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Decapod Crustacean Phylogenetics

edited by

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Is the Brachyura Podotremata a Monophyletic Group?

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ABSTRACT

We undertook a morphological analysis to test whether the Podotremata or primitive crabs including Dromiacea, Homoloidea, Raninoidea, and Cyclodorippoidea form a monophyletic group. We can show that the podotrematan subgroups are all monophyletic. Furthermore, our data clearly suggest that Cyclodorippoidea is the sister group to Eubrachyura, that the Raninoidea is the sister group to both, that the Homoloidea is the sister group to this clade, and that all of them are the sister group to Dromiacea (((Eubrachyura, Cyclodorippoidea), Raninoidea), Homoloidea), Dromiacea). Hence the Podotremata is a paraphyletic assemblage. With this result we corroborate recent molecular studies.

1 INTRODUCTION

With almost 7000 species the Brachyura or true crabs form the largest and most diverse decapod group (Ng et al. 2008). Brachyura are found in the deep sea, at thermal vents, and in freshwater and terrestrial habitats. Based on a number of morphological and molecular analyses, there is now a growing consensus that the sister group of Brachyura is the Anomala or Anomura, with both groups together forming the Meiura (Scholtz & Richter 1995; Schram 2001; Dixon et al. 2003; Ah Yong & O'Meally 2004; Miller & Austin 2006; Ah Yong et al. 2007; Tsang et al. 2008). However, brachyuran internal phylogenetic relationships are far from clear, and even their monophyly has been doubted (e.g., Gordon 1963; Williamson 1974; Rice 1980; Spears et al. 1992). This relates in particular to the brachyuran taxa whose representatives do not show the characters that are considered to make a true brachyuran crab. These taxa, the Dromiacea, Homoloidea, Raninoidea, and the Cyclodorippoidea, are often either seen as primitive brachyuran crabs or their brachyuran status is doubted. For instance, H. Milne Edwards (1837) excluded Raninoidea and Dromiacea (including Homoloidea) from Brachyura, Gordon (1963) proposed the exclusion of all podotreme crabs, Ortmann (1896) excluded the Dromiacea (including Homoloidea), and Williamson (1974) and Rice (1980, 1981b, 1983) excluded the Dromiacea. Even a relatively recent molecular phylogenetic analysis suggested the exclusion of dromiaceans from the Brachyura (Spears et al. 1992). Since the seminal work on Brachyura systematics by Guinot in the 1970s, these "primitive" crabs have been unified in a taxon called Podotremata as opposed to the sternitreme crabs or Eubrachyura containing the brachyuran crabs *sensu stricto*. According to de Saint Laurent (1980), the monophyly of Eubrachyura is well supported by the apomorphic sternal position of the female gonopores in combination with a seminal receptacle connected to the oviduct, which leads to internal fertilization. The problem is that Guinot (1977, 1978, 1979a) erected the group Podotremata based on the coxal position of the gonopores. However, coxal genital openings are found in all other decapods and in most

malacostracans, and this is a clearly plesiomorphic character. Since then the Podotremata has remained problematic. Several authors, using sperm characters and other morphological data, argued for a monophyletic Podotremata, although an unambiguous apomorphy for this group has not been established (Guinot 1978, 1979a; Jamieson 1994; Jamieson et al. 1995). Guinot & Tavares (2001), Tavares (2003), and Guinot & Quenette (2005) discuss the spermathecal invagination at the sternal boundary between the 7th and 8th thoracic segment as an apomorphy supporting the Podotremata. And indeed, this complex character involving two sternites is restricted to podotrematan representatives, but it suffers from a problematic polarization because nothing comparable exists in other reptant groups. However, we must note that the seminal receptacle and spermathecae may not be homologous structures, so the derivation of one from the other (see Hartnoll 1979) is difficult. Accordingly, several authors suggested a paraphyletic Podotremata (e.g., Scholtz & Richter 1995; Martin & Davis 2001; Dixon et al. 2003; Brösing et al. 2007), and an older (Spears et al. 1992) and a recent (Ahyong et al. 2007) molecular analysis support this view. In addition to the general question of podotrematan monophyly versus paraphyly, the internal relationships between the major podotrematan groups are a continuous matter of debate. For instance, some authors include Homoloidea within Dromiacea (e.g., Boas 1880; Borradaile 1907), while other authors (e.g., Guinot 1978) separate them. Števíć (1995) even synonymizes Dromiacea with Podotremata. Furthermore, Guinot (1978) erected a group Archaeobrachyura that includes Homoloidea, Cyclodorippoidea, and Raninoidea, although later she excluded the Homoloidea from the Archaeobrachyura (Guinot & Tavares 2001).

