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**ABSTRACT.** - A review of the carrying behaviour in brachyuran crabs and their association with sea anemones is presented. A new type of symbiosis between a sea anemone and a deep-water homolid crab from French Polynesia is described.

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### INTRODUCTION

The Brachyura form a very diverse group of crustaceans showing a wide variety of life styles. The habit of certain brachyuran crabs to seek safety by masking their body and appendages with sponges and other invertebrates or with seaweeds has evolved independently in different groups. Majids place on their hooked hairs fragments of seaweeds, sponges, ascidians, etc., while some spider crabs live in association with a sea anemone or under the protection of one or more sea anemones. Dromiid, homolid and dorippid crabs hold with their last pair of walking legs a sessile animal or a flattened shell which they use for concealment or protection. Boxer crabs, such as *Lybia*, always carry tiny sea anemones in their claws; other crabs, such as *Hepatus*, may carry the anemones on their bodies. The common habit of some dorippids of carrying a sea anemone attached to a shell is similar to the behaviour of pagurids which carry sea anemones on the shells where they hide their soft abdomen.

The existence of biotic interactions between cnidarians and crustaceans has been known for a long time (see reviews by Balss, 1924, 1956; Dales, 1957; Caullery, 1950; Patton, 1967; Ross, 1967, 1974 a, 1974 b, 1983; Castro, 1988). The cohabitation of sea anemones and hermit crabs has been the basis of numerous investigations, experiments and hypothesis on its adaptative significance. However, no comprehensive review of the symbiosis between sea anemones and brachyuran crabs exists.

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The term **symbiosis** is used in this paper in accordance with de Bary's (1879) original definition ("a phenomena of dissimilar organisms living together") and also as a "close heterospecific associations irrespective of harm or benefit to the partners" (Castro, 1988).

The starting point of our work was the discovery of the co-existence between the deep-water homolid crab *Hypsophrys inflata* Guinot & Richer de Forges and a sea anemone which is carried by the last pair of pereopods (Guinot & Richer de Forges, 1995; Chintiroglou et al., 1995). The first part of the paper examines this particular symbiosis in detail (Pl. 1A), and the carrying behaviour of two additional homolid crabs, *Homola orientalis* Henderson and *H. vigil* A. Milne Edwards, is also commented on. The second part of the paper is mainly a review, and deals with the different groups of crabs found living in symbioses with various organisms, especially sea anemones.

## MATERIALS AND METHODS

It has only been during the last three decades that our knowledge of the behaviour of bathyal symbiotic crustaceans has begun to grow with the utilisation of scuba diving, in situ photography, videophotography and other modern techniques. Similarly, the collection by baited traps preserves the crabs with their partners, permitting the study of the symbiotic relationships. It is then possible to confirm the scant information on the symbiotic crabs and to analyse the functional anatomy of their peculiar adaptations. The dredges or trawls previously used were nonselective procedures which tended to injure the organisms and did not allow the collection of crustaceans with their living partners (attached, fixed or carried) and/or any non-living camouflaging material.

During the biological investigations of the "Service Mixte de Contrôle Biologique" (SMCB) in French Polynesia (1986-1990), 3000 baited traps (Noirmoutier type), possessing a relatively small opening (size 8 cm), were set at depths of 100 to 1120 meters. This type of trap allows the collection of individuals without injuring them (see Poupin et al., 1990, figs 1, 2, pls 1-3) and, more importantly, crabs which still carry their symbiotic partner. The contents of the traps were photographed alive on the deck of the R. V. *Marara*.

Two species of homolid crabs, *Hypsophrys inflata* Guinot & Richer de Forges, 1981, and *Homola orientalis* Henderson, 1888, sensu lato, were nearly always found living either with a sponge or a sea anemone. The partner was grasped by the crab's chelate or subchelate fifth pair of pereopods, a modification that allows the crab to carry an object over its back. Nearly all samples now deposited at the Muséum national d'Histoire naturelle (Paris) contain crabs associated either with a sponge or a sea anemone. J. Poupin (pers. comm.) observed numerous many individuals of both these species on the *Marara*, which too demonstrated carrying behaviour.

Other homolids collected from French Polynesia, again using baited traps, were not found carrying a partner. These species and the sampling sites in which they were found were: *Moloha* aff. *majora* (Kubo, 1936): Fatu Hiva, Marquesas Islands, 250 m; *Yaldwynopsis* aff. *spinimanus* (Griffin, 1965): Fangataufa Atoll, Tuamotu Archipelago, 270 m; *Hypsophrys personata* Guinot & Richer de Forges, 1981, which is known also from New Hebrides and Samoa: Mururoa and Fangataufa Atolls, Tuamotu Archipelago, 450 m; Marotiri, 500-600 m, and Rimatara Island, 500-700 m, Tubuai Islands. *Homola ikedai* Sakai, 1979, described from Japan, was dredged in the Tuamotu Archipelago (Mururoa, Makemo) and in the

Marquesas Islands (350-600 m) without a partner. Another species, *Homola vigil* A. Milne Edwards, 1880, was found in Guadeloupe, West Indies, associated with sponges. All these homolid crabs are included in a revision of the family (see Guinot & Richer de Forges, 1995).

Abbreviations: MNHN: Muséum national d'Histoire naturelle, Paris; ORSTOM: Institut Français de Recherche Scientifique pour le Développement en Coopération; RMNH: Nationaal Natuurhistorisch Museum, Leiden; SMCB: Service Mixte de Contrôle Biologique; ZRC: Zoological Reference Collection, National University of Singapore; P1, P4, P5: first, fourth and fifth pair of pereopods.

# I. *Hypsophrys* in symbioses with sea anemones

## *Hypsophrys inflata* Guinot & Richer de Forges

(Figs. 1 C, 2 E, Pl. 1A)

*Hypsophrys inflata* Guinot & Richer de Forges, 1981: 547, figs. 3C, 4C, pl. 4, fig. 2; 1995: 454, figs. 1B, 55A-B, 57a-b, 58C, 61c, j; Chintiroglou et al., 1995, figs 1-3.

The deep-water crab *Hypsophrys inflata* has been found for the first time in association with a sea anemone, which belonged to a new species of *Isanthus* Carlgren, 1938 (Anthozoa, Actiniaria, Isanthidae) (Doumenc & Chintiroglou, in preparation). The anemone was held by the crab in a way suggesting that the anemone was deliberately detached by the crab. In all cases, the anemone was grabbed a little over the limbus of the basal disc, while the orientation of the oral disc varied.

Examined material of *Hypsophrys inflata* associated with a sea anemone: French Polynesia, Tuamotu Archipelago, J. Poupin (SMCB) coll. - Mururoa Atoll, st. 223, 21°50,9' S - 138°58,2' W, 500 m, 15 May.1990: 1 male, 1 ovigerous female (MNHN-B 24343), two sea anemones found in the container. Colour photographs taken by J. Poupin revealed the crabs holding the sea anemone over their bodies. - Reao Atoll, st. 70, 18°30'S - 136°27'W, 300-400 m, 07 Jun.1988: 1 ovigerous female 26,9 x 22,2 mm (MNHN-B 24311). - Makemo Atoll, st. 309, 16°34,2'S - 143°38,7'W, 580 m, 07 Oct.1990: 1 male (MNHN-B 24446) holding a sea anemone with the dactyli of P5.

Three other specimens from Mururoa Atoll [21°53,2'S - 138°53,2'W, 700-900 m, 25 Jun.1988: 1 female 35 x 30 mm (MNHN-B 24310); st. 159, 21°48,1'S - 138°55,6'W, 540 m, 21 Jun.1989: 2 female 28,7 x 24 mm, 30 x 24,8 mm (MNHN-B 24312)] and Hao Atoll, 1020 m, also collected with a baited trap, were not preserved but were photographed alive by J. Poupin (Pl. 1A). We observed that the last specimen was holding the basis of the sea anemone's column with its dactyli.

The crabs occur on hard substrata (J. Poupin, pers. comm.).

*Hypsophrys inflata* was initially collected with fishing nets from the bathyal zone (400 m) from the Loyalty Islands (near New Caledonia) and Samoa (Guinot & Richer de Forges, 1981). It is now also known from the Tuamotu Archipelago, from depths of 400 to 1020 m. Both *H. inflata* and *H. personata* are found in Samoa and in Tuamotus, but the two species were never collected from the same stations.

The genus *Hypsophrys* Wood-Mason, in Wood-Mason & Alcock, 1891, includes eight species which have been collected from depths of 400 to 2000 m. Seven of these were found in the Indo-west Pacific: *Hypsophrys superciliosa* Wood-Mason, 1891; *H. longipes* Alcock

& Anderson, 1899; *H. murotoensis* Sakai, 1979; *H. williamsi* Takeda, 1980; *H. personata* Guinot & Richer de Forges, 1981; *H. inflata* Guinot & Richer de Forges, 1981; and *H. futuna* Guinot & Richer de Forges, 1995. The eighth, *H. noar* Williams, 1974, is known from the Florida coast and the French Antilles. No known records of carrying behaviour in this genus were found. To our knowledge, the case of *H. inflata* is the first of an association between a homolid crab and a sea anemone (see Chintiroglou et al., 1995).

## II. Other symbiotic homolids collected

Two additional homolid species of the genus *Homola* Leach, 1815 (both collected with baited traps) are reported for the first time associated with sponges. *H. orientalis* Henderson, 1888, sensu lato (perhaps several species confused under this name; see Guinot & Richer de Forges, 1981, 1995), is an Indo-west-Pacific species distributed from the East-African coast to Polynesia and Hawaii at depths of 30-650 m. *H. vigil* A. Milne Edwards, 1880, is an Atlantic species known from Georgia and Florida, the Gulf of Mexico, Bahamas and West Indies (Cuba, Guadeloupe, Martinique) at depths ranging between 300-800 m. The sponges associated with both species belong to different families and genera.

### *Homola orientalis* Henderson, 1888, sensu lato (Pl. 2B)

*Homola orientalis* Henderson, 1888: 19, pl. 2, figs. 1, 1a.

*Homola orientalis* sensu lato: Guinot & Richer de Forges, 1981: 530, figs. 1A, B1, 2B, C, pl. 1, figs. 2, 3, 4; 1995: 331, figs. 9e, 10A-C, 12A-B, 13h, 16 c-f.

Examined material associated with sponges (C. Lévi det.): French Polynesia. Tuamotu Archipelago, J. Poupin (SMCB) coll. - South Marutea Atoll, st. 243, 21°30,8'S - 135°38,5'W, 130 m, 30 May.1990: 1 female (MNHN-B 24349). With sponge (Astrophorida Lévi, 1973, cf. *Dorypleres* Sollas, 1888): massive and hard, with a smooth, greyish surface. - Fangataufa Atoll, st. 234, 22°15,0'S - 138°46,0'W, 250 m, 22 May.1990: 1 male (MNHN-B 24555). With a dead sponge, genus *Spongia* Linné, 1759 (Dictyoceratida Minchin, 1900, Spongiidae Gray, 1867). - Tuanake Atoll, st. 252, 16°38,4'S - 144°14,6'W, 120 m, 04 Jun.1990: 1 male (MNHN-B 24347). With a conical sponge (Haplosclerida Topsent, 1928, Halicionidae Delaubenfels, 1932) (colour photographs). Nihuru Atoll, 16°42,8'S - 142°52,8'W, 220 m, 15 Nov.1989: 1 female (MNHN-B 22383). With a spherical sponge (Haplosclerida, Halicionidae).

Examined material carrying plant debris: Tubuai Islands, Raevavae Atoll, 23°50,6'S - 144°42,5'W, 100 m, 3 Dec.1990: 1 female. Probably, wood (MNHN-B 24451). - Society Islands, Bora Bora, st. 275, 16°26,5'S - 151°46,2'W, 190 m, 25 Jun.1990: 1 male (MNHN-B 24348).

### *H. vigil* A. Milne Edwards, 1880

*Homola vigil* A. Milne Edwards, 1880: 33.

*Homola barbata* : Paulmier (nec Fabricius, 1793), 1993: 23, pl. 27, fig. 1.

*Homola vigil* : Poupin, 1994: 40.

Examined material associated with sponges (C. Lévi det.): Guadeloupe, French West Indies Expedition, *Polka*, West coast of Basse Terre, trap, J. Poupin (SMCB) and G. Leblond coll., Mar.1993: st. X11, 16°00,14'N - 61°45,88'W, 500 m: 1 female (MNHN). With the sponge *Neoaulocystis grayi* (Bowerbank, 1869). St. Y11, 16°00,01'N - 61°45,82'W, 500 m: 3 male 28 x 26 mm, 21 x 19 mm, 19,8 x 20 mm, 2 female, 3 female ovig. 19 x 17 mm, 25 x 23,8 mm, 24 x 23 mm (MNHN). With a sponge of the genus *Farrea* Bowerbank, 1862.

### III. Morphological adaptations in host-carrying brachyuran crabs

#### 1. Carrying behaviour involving P5 or P4+P5

One type of characteristic carrying behaviour is that in which the the last pair (P5), or the two last pairs (P4+P5), of pereopods are used to grab an object. This can then be held and moved upwards and anteriorly dorsally over the body. The chelipeds are not directly involved in this behaviour pattern, although they may be used in probing and cutting materials prior to being selected. This behaviour is only observed in those crabs which possess subdorsal last pair(s) of legs provided at the tip with a prehensile grip of the subchelate or chelate mechanism. Nearly all of the primitive crabs taxa, i.e. the Podotremata of Guinot's classification (1977, 1978a), possess such a structure. The P4+P5 or P5 are no longer ambulatory. Two exceptions are the Poupiniidae, in the superfamily Homoloidea, and the Raninoidea, which burrow (see Guinot, 1993a,b, and below).

Only one non-podotrematous family, the Dorippidae, exhibits similar morphological characteristics which perform the same task and seem to be efficient in analogous behavioural patterns. It is interesting to note that in 1825, A. H. Haworth named "Dorsipedata" the brachyuran group with subdorsal last legs, including *Dromia* Weber, *Homola* Leach and *Dorippe* Weber.

The carrying behaviour thus differs from the decorative or masking behaviour found in the Majidae family, where the chelipeds cut, manipulate, and affix camouflaging material on specialized hooked setae (see Wicksten, 1986a, 1993; and below).

#### SUPERFAMILY HOMOLOIDEA DE HAAN, 1839: ONLY P5 MODIFIED

##### FAMILY HOMOLIDAE DE HAAN, 1839

The family Homolidae (Brachyura: Podotremata) is characterized by a modified fifth pair (P5) of pereopods that is always in a postero-dorsal position and is provided with a special end (Fig. 1 A-D). In all known fossil and recent genera, the fifth pereopod is different, not being ambulatory and being shorter + narrower than the rest. The entire appendage has a distinct mobility, being able to move dorsally and held above the carapace. Furthermore, the mobility between the merus and the carpus is increased facilitating the folding of the distal part of the leg. There is also a peculiar articulation between the propodus and the dactylus. The crab can thus partially extend the P5 so that an object can be held nearly perpendicular to the crab's body and far from the carapace.

The last segments of the fifth pereopod are modified, forming a subchelate or chelate end. There are various types of modifications (Figs. 2 A-I) in both the propodus and dactylus enabling them to become a prehensile organ, allowing the crabs to carry various objects (see Guinot & Richer de Forges, 1981, 1995). The propodus varies from long and slender to short and curved, and possesses a process against which the dactylus comes in contact. This process is more or less prominent, varying in position (proximal to medial) and ending in one stout spine or bearing setae that are filiform (as in *Homologenus* A. Milne Edwards, 1888) or corneous (most of genera of the family Homolidae). The setae are concentrated in particular areas, or are sparsely distributed along the inferior border. The dactylus can be very small (as in *Hypsophrys*) or long (*Homologenus*), and, in *Hypsophrys* Wood-Mason, 1891, the

propodus-dactylus of P5 resembles a small chela, with a movable finger acting as a claw (Figs. 1 C-D, 2 E-F).

A chelate P5 characterizes the genus *Homolochunia* Doflein, 1904, in which the propodus forks with a long process similar to a finger. The true dactylus, which is very mobile, together with this false dactylus constitutes a kind of forceps ("pince à sucre" in French; Fig. 2 I), or a small hand similar to the cheliped's chela (Fig. 2 H).

There are few or no reports of carrying behaviour in homolids, even when the chelate or subchelate last legs are turned dorsally over the carapace. According to Wicksten (1980, 1983, 1985, 1986a), several species of this family carry pieces of sponges, antipatharians or gorgonians between the dactyli and propodi of their fifth perieopods. Carrying behaviour in homolids is now being confirmed by various reports and is probably more frequent than originally thought.

Recorded instances include the following genera and species. In the genus *Paromola* Wood-Mason, 1891, *P. cuvieri* (Risso, 1816) and *P. japonica* Parisi, 1915, have been observed, in the field or in aquaria, carrying various animals: sponges, gorgonians, and antipatharians. Four individuals of *Paromola cuvieri*, collected off Port-Vendres, south France, were observed by Guinot & Richer de Forges in aquarium in Banyuls-sur-Mer in 1981, always holding a large living sponge over the body, using the P5. In the submersible *Cyana*, at 51°N (Ireland) at depths of 560, 720 and 922-931 m, Tyler & Zibrowius (1992: 216, 219, 220, fig. 3c) observed *Paromola cuvieri* holding the gorgonian *Calogorgia verticillata* (Pallas, 1766), and probably a sea anemone, belonging to *Bolocera* sp. *Paromola japonica* is known to be associated with sponges, gorgonians and antipatharians (Wicksten, 1985: 476, fig. 1) (Fig.

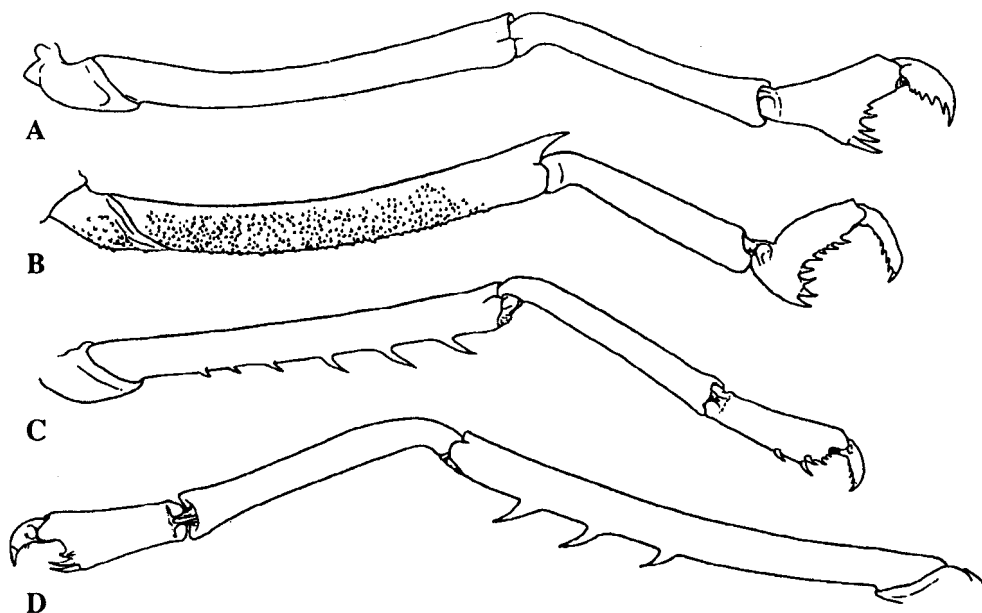


Fig. 1 A-D. Last pair of pereopods (P5) with the terminal subcheliform process in homolid crabs. A, *Gordonopsis profundorum* Alcock & Anderson, 1899, Madagascar (MNHN-B 7026); B, *Paromolopsis boasi* Wood-Mason, 1891, Madagascar (MNHN-B 6991); C, *Hypsophrys inflata* Guinot & Richer de Forges, 1981, Samoa (MNHN-B 7024); D, *Hypsophrys murotoensis* Sakai, 1979, Madagascar (MNHN-B 7025).

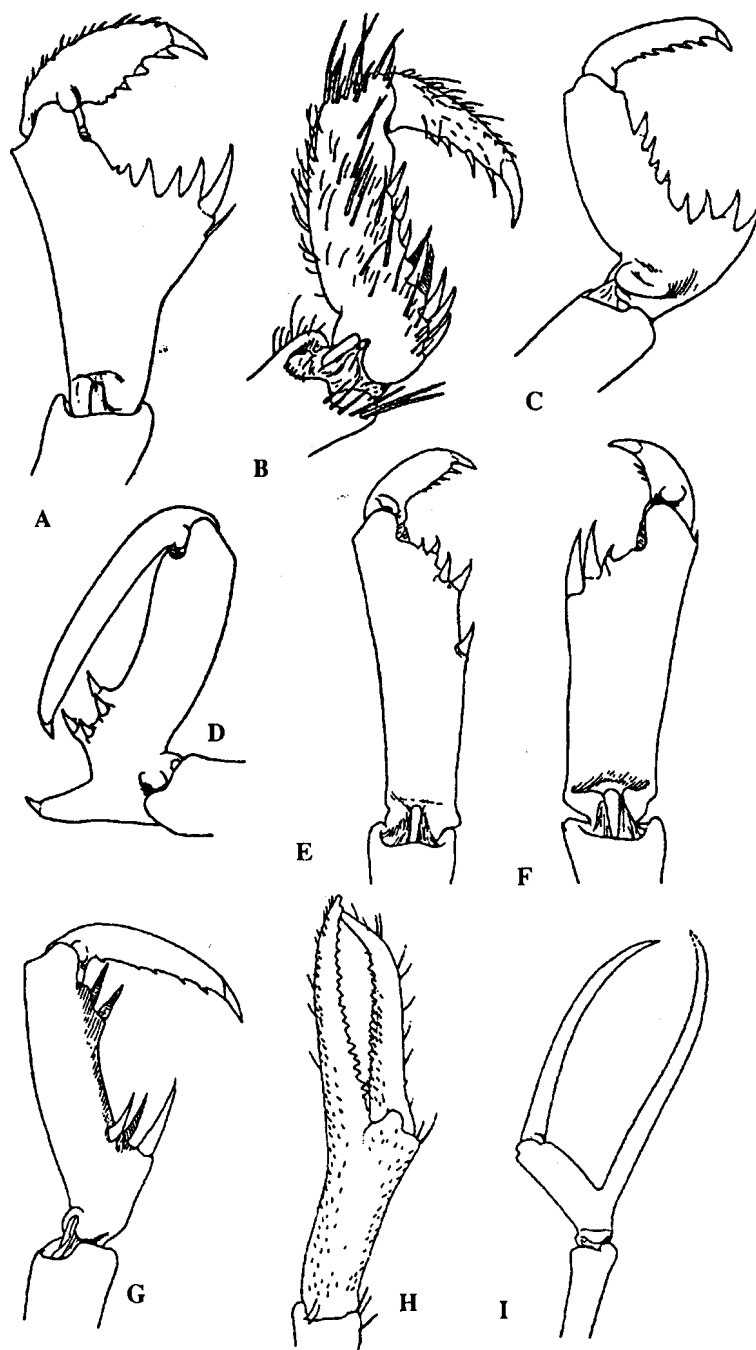


Fig. 2 A-I. Terminal subcheliform process of the last pair of pereopods (P5) in homolid crabs. A, *Gordonopsis profundorum* Alcock & Anderson, 1899, Madagascar (MNHN-B 7026); B, *Homola barbata* (Fabricius, 1793), east Atlantic coast (MNHN-B 7026); C, *Paromolopsis boasi* Wood-Mason, 1891, Madagascar (MNHN-B 6991); D, *Homolomannia occlusa* Guinot & Richer de Forges, 1981, Madagascar, MNHN-B 6992); E, *Hypsophrys inflata* Guinot & Richer de Forges, 1981, Samoa (MNHN-B 7024); F, *Hypsophrys murotoensis* Sakai, 1979, Madagascar (MNHN-B 7025); G, *Ihloopsis tirardi* Guinot & Richer de Forges, 1995, New Caledonia (MNHN-B 7030); H, *Homolochunia kullar* Griffin & Brown, 1976, Australia (after Griffin & Brown, 1976); I, *Homolochunia valdiviae* Doflein, 1904, Madagascar (MNHN-B 7020).

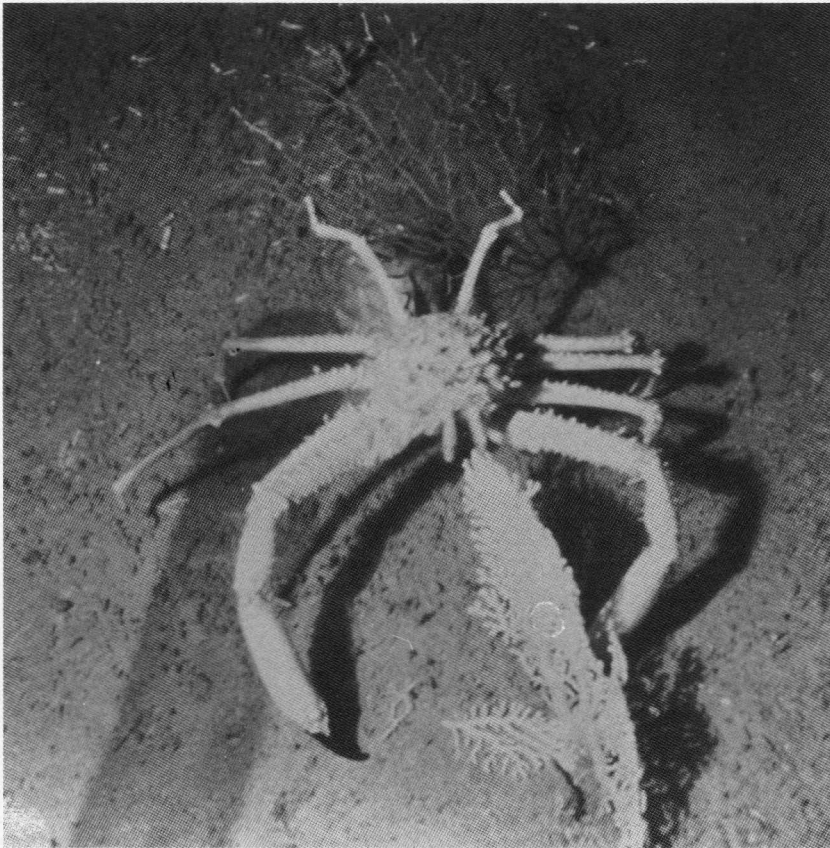


Fig. 3. *Paromola japonica* Parisi, 1915, Hawaiian Islands, Oahu, holding a gorgonid with its P5 but searching for another object to carry (411 m deep, from submarine video, Hawaii Undersea Research, 14 Jan.1984, with the authorization of. M. K. Wicksten).

3). We have examined a specimen collected off Pearl Harbor, Oahu, Hawaiian Islands, which was found walking on the substratum at 370 m, holding a sponge with its P5. A photograph taken from the submersible *Star II* (Grigg, 1977, under the name *Latreillopsis hawaiiensis* Edmondson) shows another *P. japonica* carrying a sponge. A spinose homolid, which was perhaps carrying something at the tips of its upraised P5, was photographed from the mini-sub *Diving Saucer* in Red Sea, off Port Sudan (Cousteau, 1965).

During a dive of the mini-submersible *Deepstar*, Church (1971: 113) a *Moloha faxoni* (Schmitt, 1921) (under the name *Paromola faxoni*) individual was photographed carrying a piece of sponge on its hind legs at a depth of 369 m, off San Diego, southern California (Wicksten, 1983: 187, fig. 1b; 1985: 477). For *Homolochunia valdiviae* Doflein, 1904, Gordon (1950: 224) notes without giving more details: "legs bear some Gorgonid and Sponges" (cf. Fig. 2I).

Two species of the genus *Homola* - *H. orientalis* and *H. vigil* - are reported here (cf. above and Pl. 2B) carrying sponges. During a Calsub Expedition dive, off southern New Caledonia (île des Pins), several individuals of *Homola ranunculus* Guinot & Richer de Forges, 1995, were observed holding small, white sponges with the last pair of their walking legs (B. Richer de Forges, pers. comm.).



Newbert (1984, fig. 102) photographed an unidentified "latreilliid", but more probably an homolid species, from the Red Sea carrying a piece of gorgonian (Wicksten, 1986a: 364).

#### FAMILY LATREILLIIDAE STIMPSON, 1858

The family Latreilliidae, represented by tiny spider-like crabs, contains two genera (Williams, 1982). *Latreillia* Roux, 1830, includes species which have P5 that end as a small dactylus closing against propodal spinules, in the form of a weak subchela. Others species have P5 with a minute dactylus which is not folded against the propodus. In *Eplumula* Williams, 1982, the propodal subdistal spinules are opposed by a short dactylus, closing to form a rather strong subchela.

#### FAMILY POUPINIIDAE GUINOT, 1991

The unique bathyal crab *Poupinia hirsuta* Guinot, 1991, from the Society Islands, belongs to the Homoloidea but is included in a separate family. Its last pair of legs, although subdorsal and similar to the other legs with regards to size and general morphology (propodus not broadened nor equipped with dactylus to form a subchela), are extremely mobile and can be extended dorsally. When the P5 are held in a dorsal position, the body is partly covered by the very long setae which cover these appendices so that the crab can be efficiently camouflaged. Thus, it may not be necessary for it to carry a foreign object to achieve concealment. In this case, the P5 may possibly share a dual role, both of concealment and of walking (Guinot, 1991).

#### SUPERFAMILY DROMIOIDEA DE HAAN, 1833

##### FAMILY DROMIIDAE: MODIFIED P4 AND P5

The various members of the family Dromiidae are said to lead a more or less sedentary life. Most dromiids carry a shell, a sponge, colonial tunicates, or any other hard or flexible object on their backs (Dembowska, 1926; McLay, 1982, 1983, 1993). These objects permanently cover the dorsal surface of the crab's body. Only the two anterior walking legs are used in locomotion, while the reduced, subdorsal and specialized P4 and P5 firmly hold a living sponge, ascidian or a shell. In some cases, a tight seal forms between the covering object and the carapace, as in *Hypoconcha* Guérin-Méneville, 1854 (see Wicksten, 1986b), which is also known as the "Faux Bernard l'Hermite" (Rodríguez, 1993: 44).

McLay (1993) considered that dromiids evolved towards the loss of carrying behaviour, coupled to the development of a strongly ornamented carapace and with the subchelate mechanism of the last legs becoming obsolete. The sponge-carrying behaviour appears in early juvenile instars of *Dromia dormia* (Linné, 1763), reared in the laboratory (Shenoy & Sankolli, 1993).

Dromiid-cnidarian partnerships are known but are very rare. *Dromia personata* (Linné, 1758) was described carrying a colony of the soft corals *Alcyonum palmatum* Pallas, 1766, or with the sea anemone *Calliactis parasitica* (Couch, 1838) (= *Adamsia rondeletii* Andres, 1883) (see Fenizia, 1935: 512, 514, fig. 5). *Cryptodromiopsis unidentata* (Rüppell, 1830) was reported in Mozambique usually covered by a small colony either of Zoanthids *Palythoa nelliae* or *Zoanthus natalensis* (Kalk, 1958: 71; Macnae & Kalk, 1962: 118).

## FAMILY DYNOMENIDAE ORTMANN, 1892: ONLY P5 MODIFIED

There are no reports of carrying behaviour in this family. The dorsal surface of the carapace is not soft as in many dromiids. The very reduced last pair of pereopods is located between the body and the fourth pair and, sometimes, ends in a very small chela. It is not known if this last pair of legs is prehensile and thus involved in carrying behaviour.

## SUPERFAMILY HOMOLODROMIOIDEA ALCOCK, 1900: MODIFIED P4 AND P5

The Homolodromioidea, one of the most primitive group of Brachyura, possess dorsal and subchelate fourth and fifth pereopods. Their use in carrying objects is not known in this group. No homolodromiid specimens were ever observed or collected carrying any associated partners (Báez & Martin, 1989; Guinot, 1978a, 1995). Thus, it is possible that the last pereopods are not used for protection in contrast to the Dromiidae, where the carried objects cover the entire soft body as a permanent protective cap, and to the Homolidae where the material carried is held far above the body. It is possible however, that in the homolodromiids, whose body is thin and their branchiostegae often soft, a carrying behaviour similar to that of the dromiids and homolids might be exhibited.

## SUPERFAMILY CYCLODORIPPOIDEA ORTMANN, 1892: MODIFIED P4 AND P5

In this group the last two pairs of pereopods are subdorsal and subcheliform and smaller than the precedent pairs. The propodus and the dactylus are very short, with the dactylus strongly curved. The last segments of P4 and P5 are modified to form a subchelate apparatus, in which the dactylus closes on the propodus with various ways.

Only a few cases of carrying behaviour have been recorded, and those only in the family Cymonomidae. Garth (1946: 353, pl. 50) indicates that *Deilocerus* (= *Clythrocerus*) *laminatus* (Rathbun, 1935) "carries a bit of shell". Tavares (1994: 164) observed two individuals, each of which held a piece of shell, similar in size to the crab's carapace, with P4 and P5. A similar behaviour of carrying sea urchin spines, sticks, bits of seaweeds, pebbles, pieces of shells, or entire shells above the carapace (Schmitt, 1921), has been observed by Wicksten (1982: 306-308) in *Deilocerus* (= *Clythrocerus*) *planus* (Rathbun, 1900) kept in aquaria: "the distal two segments of the fourth and fifth pereopods hold the object as if in a pair of salad tongs. The piece can be carried directly behind the crab or raised over the carapace" [...] or "thrust upwards over the crab if the animal is disturbed". These materials varied from bits of shells, chips of rock, or entire shells placed over the posterior part of the carapace. While preserved, the specimens lost the material previously carried.