Here we test whether morphological data contribute to the question of podotrematan monophyly or paraphyly and whether the Archaeobrachyura is a valid taxon. We investigate a comprehensive number of different characters. Our analysis indicates that podotrematan Brachyura are a paraphyletic assemblage. Our results are largely congruent with those of a recent analysis based on a molecular data set (Ahyong et al. 2007).

2 MATERIALS AND METHODS

2.1 Animals

We examined the following brachyuran species from our personal collections: Homolodromiidae: *Dicranodromia karubar* Guinot, 1993; Dromiidae: *Moreiradromia sarraburei* (Rathbun, 1910), *Hypoconcha arcuata* Stimpson, 1858; Dynomenidae: *Dynomene pilumnoides* Alcock, 1900; Homolidae: *Dagnaudus petterdi* (Grant, 1905), *Homola barbata* (Fabricius, 1793); Latreilliidae: *Eplumula australiensis* (Henderson, 1888); Raninidae: *Lyreidus tridentatus* de Haan, 1841, *Ranina ranina* (Linnaeus, 1758); Cyclodorippidae: *Krangalangia spinosa* (Zarenkov, 1970); Cymonomidae: *Cymonomus aequiloni* Dell 1971; Cyclodorippidae: *Tymolus brucei* Tavares, 1991; Majidae: *Prismatopus filholi* (A. Milne Edwards, 1876); Dorippidae: *Medorippe lanata* (Linnaeus, 1767); Xanthidae: *Xantho poressa* (Olivi, 1792); Portunidae: *Nectocarcinus antarcticus* (Hombron & Jacquinot, 1846), *Ovalipes catharus* (White in White & Doubleday, 1843); Varunidae: *Eriocheir sinensis* H. Milne Edwards, 1853, *Hemigrapsus crenulatus* (H. Milne Edwards, 1837). For outgroup comparison we used the following species: Anomala: *Petrolisthes elongatus* (H. Milne Edwards, 1837), *Galathea strigosa* (Linnaeus, 1767); Astacida: *Paranephrops zealandicus* (White, 1847), *Procambarus clarkii* (Girard, 1852). In addition, we considered data from the literature.

2.2 Microscopy

The morphological investigations were done with the aid of a dissecting microscope and a scanning electron microscope (SEM) (Leica). Some dissected specimens were boiled with 5% KOH to remove the soft parts. Alizarin-red stain was used to highlight calcified parts of the skeleton and appendages (for detail see Brösing et al. 2002). The specimens prepared for SEM were transferred

to an ethanol series up to pure ethanol for dehydration and then dried at critical point, mounted on stubs, and sputter-coated with gold.

2.3 Analysis

In this analysis we reconstruct the phylogenetic tree "by hand" and brain following a Hennigian approach (Hennig 1966). In the first step we provide evidence that the brachyuran subgroups under consideration are monophyletic, and in a second step we reconstruct their phylogenetic relationships following a top-down approach starting with the Eubrachyura and looking for its sister taxon, then looking for the sister taxon to this unified clade, etc. (see below).

3 RESULTS

3.1 *The monophyly of the brachyuran subtaxa*

3.1.1 *Dromiacea*

The Dromiacea *sensu* Guinot (1978, 1979a) consist of the Homolodromiidae, the Dynomenidae, and the Dromiidae (see McLay 1999). The Homoloidea, which in older concepts were part of the Dromiacea, are excluded. The clade Dromiacea *sensu* Guinot is well supported by a number of apomorphies (character set 1):

The renal opening in the coxal segment of the 2nd antennae is surrounded by upper and lower projections in a beak-like manner (Fig. 1). A corresponding structure is not found in any other decapod taxon (see below). We find this character in all investigated species of the Homolodromiidae, Dynomenidae, and Dromiidae, including *Hypoconcha*. In the relevant literature we see no exception.

The fingers of the chelae are hollow and serrated, and the serrate tips of the fingers engage (Fig. 2). Plesiomorphically, the fingers are compact and show pointed tips. As with the previous character, this is seen in all investigated dromiacean species and also found in the literature (McLay 1993, 1999; Guinot 1995; Guinot & Tavares 2003).

The 2nd pleopod of the male is flagellate with a needle-like tip and a multi-segmented basal part. The plesiomorphic condition is a stout 2nd pleopod (see McLay 1993, 1999; Guinot 1995).

In addition, the shape of the flattened acrosome of the sperm (Jamieson 1994) and the set of foregut ossicles (Brösing et al. 2002, 2007) corroborate dromiacean monophyly.

3.1.2 *Homoloidea*

The Homoloidea include the Homolidae, the Latreilliidae, and the Poupiniidae (Guinot & Richer de Forges 1995). All these subgroups share the following apomorphies (character set 2):

The telson projects between the bases of the third maxillipeds (Fig. 3). In most other cases, the telson ends posterior to the maxilliped segments. Only some leucosiids are slightly similar in this respect, but a detailed analysis reveals the fundamental difference (see Guinot 1979a). The representatives of Latreilliidae and Homolidae studied by us all showed the same pattern. For Poupiniidae, we find a corresponding character state in the publication of Guinot (1991).

The retention of the pleon is achieved by two devices, namely paired projections on the 3rd thoracic sternite and little protrusions of the basal parts of the 3rd maxillipeds. All other brachyurans show a different pattern of pleon retention structures (see below and Guinot & Bouchard 1998).

These are not many apomorphies, but as far as we know there are no exceptions found within the Homoloidea. Jamieson (1994) and Jamieson et al. (1995) mentioned several sperm characters such as numerous radial extensions of the operculum and a spiked wheel form of the anterior expansion of the perforatorium supporting the Homoloidea clade. Furthermore, larval features are interpreted as homolid apomorphies (Rice 1980).

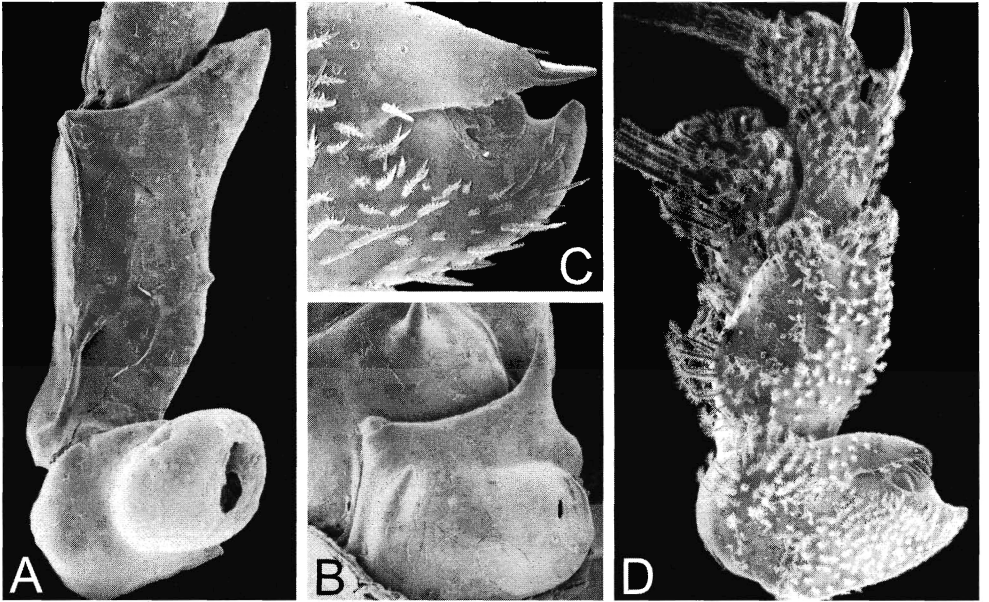


Figure 1. Renal openings, I. The renal opening of a homolid (*Dagnaudus petterdi*) (A) and an astacid (*Paranephrops zealandicus*) (B) showing the plesiomorphic condition of a tube positioned on the proximal part of the 2nd antenna. The beak-like structure around the renal opening is exemplified in a dromiid (*Moreiradromia saraburei*) (C) and a dynomenid (D) (*Dynomene pilumnoides*) apomorphic for Dromiacea.