The genus *Elassopodus* Tavares, 1993 (Cymonomidae) has vestigial P4 and P5 which consist of one, not very movable segment which is probably not involved in the carrying behaviour. Some advanced dromiids can similarly show a notable reduction in the size of the last two pairs of legs, with the subchelate mechanism becoming obsolete, and with a subsequent loss of camouflage (see below).

## SUPERFAMILY DORIPPOIDEA MACLEAY, 1838: MODIFIED P4 AND P5

Members of the Dorippidae MacLeay, 1838, the only family of the superfamily Dorippoidea, do not belong to the Podotremata but to the Heterotremata. Their last two pairs of legs are turned upwards. Their tip forms a small, strongly hooked subchela, which is able to hold organisms or objects. The range of materials varies from pieces of shell to anemones and plant leaves brought by currents. Jamieson (1994: 390-391), who used spermatozoal ultrastructure to analyse the phylogeny of Brachyura, concluded that the dorippids appear as the least modified members of the Heterotremata-Thoracotremata assemblage and that the shell carrying habit found in many dorippids might have been inherited from a podotrematous ancestor.

## SUBFAMILY DORIPPINAE MACLEAY, 1838

*Dorippe quadridens* (Fabricius, 1793) [= *D. dorsipes* (Fabricius, 1793)] has been recorded carrying a sponge (Borradaile, 1903: 439), pieces of shell or debris (Ng, 1987: 15), broken or intact valves or lamellibranchs (Ng & Tan, 1986, table 1), scutellid sea urchin (Kalk, 1958: 44, 71, fig. 17j), a starfish (McNeill, 1923: 246, fig.), stalked barnacles (Stephensen, 1945: 63), even a jellyfish in which the dactyli were hooked onto the umbrella (Estampador, 1937: 514; 1959: 65). *Medorippe lanata* (Linné, 1767) also carries living organisms (Pesta, 1918). Rathbun (1924: 27) recorded an individual of *Paradorippe australiensis* (Miers, 1884) carrying the valve of *Antigona* (*Venus*) *laqueta* Sowerby, 1851 [= *Antigona* (*Antigona*) *chemnitzii* Hanley, 1844]] on its back. *Paradorippe cathayana* Manning & Holthuis, 1986, carries a bivalve shell with the last pair of legs and can also bury itself in the sand. Shen (1932: 11) commented that "this crab always protects itself by holding a bivalve shell upon its dorsal surface with its two prehensile posterior legs. When it was frightened, it soon stopped to move in water to conceal quietly under the shell or suddenly threw it off and fled away when any danger approaches" (see also Shen, 1937: 171; André, 1937: 79, both under the name *Dorippe polita*; Holthuis & Manning, 1990: 33). Another dorippid, *Heikea japonica* (Von Siebold, 1829) from China and Japan was recorded protecting itself with a dead shell or other dead material, such as a piece of dead *Laganum* [a sand dollar] or wood; they were held with the reduced posterior two pairs of legs (Sakai, 1937: 73; 1976: 61).

*Neodorippe callida* (Fabricius, 1798) (Pl. 2A). The "leaf-porter crab" *Neodorippe callida*, an inhabitant of mangroves, is known to invariably carry a leaf, sometimes so large as to cover its whole body (Walker, 1887: 108; Lanchester, 1900: 770; Rathbun, 1910: 5; Shelford, 1916: 300; Serène & Romimohtarto, 1969: 12; cf. Holthuis & Manning, 1990: 101-103) (Pl. 2A). Ng & Tan (1986: 45-47, fig. 1, table 1), Ng (1987: 14-15), Tan & Ng (1992: 102), Lim et al. (1994: 108, 127) provided observations and figures. "Even during the day when the individual is buried in the mud, it holds a leaf; at night, it is a slow but competent swimmer, reversing its orientation with the ventral sternal plate facing the water surface and the leaf downward". Ng (*in litt.*, 11 Aug. 1993) sent to us drawings of the terminal segments of the last pair of legs and commented that "the base of the propodus has a ring of short stiff hairs on the inner surface; there is also a fringe of short, stiff hairs lining the distal edges of the carpus, also on the inner surface. So, when the propodus flexes (bents), the two tufts of hairs meet. The crab uses the point of articulation between the carpus and propodus to grip the leaf. Between the opposable tufts of hairs and hooked dactylus, the animal has an excellent hold on the leaf. The legs grasp four different corners of the leaf for

additional stability" (see also Lim et al., 1994: 127). Lim et al. (1994: 143) have recently described the mating behaviour of this species. The rear legs of the male have an additional purpose, that of grasping the female to immobilize her. The association between *Neodorippe callida* and the mangrove leaf seems to be relatively obligatory. Perhaps *Dorippe tenuipes* Chen, 1980, exhibits the same habits.

***Dorippoides facchino* (Herbst, 1785) (Pl. 1B).** The association of the "porter crab" *Dorippoides facchino* with sea anemones is well known. Herbst (1796: 215) cited observations made by the missionary John of Tranquebar, namely the use of the last two pair of legs to hold "a bivalve in which a small fish, small crustacean, or some other small animal was enclosed". It is likely that what Tranquebar "thought to be a shell was the hardened base of the sea anemone, and that he took the rest of the sea anemone to be (a piece) of fish" (Holthuis & Manning, 1990: 59).

Stimpson (1855: 376) described a new genus and species of sea anemone (as *Cancrisocia expansa*), found attached to the posterior legs of a common *Dorippe* species from the South China Sea. Verrill (1869a: 58-60; 1869b: 249-250, pl. 2, fig. 1) dealt more extensively with this association and published a striking figure. It was also added that "*D. facchino* was dredged at Hong Kong, carrying upon its back a beautiful Sea-anemone *Cancrisocia expansa* St., which completely covers the back of the crab, and like *Adamsia*, secretes from its base a thin, firm pellicle, to which it adheres, and by which the crab holds it in position with his four posterior legs. It appears that when very young the crab holds over its back a minute bit of shell or gravel upon which the Anemone lodges, and afterwards by expanding its basal pellicle as the crab grows, provides it with a permanent protection. This Anemone was never found except upon the crab's back, and the crab was not found without it". Holthuis & Manning (1990: 60, fig. 25a, b) and Manning (1993: 114, fig. 3 a, b) reproduced Verrill's 1869 original figure and provided a previously unpublished figure of *Dorippoides facchino*, found in the files of the National Museum of Natural History, Washington. Verrill (1928: 16) referred to the anemone, found on the back of a Chinese *Dorippe*, as *Carcinophila expansa*; it secreted a thin horny plate, which the crab held.

Henderson (1893: 405) observed that individuals of *D. facchino* were often "protected by the valve of some flat Lamellibranch, e. g. *Placuna*, to which an Actinia is attached". Alcock (1896: 279) "rarely found it without a protective bivalve shell and sea-anemone". Lanchester (1900: 769; 1902: 553; see also Sheldon, 1905) described a case where the crab "carries on its dorsum a small anemone, with a bivalve shell interposed" or "bears a small anemone on its back with a bivalve shell and ? Gastropod operculum interposed". Shelford (1916: 299-300) observed the habits of living crabs in Borneo (even if his interpretation of the basal plate "secreted by the crab itself" is erroneous; see Holthuis & Manning, 1990: 61-62). He mentioned that "the two hinder pairs of legs [...] hold in their claws an oval gelatinous plate on which grows a little Sea-Anemone; the crab rests with the hinder part of the body buried in the soft mud or sand [...], the former [part of the body] partially sheltered by the sea-anemone growing on the plate [...]. If a crab be deprived of its burden, it manifests every sign of disturbance, and hunts about the vessel in which it is confined until it finds the object of its search, which is then hoisted up in the two hinder legs into the old position, the crab then backing down into the mud until almost concealed from view. It is difficult to imagine how the association of the two creatures commences; how does the newly formed crab succeed in getting hold of a young unattached Sea-Anemone ?". Hornell (1922: 934-935, fig. 5) also observed the habits of two dorippids from the Madras coast, India, which "carry over their back a valve of some species of thin bivalve shell, concave side down, of size suitable for

effective concealment. [...] In many cases, the defence is increased by the presence on the surface of the shell of a little pale-coloured anemone". (Fig. 4A).

Many authors confirmed this association from different geographic areas, often with a sea-anemone held like an umbrella. Always the crab carried something: "an oval gelatinous plate, on which there grows a little Sea-Anemone" (Hose, 1929: 31; 1985: 31; see also Shen, 1931: 101), or a lamellibranch shell, "usually a Tellinid" or "the clam *Catelsia opima*, without a sea anemone attached" (Gravely, 1941: 81; see also Chopra, 1933). Serène and Romimohartarto (1969: 11) observed a large number of individuals always found with "a small valve of lamellibranch in the middle of the ventral face of the sole of the Actinian. The shell is much smaller than the dorsum of the carapace of the *Dorippe*, the sole of the Actinian on the contrary is much larger and laterally extends over the carapace covering partly the pereopods 2-3. Probably the young crab hooks a small valve of lamellibranch on which the Actinian begins to develop. The Actinian becomes larger and larger at the same time that the carapace of the crab increases (but comparatively much less) in size. The crab can always let slip away the Actinian, but we think that the association of the two organisms is the same individual one for the life time".

Morton & Morton (1983: 187, figs 10. 4, 7) showed a crab from Hong Kong (referred to as *Dorippe granulata*) holding a grey sea anemone "by its flat hardened base". Morton (1988: 62, pl. 18) added that the sea anemone "is never found alone" [...]; when the crab moults [...] the process of anemone removal will not to be excessively complicated, since the anemone will remain attached to the discarded exuvium until it is removed and replaced on the back of the newly hardened skeleton [...]; the basal portion [of the anemone] must steadily expand, to form a flexible covering for its partner. The mouth of the anemone therefore appears to be much smaller than that the other species in relation to the area of the basal disc [...]; its tentacles hang down behind the crab and sweep along the sea bed collecting some creatures stirred out by the scurrying host". The anemone reported here is not *Carcinactis ichikawai* Uchida, 1960, normally associated with *Paradorippe granulata* (see below), but the *Cancrisocia* species used by *D. facchino* (Holthuis & Manning, 1990: 63).

Tan & Ng (1988, 1992: 149), who provide an excellent colour photograph of the crab with its sea anemone, think that the association is "most intimate, the anemone actually growing with the crab !". From all these accounts Holthuis & Manning (1990: 63) conclude that the association between the dorippid *Dorippoides facchino* and *Cancrisocia expansa* is very close and obligate, the young crab beginning with "a small bivalve shell, or part of one, on which the anemone settles".

Two specimens of *D. facchino* from Thailand were examined, one ovigerous female and one male (RMNH 36087 and 37598). The female carries a very small shell and holds with the dactyli of P4 and P5 a plate on which a sea anemone is sitting. In the male the shell is broader and therefore larger than the anemone; a similar plate adheres strongly onto the shell and is intercalated between the crab's carapace and the sea anemone, which is held by the dactyli of the dorippid's last pair of legs (as in Fig. 4 A). This plate does not belong to the mollusc (P. Bouchet, pers. comm.) but is a chitinoid secretion of the sea anemone's pedal disc. It extends beyond the original shell and offers the crab a larger cover. The widening of the general shape of the actinian and the presence of a chitinous secretion is known in sea anemones (Actiniidae and Hormathiidae) associated with hermit crabs. This phenomenon was also encountered in the abyssal genus *Paracalliactis* Carlgren, 1928 (see Doumenc, 1975: 168, fig. 4). We can confirm here that the same complex exists in the association *Cancrisocia* - *D. facchino*.

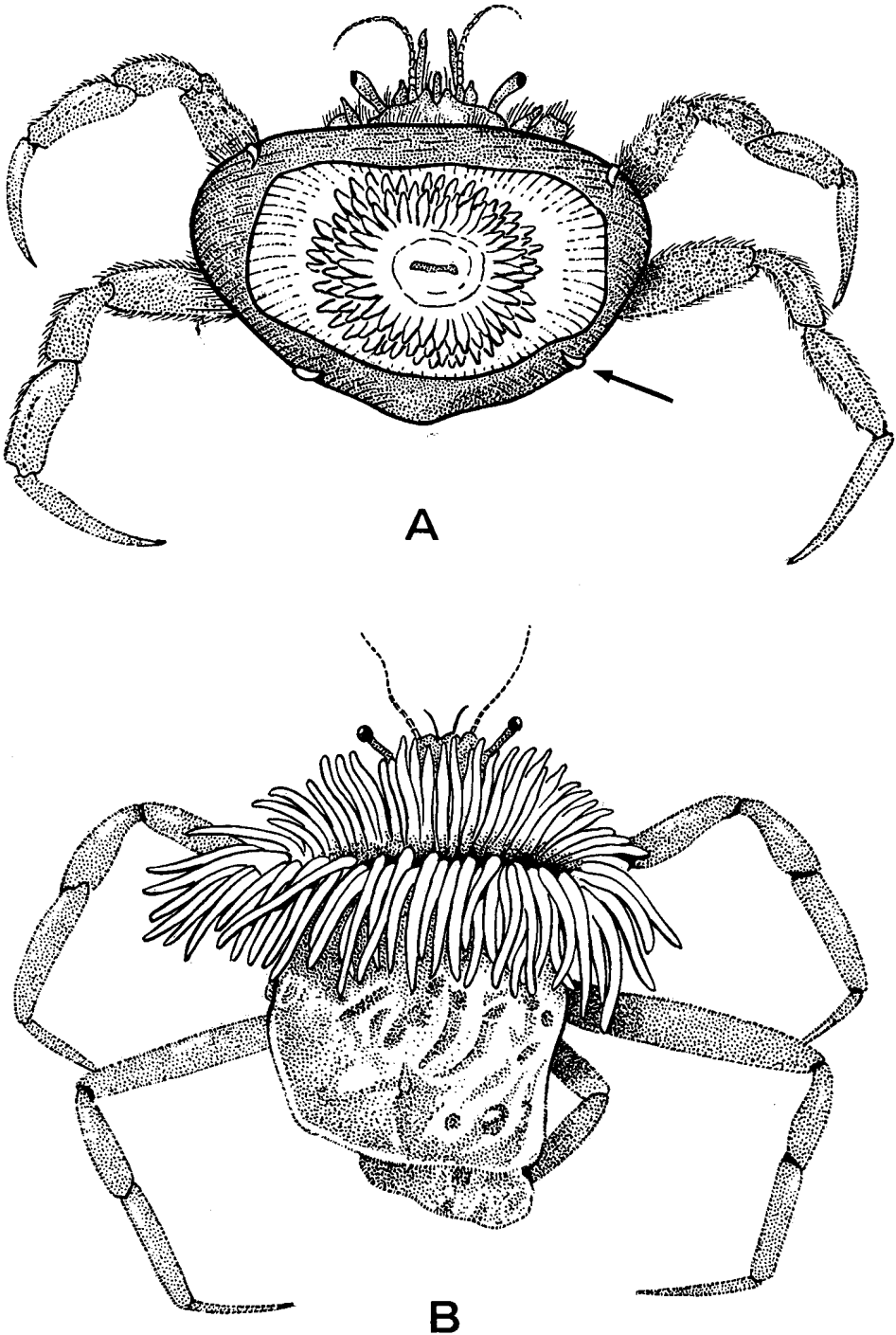


Fig. 4 A-B. Two Dorippidae symbiotic with sea anemones. A, The dorippid *Dorippoides facchino* (Herbst, 1785) associated with a sea anemone "scated upon a shell" (after Hornell, 1922: fig. 5, under the name *Dorippe dorsipes*); B, The ethusid *Ethusa mascarone* (Herbst, 1785), carrying with its P4 and P5 a shell covered by a sea anemone (after Fenizia, 1937: fig. 5). The arrow shows the crab's dactyli of P4 and P5.