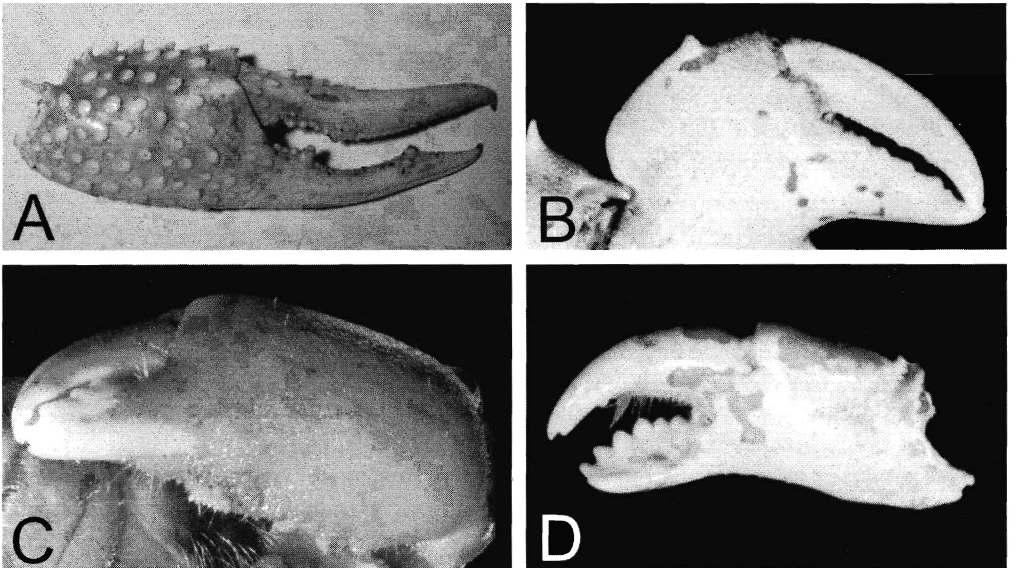


Figure 2. Chelae. (A) Chela of an astacid (*Procambarus clarkii*) and (B) of the raninoid crab *Lyreidus tridentatus* showing the pointed tips of the dactylus and propodus. (C, D): The chelae of a dynomenid (*Dynomene pilumnoides*) (C) and a homolodromiid (*Dicranodromia karubar*) (D) with hollow fingers and serrated margins that show interlocking teeth.

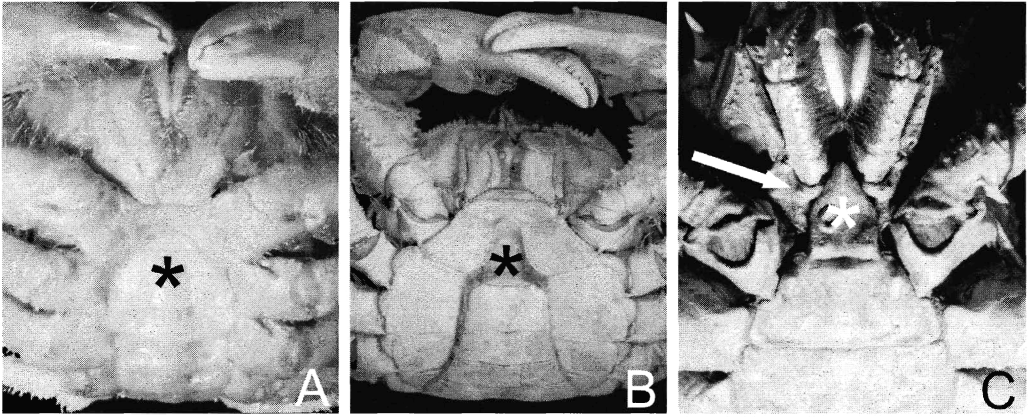


Figure 3. Telson position. (A) The telson of a dynomenid (*Dynomene pilumnoides*), (B) of a eubrachyuran (*Eriocheir sinensis*), and (C) of the homoloid species (*Dagnaudus petterdi*). Telsons marked with (*). The telson in *Dagnaudus* reaches apomorphically between the basal parts of the 3rd maxilliped, which possesses a coxal process as a pleon retention device (arrow).