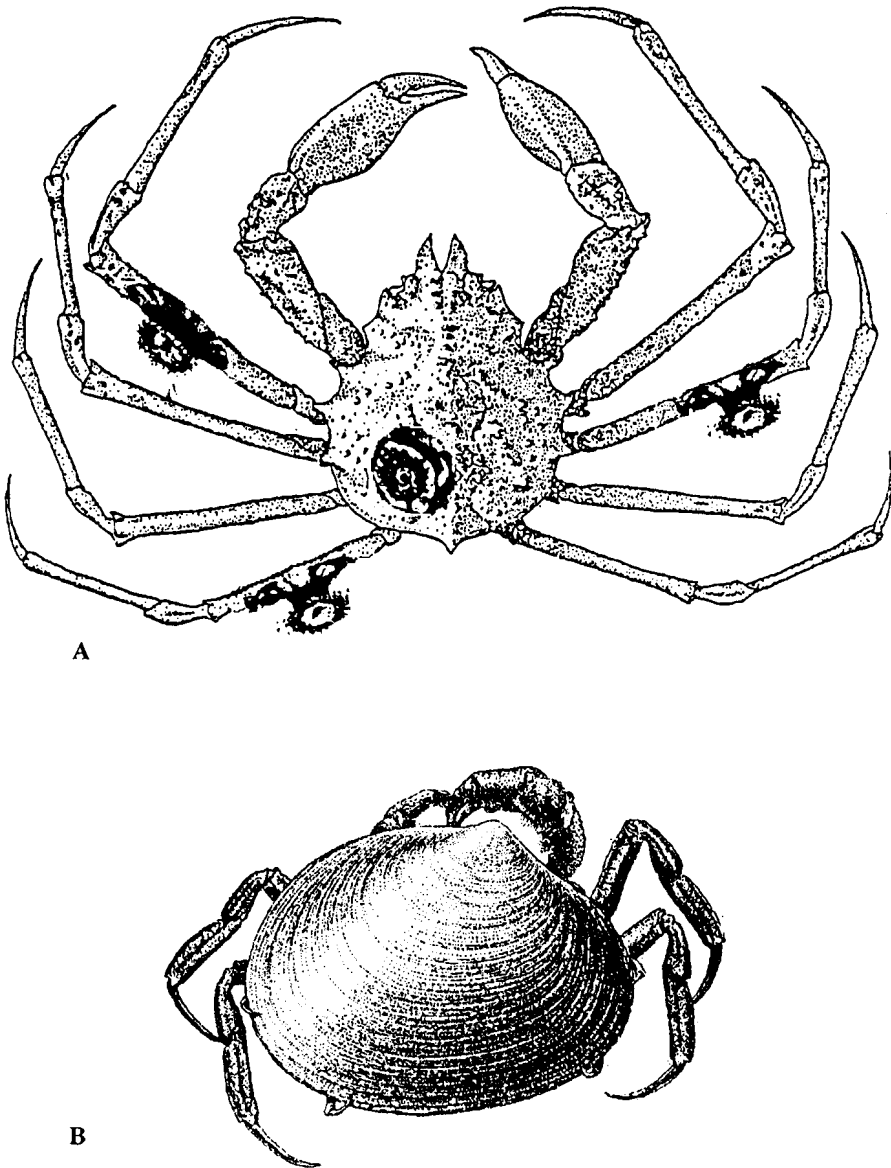


Fig. 5. A, The majid *Leptomithrax edwardsi* (de Haan, 1839), from Japan, with sea-anemones on its carapace and legs (after Sakai, 1976: pl. 86). B, The dorippid *Paradorippe granulata* (de Haan, 1841), from China and Japan, holding the lamellibranch *Macoma* without a sea anemone fastened on the shell (after Kobjakova, 1955: pl. 40, fig. 1a, under the name *Dorippe granulata*). The crab's dactyli of P4 and P5 can be observed grasping the edges of the shell.

Another sample of *D. facchino* collected from Bedok, Singapore (ZRC) was also examined. It contained an anemone, separated from a male individual, but no trace of a shell was found in the container; perhaps it was lost during the preservation processes.

***Paradorippe granulata* (de Haan, 1841)** (Fig. 5 B). The sublittoral dorippid *Paradorippe granulata*, also from China and Japan, chooses to carry shells mostly of the lamellibranch genus *Macoma* on which sea anemones are often fastened. Uchida (1960) described a new

genus and species, *Carcinactis ichikawai*, found on a dead shell of *Macoma sector* (von Martens) or *M. incongrua* Oyama and was carried by the crab *Paradorippe granulata* in Japan. Usually one anemone, but sometimes two or three, are found on a single shell carried by the crab. In aquaria, crabs select shells which include anemones. It "will seize a clam shell with its pincers and transfers the shell to the back legs" (Uchida, 1960: 595; see also Patton, 1967: 1232). Burton (1969: Fig. p. 64) misinterpreted the crab's habits, by showing a large spider crab with eleven legs and holding in each cheliped an entire bivalve to which an anemone is attached. Several authors report the crabs carrying a clam without an anemone (Döderlein, 1883: 109; Kobjakova, 1955: 155, pl. 40, fig. 1a; 1966: 212, pl. 49, fig. 1a; Levin, 1976, fig. 106a; Sakai, 1956: 26, fig. 9; 1980: 43, fig. 15; Sakai et al., 1983, fig. p. 29; see Holthuis & Manning, 1990: 126, figs. 51, 52).

Ross (1983: 178) concludes that "although not involving a hermit crab, the analogous use of bivalve shells as shelters by some dorippids is utilized by some actinians as their preferred locations".

#### SUBFAMILY ETHUSINAE GUINOT, 1977

The Mediterranean and Atlantic *Ethusa mascarone* (Herbst, 1785), named "porter crab" or "Gepäckträgerkrabbe", carries shells of bivalves, gastropods, or bits of calcareous algae and sponges using P4 and P5 (Fig. 4 B). Fenizia (1937: 6, 11, fig. 5) demonstrated that *Ethusa* in aquaria can accept a sea anemone in different ways. If the crab covers its dorsal surface directly with *Calliactis parasitica* (Couch, 1838) [= *Adamsia rondeletii* Andres, 1883], the association does not last. If there is a shell bearing *Adamsia palliata* (Bohadsch, 1761), the association lasts indefinitely (see also Schöne, 1976).

#### IV. Other instances of symbiosis with sea anemones

Another type of carrying behaviour between crabs and anemones involves the use of chelipeds (P1). Better known than in homolids, it occurs in heterotrematous polydectine crabs (Xanthidae, superfamily Xanthoidea). Other types of symbiosis with sea anemones are found in some heterotrematous crabs. In the Majidae, crabs are the active partners, whereas crabs of the family Hepatidae are only sometimes the active partners.

##### 1. Carrying behaviour involving sea anemones in claws (P1)

This association occurs in two genera, *Lybia* H. Milne Edwards, 1834, and *Polydectus* H. Milne Edwards, 1837, both members of the subfamily Polydectinae Dana, 1852 (see Guinot, 1976). Crabs are always found holding a single small anemone with two specialized claws (Pl. 3A, B). The anemones are held tightly by the middle of the column below the tentacles, with the sharp hooks of the fingers dug into the tissues. This partnership is obligate. Almost all specimens of crabs deposited in museums are preserved with their anemones.

Species of *Lybia* are named "boxer crabs" or "boxing crabs" because the claws are positioned in front of the body in a defensive or aggressive position. They usually advance first the left claw and then the right one, an action resembling the "left-right combination" of a boxer (Debelius, 1984: 98). Little else is known of this behaviour.



Latreille (1825: 124) was the first to report in the "Pilumne porte-cupules", the actual *Polydectus cupulifer* (Latreille, 1812), "une substance peut-être gommeuse et glutinante formant un empâtement à l'extrémité des [serres]". An illustration is provided in H. Milne Edwards's Atlas (in Cuvier, Règne Animal, 1837 and 1849: pl. 14, fig. 4). Dana (1852: 227) observed in *Polydectus*: "The hands in specimen procured were overgrown with a kind of sponge, which had grown around and enclosed the fingers". It was Richters (1880: 149-151, figs 72-73, pl. 15, figs 17, 18, pl. 16, figs 19, 22) who pointed out the fact that an actinian was carried in the fingers of both *Lybia* (at that time, *Melia* Latreille) and *Polydectus*. Möbius (in Richters, 1880: 174, footnote). This indicated that it was impossible to remove the anemone from the crab without injury and, if the anemone were cut into pieces, these were quickly found in the claws. Borradaile (1902: 249, fig. 49) illustrated *Lybia* living among branches of corals. He also explained the active involvement of the crab in using the anemones.

Duerden (1905: 494-511, figs 72-76) was the only researcher who conducted laboratory experiments, studying *Lybia* and *Polydectus* in the Hawaiian Islands. He concluded that the partnership was restricted to various species of actinians: *Bunodeopsis* Andres, 1880, or *Sagartia* Gosse, 1855, for *Lybia*; and *Phellia* Gosse, 1858, for *Polydectus*. Specimens of the same anemone were also found on rocks in the same environment. Duerden (1905) observed that the crab released the sea anemone when it molted, placing it aside for a moment and seizing it again after the molt.

The crab seems to obtain the cooperation of the anemone when it transfers it on its claws (see Ross, 1967: 308; 1974a: 297; 1974 b: 113; 1983: 170). Verrill (1928: 18-19, fig. 2 j, pls 3 B, 4 A) reported *Sagartia pugnax* Verrill, 1928, as the associate of both Hawaiian *Lybia* (*L. edmondsoni*) and *Polydectus*, and gave an illustration (*ibid.*: pl. 5 A, B) of *Polydectus* associated with a large live *Bunodactis* (= *Tealiopsis*) *nigrescens* Verrill, 1928.

Rathbun (1906: 866, 867) reported about *Polydectus cupulifer* from Hawaii: "Three of the specimens hold an actinian in each hand; two specimens, the smallest of all, have an actinian in one hand, not in the other; the sixth specimen lacks the right cheliped altogether, but the left grasps an actinian". Edmondson (1946: 301-302; 1962: 216, 304, fig. 34) observed in captivity *Polydectus* carrying *Sagartia pugnax* Verrill, 1928, in Hawaii [? = *Adamsia paguri*] Verrill, 1869). When *Sagartia* had been forcibly removed from its claws, other species of sea anemones were accepted, even a much too large *Bunodactis* (= *Tealiopsis*) *nigrescens* Verrill, 1928, individual.

The well-known *Lybia* species are the Indo-west-Pacific *L. tessellata* (Latreille, 1812) and *L. edmondsoni* Takeda & Miyake, 1970 (cf. Pl. 3A), from Hawaii, both characterized by a reticulated pattern on their carapace and by striped legs. These species have been observed fighting using the anemones as weapons. Debelius (1984: 96, 97) has published a few good photographs in which two species could be distinguished by the different reticulated pattern. *Polydectus*, which is densely haired, is more sluggish and more prone to "play possum" (cf. Pl. 3B).

Schmitt (1965: 148-150, fig. 66) recorded the anemone *Triactis producta* Klunzinger, 1877, for *Lybia tessellata* and *L. leptochelis* (Zehntner, 1894), and the anemone *Telmatactis decora* (Hemprich & Ehrenberg, 1834) for *Polydectus*. He added that "unlike the more choosy *Lybia*, in some localities [*Polydectus*] will carry other species and sometimes even small holothurians". Sakai (1965: 162; see also 1967: 77) reported *Lybia hatagumoana* Sakai, 1961, from Japan, carrying a tiny sea-anemone or a tiny nudibranch, both unclassified. He observed

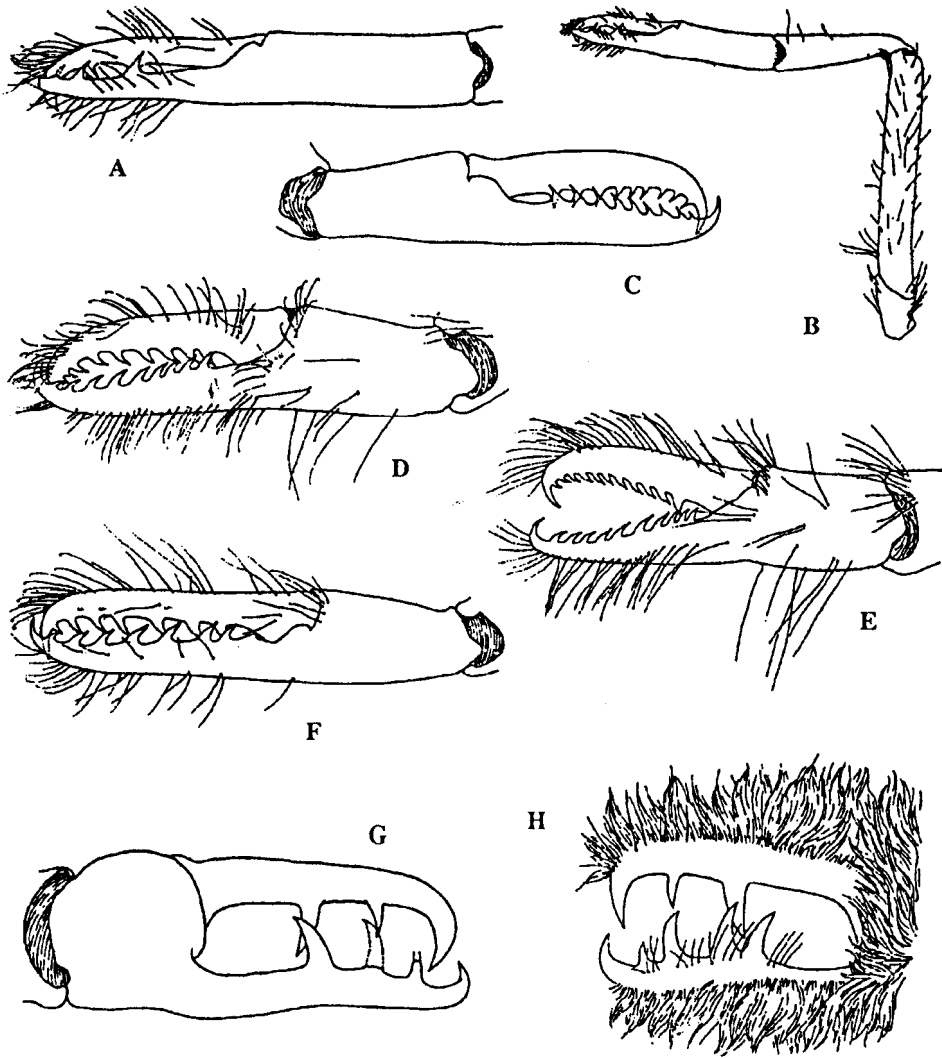


Fig. 6 A-H. Chelipeds with specialized fingers in the Polydectinae Dana, 1851 (A-F, genus *Lybia* H. Milne Edwards, 1834; G-H, genus *Polydectus* H. Milne Edwards, 1837). A-B. *Lybia denticulata* Nobili, 1906, Red Sea; C, *L. leptochelis* Zehntner, 1894, Amboina; D, *L. tessellata* (Latreille, 1812), Mauritius; E, *L. edmondsoni* Takeda & Miyake, Hawaii; F, *L. plumosa* Barnard, 1947, Madagascar; G-H, *Polydectus cupulifer* (Latreille, 1812) sensu lato, Indian Ocean, with the tomentum (H) or brushed (G). All after Guinot, 1976.

that the crab “was seen to hide its chelipeds beneath the mouth region and the first ambulatory legs seem to play the role of the cheliped”. It seems that this leg is also used to remove the anemone from the substratum.

Guinot (1976: 62-99, figs 15-22, pl. 2) showed that the shape of the slender chela and fingers and the number and shape of the hooks along the prehensile border are species specific in *Lybia* (Fig. 6 A-F) and *Polydectus* (Fig. 6 G-H). The cheliped is particularly mobile due to the disposition of the articulations, which allows it to stretch it in front of the carapace. The claws are no longer used for taking food, a task which has been taken over by the very mobile third maxillipeds and to the pereiopods, specially the first pair of walking legs. In

the Polydectinae, the morphological differentiation is striking and the association between the partners is very close.

The Japanese pagurid *Diogenes edwardsii* de Haan also carries a sea anemone, *Adamsia paguri* (Verrill, 1869) with its left claw (see Balss, 1924: 774, fig. 29; Carlgren, 1949: 98). The sea anemone is attached to a non-granulous area on the claw for easy attachment. The shell's opening is blocked by the pagurid's chela, which bears the sea anemone. The same anemone is also usually found on the shell inhabited by the pagurid. Ross (1967: 308) considers this "a special development of the normal pagurid association". This interaction may be similar with that of *Polydectus* which grabs the anemone with the dactylus's spines of the cheliped and with that of the hermit crab which attaches the sole's anemone on the smooth area of its pincer.

## 2. Carrying behaviour involving hooked setae of carapace (Majidae)

Many species of spider crabs select various materials from their environment and carry them using the hooked setae of their carapace and legs. Aurivillius (1889) gave a detailed account of the decorating activities of several European species. Being called "decorator crabs" or "masking crabs" and known as the masters of disguise, majid brachyurans deliberately attach to their bodies pieces of algae, bryozoans, hydroids, sponges, bits of shells, ascidians and other foreign objects (Hartnoll, 1993; Voultsiadou-Koukoura & Koukouras, 1993). The movements of the mouthparts involved in acquiring plus manipulating the camouflaging material, before using the chelae to position it, are very similar to those of feeding.

The most primitive spider crab species (Inachinae) feed mainly by picking material off the substrate but also by seizing floating debris on their setae. In some occasions noxious organisms, such as inedible algae, didemnid ascidians, toxic sponges, living gorgonians and sea anemones are also used as concealment. On the other hand, some majids do not carry any type of camouflage. Those species may decorate themselves only as juveniles, at which time their body is covered by setae, which disappear with age.

Masking material can also be used as a food reservoir, as it has been demonstrated in field studies with *Inachus phalangium* (Fabricius, 1775) (see Wirtz & Diesel, 1983). Wicksten (1979, 1980, 1993) hypothesizes that early majids acquired food this way and that they evolved specialized fishhook-shaped setae for storing material as part of their food-storing behaviour. The more advanced majids could attach materials which they did not eat, giving rise to decorating activities which ultimately provided camouflage: the mask was no more used as a source of food and served only for concealment. Woods & McLay (1994 a, b) have shown the dual role which the masking material can play in laboratory trials with *Notomithrax ursus* (Herbst, 1788). Hornell (1922) observed at Jersey, that when *Maja squinado* (Herbst, 1788) was placed in tanks without seaweeds, the crabs selected pebbles and balanced them carefully on its tuberculated carapace.

In subtropical and temperate European waters, in order to provide cover "a striking variety of majid and non-majid crab species may be found (non obligatory) associated with the sea-anemone *Anemonia sulcata* (Pennant) sensu lato" (den Hartog, 1990: 164).

The Harlequin crab *Camposcia retusa* (Latreille, 1829), ornamented with dense, coarse,

hooked hairs, is one of the most active decorating crabs. It covers itself with a mass of different types of marine life. At one instance it has been photographed being completely hidden amongst several polyps of the *Palythoa* sp. (Catala, 1979: fig. 24).

*Achaeus serenei* Griffin & Tranter, 1986, can be covered with stinging hydroids (Wicksten, 1993: 320).

Among the materials used in decorating by the large Californian majid *Loxorhynchus crispatus* Stimpson, 1857, Wicksten (1979: 45, table 3; 1993: 320) listed the sea anemone *Corynactis californica* Carlgren, 1936. Parts torn by the chelae or abraded by the mouthparts were able to regenerate. The use of detritus and non-living material may suggest that this species does not distinguish between living and dead materials, and does not have "special behavioral mechanism to avoid damage to the organisms they attach themselves" (Wicksten, 1979). Wicksten (1993: 320) indicated that the sheep crab *L. grandis* Stimpson, 1857, uses toxic materials as cover, but concluded that "most majid crabs do not specialize in attaching particularly noxious and protective species".

The Japanese *Leptomithrax edwardsi* (de Haan, 1839) was illustrated by Sakai (1976: pl. 86) with sea-anemones on its carapace and legs (Fig. 5 A). *Leptomithrax longipes* (Thomson, 1902) from New Zealand carries one of a number of species of sea-anemones: *Calliactis conchicolla* Parry, 1952, *Paracalliactis rosea* Hand, 1975, *Bunodactis chrysobathys* Parry, 1951, and *Phellia aucklandica* Carlgren, 1924. Hand (1975: 509-527) reported on the cleaning activity of the crab, which manipulated the anemone with its chelae turning it around against its maxillipeds, probably in order to remove adherent debris from the base. Some crabs attached several actinians on the body, but small males and all females were not active. *Leptomithrax longipes* also uses algae, hydroids, sponges and other foreign objects, and McLay (1988: 162-164) concluded that this behaviour is rather for camouflage than for deterring predators.

The majid *Stenocionopsis furcata* (Olivier, 1791) carries algae and sponges, as well as sea anemones. Cutress et al. (1970: 371, 373, figs 7-11) and Ross (1983: 169, fig. 1) described the behaviour involved in the association between this crab and *Calliactis tricolor* (Lesueur, 1811) in the Caribbean. The sea anemone is usually associated with shells inhabited by the pagurid *Dardanus* and sometimes on the carapace of the hepatid *Hepatus epheliticus* (see below). An individual of *S. furcata* may carry up to 20 or 30 sea anemones on its carapace and legs. When it encounters *Calliactis tricolor* attached to another surface, the crab uses its chelipeds and walking legs to remove the sea anemones. After a period of manipulation, the crab seizes the anemone firmly in one cheliped and lifts it onto its body (Cutress et al., 1970: 373). Preceding the transfer of the anemone, both of the chelipeds usually testes the carapace surface for empty areas. It was believed the crab "evolved in a program in which some central nervous representation of its carapace must be a necessary component" (Cutress et al., 1970: 376).

Another type of association is that of the Indo-west-Pacific majid *Cyclocoeloma tuberculata* Miers, 1880. In this crab the carapace is almost entirely covered with the polyps of the corallimorpharian *Actinodiscus* (= *Discosoma*). Its legs carry solitary polyps and small colonies of at least two species of xeniid alcyonaceans. The crab actively detaches the corallimorpharians from their substrate and transfer them to the carapace (den Hartog, 1990: 161, figs 1-6). Sakai (1967: 76; 1976: 192) reported that the same species of crab carried "several Zoanthids attached to the carapace and ambulatory legs". The "sea anemones"

mentioned by Griffin & Tranter (1986: 265) as camouflaging one of their two specimens of *Cyclocoeloma* in fact belonged to *Actinodiscus* de Blainville, 1830 (den Hartog, 1990).

### 3. Anemones attached to carapace

It is the belief of the present authors that the inclusion of the genera *Hepatus* Latreille, 1802, and *Hepatella* Smith, 1869, to the subfamily Calappidae de Haan, 1833, is erroneous, and that they should constitute a distinct family, the Hepatidae Stimpson, 1871, as part of the Parthenoxystomata (see Guinot, 1966-1967, 1978b). Thus, the denomination "calappids" used by biologists for *Hepatus* and *Hepatella* is not convenient and should be changed to "hepatids".

Bürger (1903: 678-679) described the association between the hepatid crab *Hepatus chiliensis* H. Milne Edwards, 1837, also named as the "box crab", and the actinostolid sea anemone *Antholoba achates* (Dana, 1949) [= *A. reticulata*] in Chile. It was observed that among the 60 specimens collected at one location only four were found not carrying an attached sea anemone. Each crab usually carried only one anemone, rarely two. When separated from their crabs, in an aquarium, the anemones quickly resettled on the crab's body, attaching themselves first to the legs and then sliding onto the carapace. Bürger believed that this was not an obligatory partnership since both species shared only part of their geographical ranges (see also Ross, 1967: 307; 1983: 169).

Carlgren & Hedgpeth (1952: 160, fig. 6A, pl. 2) report that *Calliactis tricolor*, the most common anemone on the Texas coast, can be found on the carapace of *Hepatus epheliticus* (Linné, 1763), the "calico crab" (Fig. 7). This crab was often collected with a sea anemone (Rathbun, 1937, table 76). While the crab fed, the anemone, which was located on the middle of the dorsal surface of the carapace, positioned its tentacles within the respiratory current of the crab and was thus able to feed. Hildebrand (1954; 1955) noted the same behaviour when he examined the fauna in the western Gulf of Mexico (see also Ross, 1983: 169; Williams, 1984: 279-280).

Cuttress et al. (1970: 371, fig. 12) while studying the behaviour of *Calliactis tricolor* (Lesueur, 1811) in relation to *Hepatus*, showed that *H. epheliticus* initiated the transfer of the anemone onto its body by rubbing the anemone's tentacles on its carapace, leading to its transfer to the crab. *C. tricolor* also transferred to *H. epheliticus*, but without such activity being exhibited by the crab. From various observations it appears that if *H. epheliticus* assists the transfer of *C. tricolor*, it does so on a less direct way than the pagurid *Dardanus*, which is very active toward the anemone, or the majid *Stenocionops*, which displays a very specialized behaviour pattern while transferring its partner (see below). In the Caribbean, *Calliactis tricolor* protects its host, the pagurid *Dardanus venosus* (H. Milne Edwards, 1848), from predation by the calappid crab *Calappa flammea* (Herbst, 1794) (see McLean & Mariscal, 1973).

Another hepatid, *Hepatus pudibundus* (Herbst, 1785), was often observed in eastern South America with one or more sea anemones attached to its carapace (Holthuis, 1959: 168). In aquaria, the crab seized the anemones with its chelipeds and hoisted them overhead to place them on its carapace (Tavares, pers. comm.).

The sea anemone *Sagartia carcinophila* Verrill, 1869, often lives attached to the back

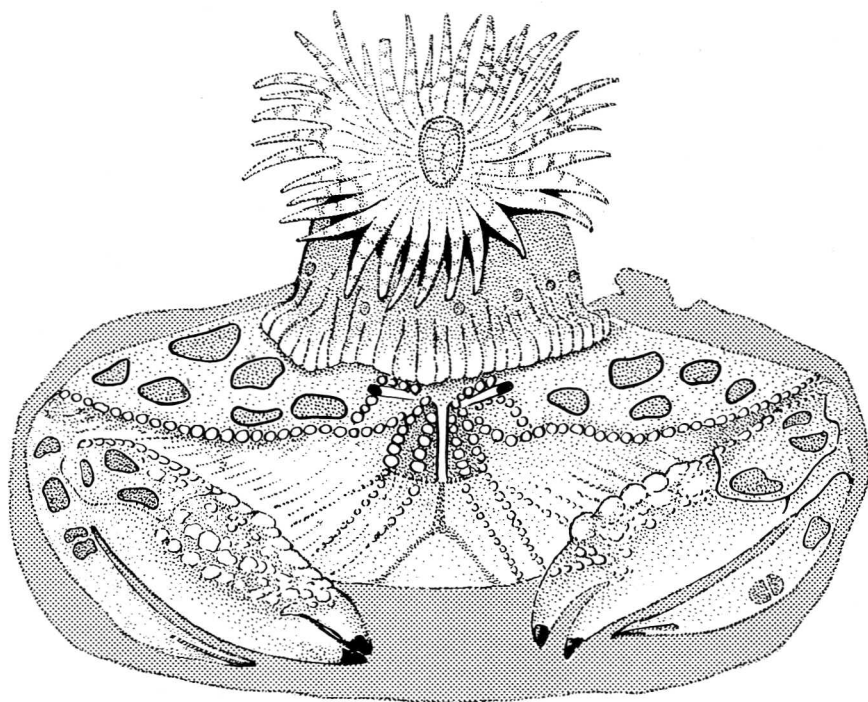


Fig. 7. *Hepatus epheliticus* (Linné, 1763) with its sea anemone (after Carlgren & Hedgpeth, 1952: table 2).



Fig. 8. The majid *Doclea ovis* (Fabricius, 1787), in aquaria. A large female collected off Bedok, 1981, by P. Ng (courtesy of P. K. L. Ng).

of the small hepatid crab *Hepatella amica* Smith, 1869, in the Bay of Panama (Verrill, 1928: 16).

From the above we can say that anemones respond to the smooth and rounded exoskeleton of hepatids, even though they may show preferences for molluscan shells and their pagurids hosts.

An association between a majid, e. g. the genus *Doclea* Leach, 1815, and anemones should be categorised here, because the anemone just seems to adhere to the soft velvet-like pubescence covering the crab's carapace (Fig. 8). Alcock (1902: 67) recorded the decorating behaviour involving sea anemones in spiders crabs of this genus. This was also confirmed by Wagner (1987: 901, pl. 1) in *D. ovis* (Fabricius, 1787): it usually carries anemones and, when they are removed, will place them back onto the dorsal part of the carapace (see also Tan & Ng, 1988, 1992: 149). P. K. L. Ng (*in litt.* 31 Mar. 1995) provided to us the following observations. Of the several *Doclea* species found in Singapore, only *D. ovis*, and mostly when it is adult, is known to have this habit. Large specimens, especially females, carry 2-4 anemones of varying sizes on their back. Only in one case, a small individual (ca. 15 mm carapace width) was seen carrying a small anemone on its back. The anemones attach themselves their sole to the dense velvet-like setae of the crab's carapace. During the day, the crabs themselves hide in the sand/mud, and only the anemones are obvious. When one physically detaches the anemones from the crab and leaves them next to it, the crab "plants" the anemones back. Ng observed the crab gently prodding the base of the anemones to encourage them to release their grip and then the crab repositioning the anemones on its back.

#### 4. Association between spider crabs and anemones

Several accounts of relationships between spider crabs and anemones have been based on aquarium observations. Thomson (1923) observed at Roscoff, both in the field and in aquaria, that *Macropodia rostrata* (Linné, 1761) (referred to as *Stenorhynchus phalangium*) consistently attached to the columns of *Anemonia viridis* (Forsskål, 1775) [= *A. sulcata* (Pennant, 1766)] as to be concealed by the tentacles. Davenport (1962) showed that young of *Hyas araneus* (Linné, 1758) associated with *Tealia felina* (Linné, 1761) (= *Urticina felina*) in aquaria. Similarly, Schrieken (1966: 276) observed in the Netherlands the relationship between *Hyas coarctatus* Leach, 1815, and *Tealia felina* and between *Macropodia rostrata* and *Anemonia viridis*. It was described how the crab tapped the anemone with its second legs. These associations seem to be facultative.

Hartnoll (1970: 37) showed during observations near Port Erin Bay, England, that the majid *Inachus phalangium* (Fabricius, 1775) was the only crab regularly found associated with sea anemones, especially with the snakelocks sea anemone, *Anemonia viridis*. *Tealia felina* was also common in the area, but it was never found accompanied by crabs. Other mentioned majids while occurring locally were not found in association with sea anemones. It was further observed that the crab usually stood on the substrate with the posterior part of the carapace against the anemone's column, which was often grasped with the fourth and fifth pereopods (Hartnoll, *ibid.*, fig. 1). *Anemonia viridis* was found to be suitable as a host mostly because of its inability to retract its tentacles, which completely concealed the crab. No touching behaviour from the part of the crab was observed, except feeling with the P4 and P5. Hartnoll concluded that there was a mutual benefit in terms of food between the two

organisms and further that the crab was immune to the sea anemone's nematocysts. Weinbauer et al. (1982: 143) studied the relationship of *Inachus phalangium* and *Anemonia* in their natural environment and observed that the crab normally moved with impunity between the tentacles. Treating the crab's surface with acetone removed its protection and resulted in a feeding response by the anemone. Immunity was regained only after the crab repeatedly contacted the anemone's tentacles.

The same association has been studied in the field in the Banyuls region, south France, by Wirtz & Diesel (1983) and Diesel (1986a, b; 1988). More than twenty crustacean species, besides *Inachus phalangium*, live in association with *Anemonia viridis* in the Mediterranean. While Hartnoll (1970) found *Inachus* both in association with *Anemonia* and living on its own in the North Sea, Diesel found that in the Mediterranean the crabs are obligate associates of sea anemones. Most crabs established relationships with *Anemonia* that lasted for several days, some being associated with the same individual for longer than a month. Crabs left the protection of their host to feed, moult, flee from larger conspecifics and search for a sexual partner. This mate searching strategy led males to learn the position of sea anemones harbouring females and the time when these were to spawn. This allowed males to arrive punctually to fertilize the next brood (see also Christy, 1987). The *Inachus-Anemonia* symbiosis is discussed by Shick (1990). Chintiroglou who made observations on *Inachus phalangium* in the Aegan Sea, concluded that the crab seems protected by the sea anemone, evading cephalopods, the main predators of crabs (Wells, 1978).

Another majid crab, *Mithrax (Mithraculus) commensalis* Manning, 1970 (pp. 157-160), from the West Indies, was collected from the disc of a broad, brown sea anemone which aggregated in large colonies. The biology of this species was investigated by Patton (1979: 55-61), who considered it a synonym of *M. cinctimanus* (Stimpson, 1860). In Discovery Bay, Jamaica, Patton recorded that juveniles of *M. cinctimanus* inhabited anemones in a rather temporary association, while the adults seemed to be free living. *M. cinctimanus* was found most frequently on the flat and short tentacles of the anemone *Stoichactis helianthus* (Ellis) and sometimes among the long, stout tentacles of *Condylactis gigantea* (Weiland). In laboratory situations, crabs always moved into associations with one or another anemone, rather than hiding under stones and pieces of coral, showing that an association with a sea anemone was strongly preferred. The experiments showed that the protection of *Mithrax* from host's nematocyst discharge depended on continued association (about seven days), since crabs isolated for only two or three days were stung. Patton concluded that, probably as in the case of anemone fish, the crabs achieve protection by virtue of host substances absorbed on their bodies. At Grand Bahama Island the same majid was seen associated with the anemones *Lebrunia danae* (Duchassaing & Michelotti, 1866) and *Bartholomea annulata* Lesueur, 1817 (Herrnkind et al., 1976).

## DISCUSSION

Based on our research we can state that the species of brachyuran crabs and anemones that live in symbioses fall into a relatively restricted number of taxonomic groups.