3.1.3 Raninoidea

The Raninoidea is a very uniform and easy to identify group of crabs. Accordingly, there are a number of clear apomorphies supporting this clade (character set 3):

The exopod of the 1st maxilliped is flattened, lacks a flagellum, and is involved in the exhalant water current channel (see also Bourne 1922) (Fig. 4). The plesiomorphic state is a more or less round exopod equipped with a flagellum.

The paired spermathecal openings lead into an unpaired median atrium. This is associated with the 7th thoracic sternite (see also Gordon 1963; Guinot 1993). In the other podotrematan crabs the spermathecal openings are separate and positioned between the 7th and 8th thoracic sternites.

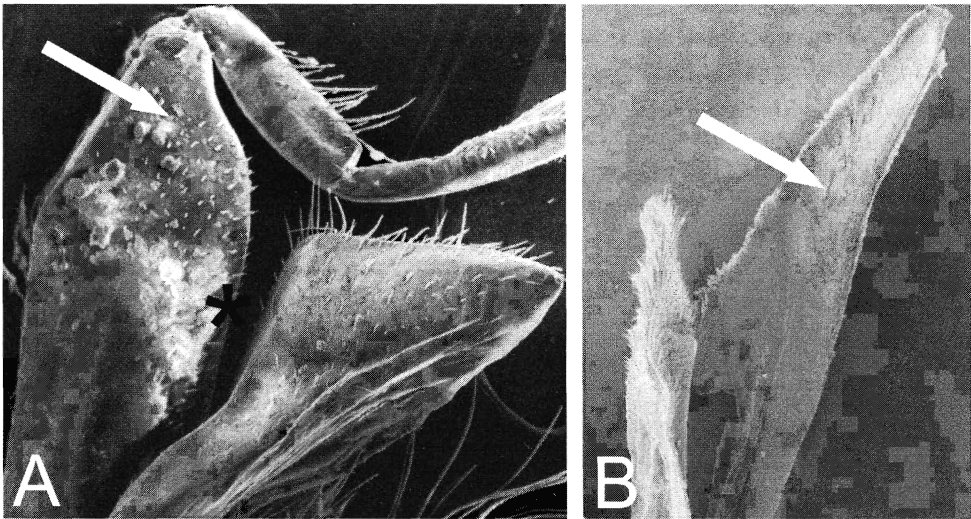


Figure 4. Exopod of the 1st maxilliped. (A) The flat and flagellate exopod of the 1st maxilliped (arrow) of a eubrachyuran (*Prismatopus filholi*) representing the plesiomorphic condition. (B) The apomorphic aflagellate and widened exopod (arrow) in *Lyreidus tridentatus*, a raninoid species.

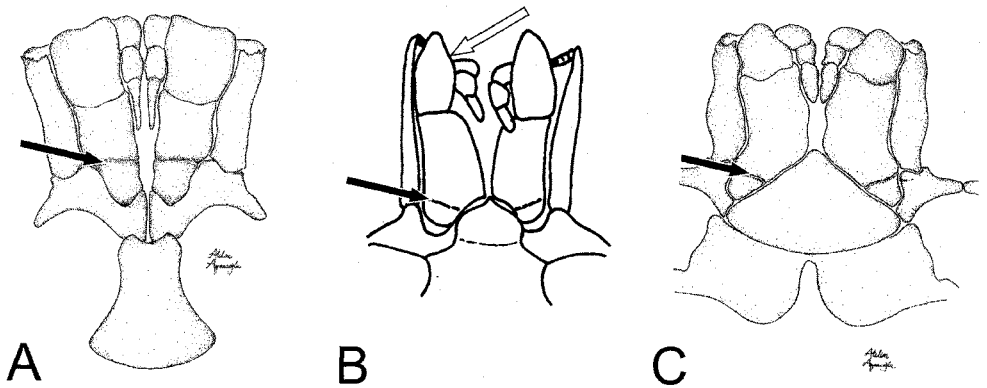


Figure 5. The 3rd maxillipeds of (A) a dromiacean (*Moreiradromia sarra burei*), (B) a cyclodorippoidean (*Cymonomus aequilonius*), and (C) a eubrachyuran (*Nectocarcinus antarcticus*). The black arrows point to the basis-ischium boundary showing that there is a characteristic pattern apomorphically shared by cyclodorippoideans and eubrachyurans. The white arrow in (B) points to the apomorphically posteriorly situated endopodal palp of the cyclodorippoidean 3rd maxilliped.