### Brachyuran crabs.

I. As a rule, carrying behaviour employing the last walking legs may be considered a



characteristic of the more primitive crabs, ie the section Podotremata Guinot, 1977, where the last pereopods are no longer functional for locomotion and are specially modified to hold an object, with the exception of Raninoidea which are burrowers (Guinot, 1993b). Examples of carrying behaviour are reported in several families. The dynomenids, although phylogenetically close to the carrying dromiids, and poupiniids (close to the carrying homolids) probably do not exhibit a carrying behaviour.

This kind of adaptation is found only in one heterotrematous family, the Dorippidae, whose last pereopods are similar to those of the dromiids.

1. Section Podotremata Guinot, 1977: always with P4 + P5, or only P5.

– Homolodromiidae Alcock, 1900. No carrying behaviour known in this archaic family (Guinot, 1995). The dorsal surface of the carapace, although weakly calcified and thin, is not very soft (only the branchiostegite, on the latero-ventral parts of the cephalothorax, is completely soft). The whole body is often ornamented with granules, spines and very dense hairs. The P4 and P5 are dorsal and possess a subchelate or chelate apparatus that may function in the same way as in the Dromiidae. No reports of carrying behaviour exists.

– Dromiidae de Haan, 1833. Carrying behaviour obligate (the dorsal surface of the carapace is soft), except in the most advanced genera in which the carapace is hard and even ornamented with granules and/or setae. The carried object is held close to the carapace. Symbiosis with sponges is frequent, but rare with sea anemones.

– Dynomenidae Ortmann, 1892. No carrying behaviour recorded in this small family. The dorsal carapace is hard, sometimes ornamented. The reduced P5, sometimes ending in a tiny chela, seems not to be prehensile, due to their position between the body and the P4. There is no report of carrying behaviour. No associated organisms have been found with the crabs deposited in museum collections.

– Cyclodorippoidea Ortmann, 1892. Carrying behaviour is known only in one genus of this group. Perhaps not uncommon, at least in those species where the last pairs of pereopods are not too much reduced.

– Homolidae de Haan, 1839. Carrying behaviour frequent, perhaps permanent, generally with sponges. The different species show many varied apparatuses at the end of P5. The P5 ends in a small chela in the genus *Homolochunia*. The carried object is held upraised, far from the carapace. An association with a sea anemone is described in the present paper: *Hypsophrys inflata* Guinot and Richer de Forges, 1981, with *Isanthus* sp.

– Latreilliidae Stimpson, 1858. Only one example reported, but doubtful.

– Poupiniidae Guinot, 1991. Probably no carrying behaviour.

2. Section Heterotremata Guinot, 1977.

– Dorippoidea, family Dorippidae MacLeay, 1838. With P4 + P5.

- Subfamily Dorippinae MacLeay, 1838. Two known anemone-carrying species: *Dorippoides facchino* (Herbst, 1785) and *Paradorippe granulata* (de Haan, 1841).

- Subfamily Ethusinae Guinot, 1977. One known anemone-carrying species: *Ethusa mascarone* (Herbst, 1785).

– Xanthoidea, family Xanthidae MacLay, 1838. With P1.  
 - Subfamily Polydectinae Dana, 1852. Carrying behaviour involving the first pair of pereopods (chelipeds or P1) in all species of the genera *Lybia* H. Milne Edwards, 1837, and *Polydectus* H. Milne Edwards, 1837. Only with tiny anemones.

– Parthenoxystomata Guinot, 1967, family Hepatidae Stimpson, 1871. Only with anemones, which probably find a smooth shell-like surface. *Hepatus chiliensis* H. Milne Edwards, 1837; *Hepatus epheliticus* (Linné, 1763); *Hepatus pudibundus* (Herbst, 1785); and *Hepatella amica* Smith, 1869.

The same habit has been observed in the majid genus *Doclea* Leach, 1815, especially in *D. ovis* (Fabricius, 1787), the anemone being attached on the velvet-like pubescence of the carapace and not to hooked setae (cf. *infra*).

– Majoidea, family Majidae Samouelle, 1819. Carrying behaviour is found in several majids, the hooked setae of which bear different objects.

1) Anemone-carrying: *Inachus phalangium* (Fabricius, 1775); *Maja squinado* (Herbst, 1788); *Halimus* sp.; *Loxorhynchus crispatus* Stimpson, 1857; *L. grandis* Stimpson, 1857; *Leptomithrax longipes* (Thomson, 1902); and *Stenocionops furcata* (Olivier, 1791).

2) Anemone-living: *Inachus phalangium* (Fabricius, 1775); *Mithrax* (*Mithraculus*) *commensalis* Manning, 1970; and *M. (Mithraculus) cinctimanus* (Stimpson, 1860).

## Sea anemones

Order Corallimorpharia Carlgren, 1949

Family Corallimorphidae R. Hertwig, 1882

Genus *Corynactis* Allman, 1846

*Corynactis californica* Carlgren, 1936

Family Actinodiscidae Carlgren, 1938

Genus *Actinodiscus* de Blainville, 1830 (= *Discosoma* Ehrenberg, 1834)

Order Actiniaria Carlgren, 1938

Family Boloceroididae Carlgren, 1924

Genus *Bunodeopsis* Andres, 1880

Genus *Bartholomea* Lesueur, 1817

*Bartholomea annulata* Lesueur, 1817

Genus *Triactis* Klunzinger, 1877

*Triactis producta* Klunzinger, 1877

Family Actiniidae (Gosse, 1858)

Genus *Anemonia* Risso, 1826

*Anemonia viridis* (Forsskål, 1775) (= *A. sulcata* Pennant, 1766)

Genus *Bolocera* Gosse, 1860

Genus *Tealia* Gosse, 1858

*Tealia felina* (Linné, 1767)

Genus *Bunodactis* Verrill, 1899

*Bunodactis chrysobathys* Parry, 1951

*Bunodactis nigrescens* Verrill, 1928 (= *Tealiopsis nigrescens* Verrill, 1928)

Sub-Tribe Mesomyaria Stephenson, 1921

Family Isanthidae Carlgren, 1938

Genus *Isanthus* Carlgren, 1938

- Isanthus*, new species (in preparation)  
 Family Actinostolidae Carlgren, 1932  
     Genus *Antholoba* R. Hertwig, 1882  
         *Antholoba achates* (Dana, 1949)  
 Family Isophelliidae Stephenson, 1935  
     Genus *Telmatactis* Gravier, 1918  
         *Telmatactis decora* (Hemprich & Ehrenberg, 1834)  
 Family Hormathiidae Carlgren, 1925  
     Genus *Paracalliactis* Carlgren, 1928  
         *Paracalliactis rosea* Hand, 1975  
     Genus *Calliactis* Verrill, 1869  
         *Calliactis tricolor* (Lesueur, 1811)  
         *Calliactis conchicola* Parry, 1952  
         *Calliactis parasitica* (Couch, 1838) (= *Adamsia rondeletii* Andres, 1883)  
     Genus *Adamsia* Forbes, 1840  
         *Adamsia palliata* (Boahadsch, 1761)  
         *Adamsia paguri* (Verrill, 1869) (= *Sagartia paguri*)  
 Family Sagartiidae Gosse 1858  
     Genus *Sagartia* Gosse, 1855  
         *Sagartia pugnax* Verrill, 1928  
         ? *Sagartia carcinophilea* Verrill, 1869  
     Genus *Phellia* Gosse, 1858  
         *Phellia aucklandica* Carlgren, 1924  
 Family Aiptasiidae Carlgren, 1924  
     *Lebrunia danae* (Duchassaing & Michelotti, 1860)

## Behaviour pattern

The associations between brachyuran crabs and sea anemones can be classified as mutualistic and regarded as behavioural associations because behavioural rather than physiological adaptations dominate the interactions between the partners (Castro, 1988: 169).

Ross (1974: table 1) has reviewed the interactions between hermit and brachyuran crabs and sea anemones, emphasizing the behavioural contribution of each of them in the detachment of the anemone prior to settlement on the host brachyuran crab or gastropod shell occupied by a host hermit crab.

1) The detachment behaviour is the result of the activity of the anemone alone in the associations *Hepatus chilensis*/*Antholoba achates*; *Hepatus epheliticus*/*Calliactis tricolor*. In that case the crustacean's exoskeleton-climbing seems an extension of the habit of shell-climbing to the shells inhabited by hermit crabs. *Calliactis tricolor* finds in the crab's carapace a similar support as with *Dardanus*, thereby gaining the advantage of transportation.

2) The detachment behaviour is the result of the activity of the crab alone in the associations *Stenocionops furcata*/*Calliactis tricolor*; *Leptomithrax longipes*/*Calliactis conchicola* or *Paracalliactis rosea*; *Hepatus pudibundus*/sea anemone; *Hepatella amica*/*Sagartia carcinophilea*.



Plate 1. A - *Hypsophrys inflata* Guinot & Richer de Forges, 1981, holding its sea anemone, *Isanthus* sp. with its P5, French Polynesia, Tuamotu archipelago, Mururoa atoll, 500 m (MNHN-B 24343) (J. Poupin coll. and fotogr., courtesy of J. Poupin).



Plate 1. B - *Dorippe facchino* (Herbst, 1785), the porter crab, off the East coast of Singapore, with its sea anemone *Cancrisocia expansa* Stimpson, on its carapace (live colour; background not natural) (P. Ng coll. 1981, and fotogr.; courtesy of P. K. L. Ng).





Plate 2. A - *Neodorippe callida* (Fabricius, 1798), the leaf porter crab, common in Malaysian and Singapore waters, swimming upside down with a leaf held by the P5 and covering its back (courtesy of P. K. L. Ng, 1987, after Ng & Tan, 1986).



Plate 2. B. - *Homola orientalis* Henderson, 1888, with its sponge (detached), French Polynesia, Tuamotu archipelago, Fangataufa atoll, 250 m, J. Poupin coll. (MNHN-B 24555) (courtesy of J. Poupin).



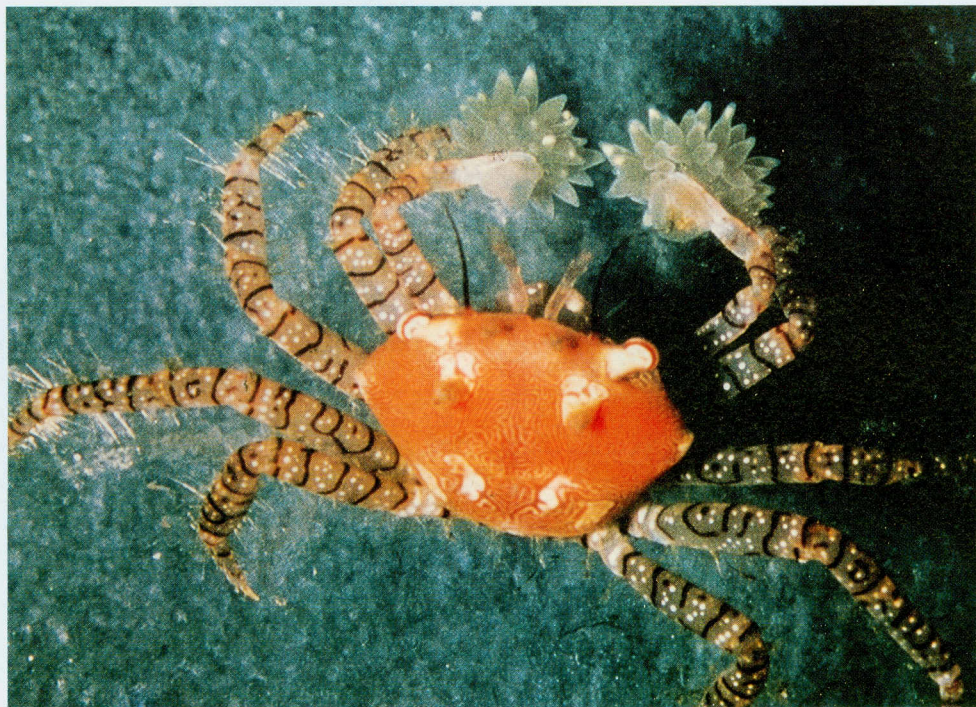


Plate 3. A - *L. edmondsoni* Takeda & Miyake, 1970, from Kaneohe Bay, Oahu, Hawaii, holding a sea anemone in each cheliped (P. Castro coll. and fotogr.; courtesy of P. Castro).



Plate 3. B - *Polydectus cupulifer* (Latreille, 1812), from Kaneohe Bay, Oahu, Hawaii, holding a sea anemone in each cheliped (P. Castro coll. and fotogr.; courtesy of P. Castro).

The carrying behaviour of Homolidae, as in *Hypsophrys inflata*, and of all other crabs with specialized last pair of legs (many Podotremata and Heterotremata Dorippidae) fall under the second category. The transfer of a sea anemone sitting on a shell to the carapace of some dorippid species seems to depend only on the activity of the crab. In the obligate partnership of *Lybia* and *Polydectus* with sea anemones held by the claws, the crab is obviously the active member but some degree of cooperation seems to be obtained by the sea anemone.

The evolution, in certain brachyuran crabs, of active behavioural patterns towards the establishment of symbioses with sea anemones is also important from a phylogenetic point of view. The carrying behaviour is a common tendency in podotrematous crabs (Guinot 1993a) and it parallels the relationships of these primitive crabs to those of the anomuran crabs. Wicksten (1982: 307) expressed the idea that the use of only the anterior two pair of walking legs for locomotion in the cyclodorippid *Deilocerus* (= *Clythrocerus*) *planus* (Rathbun, 1900) resulted in movements similar to those of anomurans which carry shells. Dorippids and Majids can in the same way be considered as primitive in the Heterotremata-Thoracotremata assemblage. In brachyuran crabs, therefore the loss of the camouflage may be regarded as an advanced behaviour.

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#### LITERATURE CITED

- Alcock, A., 1896. Materials for a Carcinological Fauna of India. N°2. The Brachyura Oxystomata. *J. Asiat. Soc. Beng.*, **65** (2): 134-296, pls 6-8.
- Alcock, A., 1902. *A naturalist in Indian seas*. London, John Murray, 328 pp., 98 figs, 2 tables.
- André, M., 1937. Coquilles vides de Bivalves habitées par des Crustacés. *J. Conchiliol.*, **81** : 72-81, figs 1, 2.
- Aurivillius, C. W. S., 1889. Die Maskierung der oxyrhynchen Dekapoden durch besondere Anpassungen ihres Körperbaues vermittelt. *Svensk. Vet. Akad. Handl.*, **23** (4): 1-72, pls 1-5.

- Báez, R., P. & J. W. Martin, 1989. Crabs of the family Homolodromiidae. I. Description of the male of *Homolodromia robertsi* Garth, 1973, based on specimens from deep waters off the coast of Chile. *J. Crust. Biol.*, **9** (3): 492-500, figs 1-3, table 1.
- Balss, H., 1924. Über Anpassungen und Symbiose der Paguriden. Eine Zusammenfassende Übersicht. *Z. Morph. Ökol. Tiere*, (1): 752-792, figs 1-35, tables 1-3.
- Balss, H., 1956. Decapoda. In: *H. G. Bronns Klassen und Ordnungen des Tierreichs*, Fünfter Band. I. Abteilung. 7. Buch. 11. Lieferung. Leipzig, Akademische Verlagsgesellschaft, pp. 1369-1504.
- Barry, A. de, 1879. Die Erscheinungen der Symbiose. Strassburg, K. J. Trübner, 30 pp.
- Borradaile, L. A., 1902. Marine Crustaceans. III. The Xanthidae and some other crabs. In: J. S. Gardiner (ed), *The Fauna and Geography of the Maldive and Laccadive Archipelagoes*, **1** (3): 237-271, figs 41-60.
- Borradaile, L. A., 1903. Marine Crustaceans. IX. The Sponge-crabs (Dromiacea). In: J. S. Gardiner (ed), *The Fauna and Geography of the Maldive and Laccadive Archipelagoes*, **2** (1): 574-578, pl. 33.
- Bürger, O., 1903. Ueber das Zusammenleben von *Antholoba reticulata* Couth. und *Hepatus chilensis* M. E. *Biol. Centralbl.*, **23** (20): 678-679.
- Burton, M., 1969. *Animal Partnerships*. New York and London, F. Warne, 107 pp.
- Carlgren, O., 1938. South African Actiniaria and Zoantharia. *K. svenska vetensk. Akad. Handl.*, (30), **17** (3): 1-141.
- Carlgren, O., 1949. A survey of the Ptychodactylaria, Corallimorpharia and Actiniaria. *K. svenska vetensk. Akad. Handl.*, (4) **1** (1): 1-121, 4 pls
- Carlgren, O. & J. W. Hedgpeth, 1952. Actiniaria, Zoantharia and Ceriantharia from Shallow Water in the Northwestern Gulf of Mexico. *Publ. Inst. Mar. Sci.*, University of Texas, **2** (2): 142-172, figs 1-9.
- Castro, P., 1976. Brachyuran Crabs Symbiotic with Scleractinian Corals: A Review of their Biology. *Micronesica*, **12** (1): 99-110.
- Castro, P., 1988. Animal Symbioses in Coral Reef Communities: a Review. *Symbiosis*, **5** : 161-184.
- Catala, R., 1979. *Offrandes de la mer*. Tahiti, Les Editions du Pacifique, 336 pp.
- Caullery, M., 1950. *Le parasitisme et la symbiose*. Paris, G. Doin, 2e édit., 358 pp. , 80 figs.
- Chintiroglou, C. C., D. Doumenc & D. Guinot, in press. Anemone-carrying behaviour in a deep-water homolid crab (Crustacea, Decapoda, Brachyura, Podotremata), *Crustaceana*.
- Chopra, B. N., 1935. Further Notes on Crustacea Decapoda in the Indian Museum. III. On the Decapod Crustacea collected by the Bengal Pilot Service off the Mouth of the River Hughli. Dromiacea and Oxystomata. *Rec. Indian Mus.*, **35** (1): 25-52, figs 1-7.
- Christy, J. H., 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. *Bull. Mar. Sci.*, **4** (2): 177-191, tables 1-3.
- Church, R. R., 1971. Deepstar explores the ocean floor. *Natn. geogr. Mag.*, **139** (1): 110-129.
- Cousteau, J.-Y., 1965. *World without sun*. New York, Harper and Row, 265 pp.
- Cutress, C., D. M. Ross & L. Sutton, 1970. The association of *Calliactis tricolor* with its pagurid, calappid, and majid partners in the Caribbean. *Canadian J. Zool.*, **48** (2): 371-376, pls 1-2.



- Dales, R. P., 1957. Interrelations of organisms. A. Commensalism. In: J. W. Hedgpeth (ed), Treatise on marine Ecology and Palaeoecology. Vol. 1. *Geol. Soc. Am. Mem.*, 67: 391-412.
- Dana, J. D., 1852. Crustacea. Part 1. In: *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N.* Philadelphia: C. Sherman, 13, VIII+685 pp.
- Davenport, D., 1962. Physiological notes on actinians and their associated commensals. *Bull. Inst. océanogr., Monaco*, 1237: 1-15.
- Debelius, H., 1983. *Armoured Knights of the Sea*. Kernen Verlag, 120 pp.
- Dembowska, W. S., 1926. Study on the habits of the crab *Dromia vulgaris* M. E. *Biol. Bull. Mar. Biol. Lab. Woods-Hole*, 50: 162-178, figs 1, 2.
- Diesel, R., 1986a. Optimal Mate Searching Strategy in the Symbiotic Spider Crab *Inachus phalangium* (Decapoda). *Ethology*, (72): 311-328, figs 1-15.
- Diesel, R., 1986b. Population dynamics of the commensal spider crab *Inachus phalangium* (Decapoda: Maiidae). *Mar. Biol.* (91): 481-489, figs 1-10, tables 1-4.
- Diesel, R., 1988. Male-female association in the spider crab *Inachus phalangium*: the influence of female reproductive stage and size. *J. Crust. Biol.*, 8 (1): 63-69, fig. 1-5.
- Döderlein, L., 1883. Faunistische Studien in Japan. Enoshima und die Sagami Bay. *Arch. Naturgesch. (Berlin)*, 49 (1): 102-103, pl. 2.
- Doumenc, D., 1975. Actinies bathyales et abyssales de l'océan Atlantique nord. Famille des Hormathiidae (genres *Paracalliactis* et *Phelliactis*) et des Actinostolidae (genres *Actinoscyphia* et *Sicyonis*). *Bull. Mus. natl. His. nat., Paris*, 3e sér. (287) Zool., 197 : 157-206, figs 1-8, maps 1-3, pls 1, 2.
- Duerden, J. E., 1905. On the habits and reactions of crabs bearing Actinians in their claws. *Proc. J. Zool. Soc. Lond.*, 2: 494-511.
- Edmondson, C. H., 1946. Reef and Shore Fauna of Hawaii. *Spec. Publs Bernice Bishop Mus.*, (22): III + 381 p., 223 figs.
- Edmondson, C. H., 1962. Xanthidae of Hawaii. *Occ. Pap. Bernice P. Bishop Mus.*, 22 (13): 215-309, figs 1-34.
- Estampador, E. P., 1937. A Check List of Philippine Crustacean Decapods. *Philipp. J. Sci.*, 62 (4): 465-559.
- Estampador, E. P., 1959. Revised Check List of Philippine Crustacean Decapods. *Nat. appl. Sci. Bull. Univ. Philipp.*, (Quezon City, Philippines), 17 (1): 1-127.
- Fenizia, G., 1935. La *Dromia vulgaris* (M. Edw.) e le sue abitudini. *Arch. Zool. Ital.*, 31: 509-539.
- Fenizia, G., 1937. Sull'istinto di mascheramento dell'*Ethusa mascarone* Herbst. *Bull. Inst. Oceanogr. Monaco*, (732), 1-15, figs 1-5.
- Garth, J. S., 1946. Littoral brachyuran fauna of the Galapagos Archipelago. *Allan Hancock Pacif. Exped.*, 5 (10): i-iv+341-600, fig 1, pls 49-87.
- Gordon, I., 1950. Crustacea Dromiacea. Part I: Systematic account of the Dromiacea collected by the "John Murray" Expedition. Part II: The morphology of the spermatheca in certain Dromiacea. *Scient. Rep. John Murray Exped. 1933-34*, 9 (3): 201-253, figs 1-26, pl. 1.
- Gravely, F. H., 1941. Shells and other animals remains found on the Madras beach. I. Groups other than snails, etc. (Mollusca Gastropoda). *Bull. Madras Govt Mus.*, new series (Natural History), 5 (1): 1-112, 30 figs.

- Griffin, D. J. G. & H. A. Tranter, 1986. The Decapoda Brachyura of the Siboga Expedition. Part VIII. Majidae, in *Siboga Exped.*, Monogr. 39C4, livr. 148, 1-335, figs 1-112, pls 1-22.
- Grigg, R. W., 1977. *Hawai 's précieux coral*. Island Heritage, 64 pp.
- Guinot, D., 1966-1977. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyours. I. Les affinités des genres *Aethra*, *Osachila*, *Hepatus*, *Hepatella* et *Actaeomorpha*. *Bull. Mus. natl Hist. nat., Paris*, 1966, (2) 38 (5): 744-762, figs. 1-24; 1966 (1967), (2) 38 (6): 828-845, figs. 25-41.
- Guinot, D., 1976. Constitution de quelques groupes naturels chez les Crustacés Décapodes Brachyours. I. La superfamille des Bellioidea et trois sous-familles de Xanthidae (Polydectinae Dana, Trichiinae de Haan, Actaeinae Alcock). *Mém. Mus. natn. Hist. nat., (A), Zool.*, 97: 1-308, figs 1-47, pls 1-19.
- Guinot, D., 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyours. *C. r. hebdomadaire. Séanc. Acad. Sci., Paris*, (D) 285: 1049-1052.
- Guinot, D., 1978a. Principes d'une classification évolutive des Crustacés Décapodes Brachyours. *Bull. biol. Fr. Belg.*, n.s., 112 (3): 211-292, figs 1-3, 1 table.
- Guinot, D., 1978b. Analyse morphogénétique d'une lignée de Crabes: la lignée "parthénostomienne" et position systématique du genre *Drachiella* Guinot (Crustacea, Decapoda, Brachyura). In: Volume jubilaire du Professeur Pierre Drach. *Archs Zool. exp. gén.*, 119 (1): 7-20, figs 1-3, pls 1-4.
- Guinot, D., 1991. Etablissement de la famille des Poupiniidae pour *Poupinia hirsuta* gen. nov., sp. nov. de Polynésie (Crustacea, Decapoda, Brachyura: Homolidae). *Bull. Mus. natl Hist. nat., Paris*, 4e sér., 1990 (1991), sect. A, 12 (3-4): 577-605, figs 1-12, pls 1-3.
- Guinot, D., 1993a. Données nouvelles sur les Crabes primitifs (Crustacea Decapoda Brachyura Podotremata). *C. R. Acad. Sci. Paris*, (III) 316 (10): 1225-1232, fig. 1-8.
- Guinot, D., 1993b. Données nouvelles sur les Raninoidea de Haan, 1841 (Crustacea Decapoda Brachyura Podotremata). *C. R. Acad. Sci. Paris*, (III) 316 (11): 1324-1331, fig. 1-7.
- Guinot, D., 1995. Crustacea Decapoda Brachyura: Révision de la famille des Homolodromiidae Alcock, 1900. In: A. Crosnier (ed), Résultats des Campagnes Musorstom. Volume 13. *Mém. Mus. nat. Hist. nat.*, 13: 155-282, figs 1-42.
- Guinot, D. & B. Richer de Forges, 1981. Homolidae, rares ou nouveaux, de l'Indo-Pacifique (Crustacea, Decapoda, Brachyura). *Bull. Mus. natl Hist. Nat., Paris* (4) 3 (2): 523-581, figs 1-7, pls 1-8.
- Guinot, D. & B. Richer de Forges, 1995. Crustacea Decapoda Brachyura: Révision de la famille des Homolidae de Haan, 1839. In: A. Crosnier (ed), Résultats des Campagnes Musorstom. Volume 13. *Mém. Mus. nat. Hist. nat.*, 13: 283-517, figs 1-76.
- Hand, C., 1975. Behaviour of some New Zealand sea anemones and their molluscan and crustacean hosts. *New Zealand J. Mar. Freshwater Res.*, 9 (4): 509- 527, table 1.
- Hartnoll, R. G., 1970. The relationship of an amphipod and a spider crab with the snakelocks anemone. *Ann. Rep. Mar. Biol. Stn Port Erin*, 83: 37-42, fig. 1.
- Hartnoll, R. G., 1993. The epibiota of spider crabs. *Bios*, 1 (1): 164-176, tables 1-4.
- Hartog, J. C. den, 1990. Associated occurrence of *Cyclocoeloma tuberculata* Miers, 1880 (Decapoda: Majidae) and species of Discosomatidae (Anthozoa: Corallimorpharia). *Zool. Meded. Leiden*, 64 (12): 161-168, figs 1-5, table 1.
- Haworth, A. H., 1825. A new binary Arrangement of the Brachyurous Crustacea. XVII. *Philos. Mag. J.*, 65 (322): 105-106.

- Henderson, J. R., 1893. A Contribution to Indian Carcinology. *Trans. Linn. Soc. Lond.*, (2) 5 : 325-458, pls 36-40.
- Herbst, J. F. W., 1782-1804. *Versuch einer Naturgeschichte der Krabben und Krebse*. Berlin und Stralsund, 3 vol., 274+226+(216) pp., 72 pls.
- Herrnkind, W., G. Stanton & E. Conklin, 1976. Initial characterization of the complex associated with the anemone, *Lebrunia danae*, at Grand Bahama. *Bull. Mar. Sci.*, 26 : 65-71.
- Hildebrand, H. H., 1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. *Publ. Inst. Mar. Sci.*, Texas, 3 (2): 233-266.
- Hildebrand, H. H., 1955. A study of the fauna of the pink shrimp (*Penaeus duorarum* Burkenroad) grounds in the Gulf of Campeche. *Publ. Inst. Mar. Sci.*, Texas, 4 (1): 169-232.
- Holthuis, L. B., 1959. The Crustacea Decapoda of Suriname (Dutch Guiana). *Zool. Verh., Leiden*, (44): 1-296, figs 1-68, pls 1-16.
- Holthuis, L. B. & R. B. Manning. 1990. Crabs of the Subfamily Dorippinae MacLeay, 1838, from the Indo-West-Pacific Region (Crustacea: Decapoda: Dorippidae). *Res. Crust.*, Tokyo, spec. n° 3: 1-151, figs 1-58.
- Hornell, J. S., 1922. Some commensals of Indian Alcyonarians and Crabs. *J. Bombay Nat. Hist. Soc.*, 28 (4): 926-936, 6 figs.
- Hose, C., 1929. *The field-Book of a Jungle-Wallah being a Description of Shore, River and Forest Life in Sarawak*. London, Oxford University Press, 1985 edition, VIII+216 pp., 14 pls.
- Jamieson, B. G. M., 1994. Phylogeny of the Brachyura with particular reference to the Podotremata: evidence from a review of spermatzoal ultrastructure (Crustacea, Decapoda). *Philos. Trans. Roy. Soc. London*, (B) 345 : 373-393, figs 1-10.
- Kalk, M., 1958. The general ecology of the shores of Inhaca Island. The Crustacea of Inhaca shores. In: W. Macnae and M. Kalk (ed), *A Natural History of Inhaca Island, Moçambique*. Johannesburg, Witwatersrand, 31-83 pp., figs 1-19.
- Kobyakowa, Z. I., 1955. [Stomatopoda and Decapoda]. In: E. N. Pavlovskii (ed) [*Atlas of the Invertebrates of the Far Eastern Seas of the U. S. S. R.*]. SSSR, Moscow/Leningrad, Akademiya Nauk, 146-158 pp., pls 34-41. (In Russian ).
- Kobyakowa, Z. I., 1966. [Stomatopoda and Decapoda]. In: E. N. Pavlovskii (ed) [*Atlas of the Invertebrates of the Far Eastern Seas of the U. S. S. R.*] Moscow/Leningrad, Akademiya Nauk SSSR, 200-215 pp. [Translation of the 1955 book by the Smithsonian Institution and National Science Foundation, Jerusalem].
- Lanchester, W. F., 1900. On a Collection of Crustaceans made at Singapore and Malacca. Part I. Crustacea Brachyura. *Proc. zool. Soc. Lond.* 1900: 719-770, pls 44-47.
- Lanchester, W. F., 1902. On the Crustacea Collected During the "Skeat" Expedition to the Malay Peninsula, Together with a Note on the Genus *Actaeopsis*, Part 1.- Brachyura, Stomatopoda, and Macrura. *Proc. Zool. Soc. London*, (2) 1901 (1902): 534-574, pls 33, 34.
- Latreille, P. A., 1825-1828. *Encyclopédie Méthodique. Histoire Naturelle. Entomologie, ou Histoire naturelle des Crustacés, des Arachnides et des Insectes*. Tome X par MM. Latreille, Le Peletier de Saint-Fargeau, Serville et Guérin [-Méneville]. Paris, Pt 1, pp. 1-344. Pt 2, 1828, pp. 345-832.
- Levin, S., 1976. Decapoda. In: A. N. Golikov *et al.* (ed), *Animals and Plants of Peter the Great Bay*. Leningrad, Akademia Nauk SSSR, pp. 49-56. (In Russian).
- Lenhoff, M. H., 1965. Some physicochemical aspects of the macro- and microenvironments surrounding *Hydra* during activation of their feeding behavior. *Amer. Zoologist*, (5): 515-524.

- Lim, S. S. L., P. K. L. Ng, L. W. H. Tan & W. Y. Chin, 1994. *Rhythm of the Sea. The Life and Times of Labrador Beach*. Singapore, Nanyang Technological University, School of Science, 160 pp.
- Macnae, W. & M. Kalk, 1962. The fauna and flora of sand flats at Inhaca Island, Moçambique. *J. Anim. Ecol.*, **31** (1): 93-128, figs 1-5, table 1.
- Manning, R. B., 1970. *Mithrax (Mithraculus) commensalis*, a new West Indian spider crab (Decapoda, Majidae) commensal with sea anemone. *Crustaceana*, **19** (2): 157-160, figs 1, 2, pl. 1.
- Manning, R. B., 1993. The scientific contributions of Williams Stimpson, an early American naturalist and taxonomist. In: F. Truesdale (ed), *History of Carcinology*, Vol. 8 of *Crustacean Issues*, F. R. Schram (ed). Rotterdam/Brookfield, A. A. Balkema, pp. 109-117.
- McLay, C. L., 1982. Population Biology of the Sponge Crab *Cryptodromia hilgendorfi* (Dromiacea) in Moreton Bay, Queensland, Australia. *Mar. Biol.*, **70**: 317-326, figs 1-11, tables 1-3.
- McLay, C. L., 1983. Dispersal and use of sponges and ascidians as camouflage by *Cryptodromia hilgendorfi* (Brachyura: Dromiacea). *Mar. Biol.*, **76**: 17-32, figs 1-12, tables 1-11.
- McLay, C. L., 1988. Brachyura and crab-like Anomura of New Zealand. *Leigh Lab. Bull.*, (22): i-v+1-463, figs 1-85.
- McLay, C. L., 1993. The Sponge Crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera. In: A. Crosnier (ed), *Résultats des Campagnes Musorstom*, Volume 10. *Mém. Mus. natn. Hist. nat.*, (A) **156**: 111-251, figs 1-19, tables 1-8.
- McLean, R. B. & R. N. Mariscal, 1973. Protection of a hermit crab by its symbiotic sea anemone *Calliactis tricolor*. *Experientia*, **29** (1): 128-130.
- McNeill, F. A. , 1923. Crustacean Camoufleurs. *Aust. Mus. Mag.*, **1** (8): 243-246, 6 figs.
- McNeil, F. A., 1936. Seaweed Crabs and their Camouflage. *Aust. Mus. Mag.*, **6** (2): 57-58, fig. 1.
- Milne Edwards, H., 1837. Les Crustacés, in G. Cuvier, *Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition accompagnée de planches gravées [...] par une réunion des disciples de Cuvier, [...] Paris, Fortin, Masson et Cie. Text, pp. 1-278. Atlas, pls 1-80.*
- Milne Edwards, H., 1849. Les Crustacés, in G. Cuvier, *Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition accompagnée de planches gravées [...] par une réunion des disciples de Cuvier, [...] Paris, Fortin, Masson et Cie. Text, pp. 1-278. Atlas, pls 1-80.*
- Morton, B., 1988. *Partnerships in the sea: Hong Kong's marine symbioses*. Hong Kong University Press, 124 pp.
- Morton, B. & J. Morton, 1983. *The Sea Shore Ecology of Hong Kong*. Hong Kong University Press, 350 pp., 28 pls.
- Newbert, C., 1984. *Within a rainbow sea*. Honolulu, Hawaii, Beyond Words Publ. Company, 208 pp.
- Ng, P. K. L., 1987. The master Camoufleurs. The Upside Down World of the Leaf Porter Crab. *Nature, Malaysiana*, **12** (2): 14-15.
- Ng, P. K. L. & L. W. H. Tan, 1986. The Leaf-carrying Behaviour of *Neodorippe (Neodorippe) callida* (Fabricius, 1798), with a Note on Carrying Behaviour of Dorippid Crabs (Crustacea, Decapoda, Brachyura). *J. Singapore Nat. Acad. Sci.*, **15** : 45-47, 1 fig., 1 table.
- Patton, W. K., 1967. Commensal Crustacea. Proceedings of the Symposium on Crustacea held at Ernakulam from January 12 to 15, 1965. *Mar. Biol. Assoc. India*, (3): 1228-1243.

- Patton, W. K., 1979. On the association of the spider crab, *Mithrax (Mithraculus) cinctimanus* (Stimpson) with Jamaican sea anemones. *Crustaceana*, Suppl. 5 (Studies on Decapoda): 55-61, fig. 1, table 1.
- Paulmier, G., 1993. *Crustacés profonds capturés aux casiers aux Antilles Françaises*. Rapport Ifremer, La Martinique, Laboratoire du Robert, et Neuil/Mer, Station de l'Houmeau, 34 pp., 34 pls.
- Pesta, O., 1918. *Die Decapodenfauna der Adria. Versuch einer Monographie*. Leipzig und Wien, IX+600 pp., 150 figs, 1 map.
- Poupin, J., 1994. *Faune marine profonde des Antilles françaises. Récoltes du navire Polka faites en 1993*. Orstom Editions, Collections Etudes et Thèses, 79 pp, 5 pls.
- Poupin, J., T. Tamarit & A. Vandenboomgaerde, 1990. *Pêches profondes aux casiers sur les pentes océaniques des îles de Polynésie Française. (N/O Marara - 1986/1989)*. Tahiti, Orstom, Océanographie, n°42, 97 pp.
- Rathbun, M. J., 1906. The Brachyura and Macrura of the Hawaiian Islands. *Bull. U. S. Fish Commn*, 23 (3), 1903 (1906): 827-930, I-VIII, figs. 1-79, pls. 1-24.
- Rathbun, M. J., 1910. Brachyura. V. In: The Danish Expedition to Siam 1899-1900. *K. danske Vidensk. Selsk. Skr.*, (7) 5 (4): 301-367, figs 1-44, pls 1-2, 1 map.
- Rathbun, M. J., 1924. Brachyura, Albuneidae and Porcellanidae. 37. In: Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910-1913. *Ark. Zool.*, 16 (23): 1-33, figs 1-7, pl. 1.
- Rathbun, M. J., 1937. The oxystomatous and allied crabs of America. *Bull. U. S. natn. Mus.*, 166: i-vi, 1-278, figs 1-47, pls 1-86, tables 1-87.
- Richters, F., 1980. Decapoda. In: K. A. Möbius, *Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen, bearbeitet von K. Möbius, F. Richters und E. von Martens [...]*. Berlin, Verlag der Guttman'schen Buchhandlung, pp. 139-178, pls 15-18.
- Rodríguez, G., 1993. From Oviedo to Rathbun: The development of brachyuran crab taxonomy in the Neotropics (1535-1937). In: F. Truesdale (ed), *History of Carcinology*, Vol. 8 of *Crustacean Issues*, F. R. Schram (ed). Rotterdam/Brookfield, A. A. Balkema, pp. 41-73.
- Ross, D. M., 1967. Behavioural and ecological relationships between sea anemones and other invertebrates. *Oceanogr. Mar. Biol. Ann. rev.*, 5 : 291-316.
- Ross, D. M., 1971. Protection of hermit crabs (*Dardanus* spp.) from *Octopus* by commensal sea anemones (*Calliactis* spp.). *Nature* (London), 230 (5293): 401-402.
- Ross, D. M., 1974a. Behavior patterns in associations and interactions with other animals. In: L. Muscatine and H. M. Lenhoff, *Coelenterate Biology*. London, San Francisco and New York, Academic Press, pp. 281-312, figs 1-3, tables 1, 2.
- Ross, D. M., 1974b. Evolutionary aspects of associations between crabs and sea anemones. In: W. B. Vernberg (ed), *Symbiosis in the Sea*. Columbia, University of South Carolina Press, 111-125 pp.
- Ross, D. M., 1983. Symbiotic relations. In: F. J. Vernberg and W. B. Vernberg, *Behavior and ecology*, Vol. 7 of *The Biology of Crustacea*, D. E. Bliss (ed). New York/London, Academic Press, 163-211 pp., figs 1-5.
- Sakai, T., 1937. Studies on the Crabs of Japan. II. Oxystomata. *Sci. Rep. Tokyo Bunrika Daig.*, sect. B, 3, Suppl. n°2: 67-192, figs 1-45, pls 10-19.
- Sakai, T., 1956. *Crabs*. Edition 1. Tokyo: Saito Press, 1-60 [List of Latin names]+1-224 [Japanese text]+1-4 [introduction], 69 figs, 6 pls (2 coloured).

Sakai, T., 1965. *The Crabs of Sagami Bay Collected by His Majesty the Emperor of Japan described and illustrated by Tune Sakai, D. Sc.* Tokyo, Maruzen, XVI+1-206, figs 1-27 (English text)+1-92 (Japanese text)+1-32, figs. 1-27, pls 1-100, 1 map.

Sakai, T., 1967. Notes from the Carcinological Fauna of Japan (III), (Tokyo). *Res. Crust., Tokyo*, 3, 68-73 (in Japanese), 74-83 (in English), figs 1, 2, 1 frontisp.

Sakai, T., 1976. *Crabs of Japan and the Adjacent Seas*. Tokyo: Kodansha Ltd. [In three volumes: (1) English text, XXIX+773 pp., figs 1-379; (2) plates volume, 16 pp., pls 1-251; (3) Japanese text, 1-461 pp., figs 1, 2]

Sakai, T., 1980. *Crabs. Their Morphology and Myth*. Second edition. Tokyo, 299 pp., 8 pls.

Sakai, T., T. Tomiyama, T. Hibiya & M. Takeda, 1983. *Fisheries in Japan, Crab*. Tokyo, 179 pp.

Schäfer, W., J. T. Hoeg & J. Lützen, 1983. Some Notes on the Morphology of an Aberrant Actinian (Hexacorallia, Actiniaria) Associated with the glaucothoe of the hermit Crab *Paguroopsis typica* Henderson (Anomura, Paguridae). *Zoologica Scripta*, 12 (4): 229-236, figs 1-12, tables 1, 2.

Schmitt, W. L., 1921. The Marine Decapod Crustacea of California with special reference to the Decapod Crustacea collected by the United States bureau of Fisheries Steamer "Albatross" in connection with the Biological Survey of San Francisco Bay during the years 1912-1913. *Univ. Calif. Publs Zool.*, 23 : 1-469, figs 1-165, pls 1-50.

Schmitt, W. L. 1965. *Crustaceans*. Michigan, Ann Arbor Science Paperbacks, 5-204 pp., figs 1-75.

Schöne, H., 1976. Zur Biologie der dekapoden Krebse. *Encyclopaedia Cinematographica, Publ. Wiss. Filmen*, (9): 461-556.

Schrieken, B., 1966. Spin Krabben en Zeeanemonen. *Levende Nat.*, 68: 176-279.

Serène, R. & K. Romimohtarto, 1969. Observations on the species of *Dorippe* from the Indo-Malayan region. *Mar. Res. Indonesia [Penelitian laut di Indonesia]*, (9): 1-35, figs 1-29, pls 1-6.

Sheldon, J. M. A., 1905. *Guide to the Invertebrates of the Synoptic Collection in the Museum of the Boston Society of Natural History*, V+505 pp.

Shelford, R. W. C., 1916. *A Naturalist in Borneo*. London, XXVIII+331 pp., pls 1-32. [A facsimile reprint edition was published in 1985 by Oxford University Press].

Shen, C.-J., 1931. The Crabs of Hong Kong. Part I. *HongKong Nat.*, 2 (2): 92-110, figs 1-11, pls 4-10.

Shen, C.-J., 1932. The Brachyuran Crustacea of North China. *Zoologia Sin.*, (A) Invertebrates of China, 9 (1): i-x+1-320, figs 1-171, pls 1-10, 1 map.

Shen, C.-J., 1937. On some account of the crabs of North China. *Bull. Fan Mem. Inst. Biol., Peiping*, 7 (5): 167-185.

Shenoy, S. & K. N. Sankolli, 1993. The larval development in the laboratory of the sponge crab *Dromia dormia* (Linnaeus) (Decapoda: Brachyura: Dromiidae). *Proceedings of the First European Crustacean Conference, Paris, August 31-September 5, 1992* (abstracts), p. 149.

Shick, J. M., 1991. A Functional Biology of Sea Anemones. In: P. Calow, *Functional Biology of Sea Anemones*. London/New York, Chapman and Hall, 395 pp.

Stephensen, K., 1945. The Brachyura of the Iranian Gulf. With an Appendix: The male pleopoda of the Brachyura. In : *Danish scientific Investigations in Iran*, Part IV. Copenhagen, E. Munksgaard, pp. 57-237, figs 1-60.

- Stimpson, W., 1855. Descriptions of Some of the New Marine Invertebrata from the Chinese and Japanese Seas. *Proc. Acad. Nat. Sci. Philadelphia*, (7): 375-384.
- Tan, L. W. H. & P. K. L. Ng, 1988. *A Guide to Seashore Life*. First edition. Singapore, Singapore Science Centre, 160 pp.
- Tan, L. W. H. & P. K. L. Ng, 1992. *A Guide to Seashore Life*. Second edition. Singapore, Singapore Science Centre, 160 pp.
- Tavares, M., 1993. Crustacea Decapoda: Les Cyclodorippidae et Cymonomidae de l'Indo-Ouest-Pacifique à l'exclusion du genre *Cymonomus*. In: A. Crosnier (ed), Résultats des Campagnes Musorstom, Volume 10. *Mém. Mus. natn. Hist. nat.*, (A) 156: 253-313, figs 1-20.
- Tavares, M., 1994. Brachyœures bathyaux récoltés par le "Marion Dufresne" au large du Brésil. Systématique et phylogénie des Cyclodorippoidea mondiaux (Crustacea, Decapoda, Brachyura). PhD thesis, University Paris 6, Paris, 324 pp., 70 figs.
- Thomson, D. L., 1923. Note upon an Association between Spider-Crab and Sea-Anemone, *J. mar. biol. Ass. U. K.*, 13, n. s.: 243-244.
- Tyler, P. A. & H. Zibrowius, 1992. Submersible observations of the invertebrate fauna on the continental slope southwest of Ireland (NE Atlantic Ocean). *Oceanologica Acta*, 15 (2): 211-226, figs 1-6.
- Uchida, T., 1960. *Carcinactis ichikawai* n. gen., n. sp., an Actinarian Commensal with the Crab *Dorippe granulata*. *Japanese J. Zool.*, 12 (4): 595-601, fig. 1, pl. 1.
- Verrill, A. E., 1869a. Actiniaria, with Supplement and Geographical Lists. Synopses of the Polyps and Corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Captain John Rodgers, U. S. N., from 1853 to 1856, Collected by Dr. William Stimpson, Naturalist to the Expedition, Part IV. *Proc. Essex Institute* (6): 51-104, pls 1-2.
- Verrill, A. E., 1869b. On the parasitic Habits of Crustacea. *American Naturalist*, (3): 239-250.
- Verrill, A. E., 1928. Havaian shallow water Anthozoa. *Bernice P. Bishop Mus. Bull.* (49): 1-30, figs 1-3, pls 1-5.
- Voultsiadou-Koukoura, E. & A. Koukouras, 1993. Remarks on sponge-decapod associations in the North Aegean Sea. *Bios*, 1 (1): 251-256, tables 1-4.
- Wagner, H. P., 1987. A revision of the genus *Doclea* Leach, 1815 (Crustacea, Brachyura, Majidae). *Bull. Mus. natl Hist. nat.*, (4), sect. A, 8 1986 (1987) (4): 893-953, figs 1-36, pls 1-9.
- Walker, A. O., 1887. Notes on a Collection of Crustacea from Singapore. *J. Linn. Soc. Lond. (Zool.)*, (20): 107-117, pls 6-9.
- Weinbauer, G., V. Nussbaumer & R. A. Patzner, 1982. Studies on the relationship between *Inachus phalangium* Fabricius (Majidae) and *Anemonia sulcata* Pennant in their natural environment. *Mar. Ecol.*, 3 (2): 143-150.
- Wells, M. J., 1978. *Octopus. Physiology and Behaviour of an Advanced Invertebrate*. London, Chapman and Hall, New York, John Wiley and Sons, 417 pp.
- Wicksten, M. K., 1979. Decorating behaviour in *Loxorhynchus crispatus* Stimpson and *Loxorhynchus grandis* (Brachyura, Majidae). *Crustaceana*, Suppl. 5 (Studies on Decapoda): 37-46, figs 1-2, tables 1-5.
- Wicksten, M. K., 1980. Decorator crabs. *Scientific American*, 242 (2): 116-122.
- Wicksten, M. K., 1982. Behavior in *Clythrocerus planus* (Rathbun, 1900) (Brachyura, Dorippidae). *Crustaceana*, 43 (3): 306-308.

- Wicksten, M. K., 1983. Camouflage in marine invertebrates. *Mar. Biol. Ann. Rev.*, **21**: 177-193.
- Wicksten, M. K., 1985. Carrying behavior in the family Homolidae (Decapoda: Brachyura). *J. Crust. Biol.*, **5** (3): 476-479.
- Wicksten, M. K., 1986a. Carrying behavior in brachyuran crabs. *J. Crust. Biol.*, **6** (3): 364-369.
- Wicksten, M. K., 1986b. Shell-carrying in *Hypoconcha sabulosa* (Herbst, 1799) (Decapoda, Brachyura). *Crustaceana*, **50** (3): 19-20.
- Wicksten, M. K., 1993. A review and a model of decorating behavior in spider crabs (Decapoda, Brachyura, Majidae). *Crustaceana*, **64** (3): 314-325.
- Williams, A. B., 1982. Revision of the genus *Latreillia* Roux (Brachyura: Homoloidea). *Quad. Lab. Tecnol. Pesca* (Ancona), **3** (2-5): 227-255, figs 1-8, table 1.
- Williams, A. B., 1984. *Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida*. Smithsonian Institution Press, 550 pp., 380 figs.
- Wirtz, P. & R. Diesel, 1983. The social structure of *Inachus phalangium*, a spider crab associated with the sea anemone *Anemonia sulcata*. *Z. Tierpsychol.*, **62** : 209-234.
- Woods, C. M. C. & C. L. McLay, 1994a. Use of camouflage materials as a food store by the spider crab *Notomithrax ursus* (Brachyura: Majidae). *New Zealand J. mar. freshw. Res.*, **28**: 97-104, figs 1-3.
- Woods, C. M. C. & C. L. McLay, 1994b. Masking and ingestion preferences of the spider crab *Notomithrax ursus* (Brachyura : Majidae). *New Zealand J. mar. freshw. Res.*, **28**: 105-111, figs 1, 2, tables 1-5.
- Woods, C. M. C., 1993. Natural diet of the crab *Notomithrax ursus* (Brachyura: Majidae) at Oaro, South Island, New Zealand. *New Zealand J. mar. freshw. Res.*, **27**: 309-315, figs 1-4, table 1.

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