The sternum is narrowed posterior to the 4th or 5th sternites (see Bourne 1922; Guinot 1993) (see Fig. 9). Plesiomorphically, the posterior part of the sternum is much wider.

Additional data from sperm morphology and the foregut ossicles also support a monophyletic Raninoidea (Jamieson 1994; Brösing et al. 2007).

3.1.4 *Cyclodorippoidea*

The Cyclodorippoidea are subdivided into the Cyclodorippidae, Cymonomidae, and Phyllotymolinidae (Tavares 1998). We found relatively few putative apomorphies, and thus the status of the group is debatable (character set 4):

The palp of the 3rd maxilliped is in a very sub-distal position (Fig. 5). The plesiomorphic condition is a more distal position. This character can be seen in *Tymolus*, *Cymonomus*, and *Krangalangia* (see also Tavares 1993).

The first three pleon segments are visible dorsally when the crab is in a horizontal position. In other crabs either no segments or at most two segments are seen in the dorsal aspect.

The tip of the telson reaches only to the segment of the 3rd pereopods. In most other crabs it extends more anteriorly, with the notable exception of some raninoids (see Fig. 3).

Further morphological evidence for a Cyclodorippoidea clade comes from sperm data (Jamieson et al. 1995).

3.1.5 *Eubrachyura*

The Eubrachyura *sensu de Saint Laurent* (1980) or sternitreme crabs (Balss 1940; Gordon 1963; Guinot 1978, 1979a) are composed of the Heterotremata and Thoracotremata (Guinot 1978). It was not the task of the present study to investigate the internal relationships of the Eubrachyura and to test the monophyly of Heterotremata and Thoracotremata (Guinot 1978). Here we discuss only the putative apomorphies of this taxon (character set 5):

The position of female gonopores is on the 6th thoracic sternite. The plesiomorphic condition is a coxal position of female gonopores. This is without exception the case in the specimens studied by us.

The seminal receptacle is part of the oviduct. Plesiomorphically, all sperm receptacles (if present) in other decapods, including podotrematan crabs, are not connected to oviducts, but are instead part of the external thoracic surface.

The fertilization is internal. In all other reptants there is external fertilization.

The epistome encircles the base of the 2nd antenna. This can even lead to the complete fusion and fixation of the base of the 2nd antenna in some groups (e.g., majids and parthenopids). Plesiomorphically, the base of the 2nd antenna is free.

Subsequent to Guinot's papers, the validity of this group has rarely been doubted. Only Brösing et al. (2007) found some evidence in foregut ossicle patterns for the resurrection of a taxon *Oxystomata*, which would include the raninoids, cyclodorippoidea, and some basal heterotreme groups.

3.2 The phylogenetic relationships among brachyuran subtaxa

Below we reconstruct, in stepwise fashion, the phylogenetic relationships of Brachyura, starting with the sister group to Eubrachyura.

3.2.1 Synapomorphies of Eubrachyura and Cyclodorippoidea (character set 6)

The 3rd thoracic sternite is wide, separating the basis and ischium of the 3rd maxilliped in a characteristic manner (Fig. 5). The plesiomorphic state is a narrow sternite, with the basis and the ischium of the 3rd maxilliped lying in an adjacent position. This character is found in all Eubrachyura without exception and in the cyclodorippoidea species investigated by us.

The coxal segment of the 2nd antenna is scale-like and conceals the renal opening (Fig. 6). The epistome forms a counterpart. This pattern is not found in any other brachyuran or other decapod group. The beak-like structure of Dromiacea is exclusively formed by the coxa, and in other groups there is a simple tube-like projection. The pattern is in detail slightly different in some Eubrachyura. For instance, in Majidae the coxa is completely fused to the epistome and is thus immobile.

The epipodite of the 1st maxilliped is elongated and strengthened with a calcified rod (dorsal gill cleaner and flabellum) (Fig. 7). The epipod is triangular and relatively short and lacks the calcified rod in the other Brachyura. This character seems to occur in all eubrachyuran species studied by

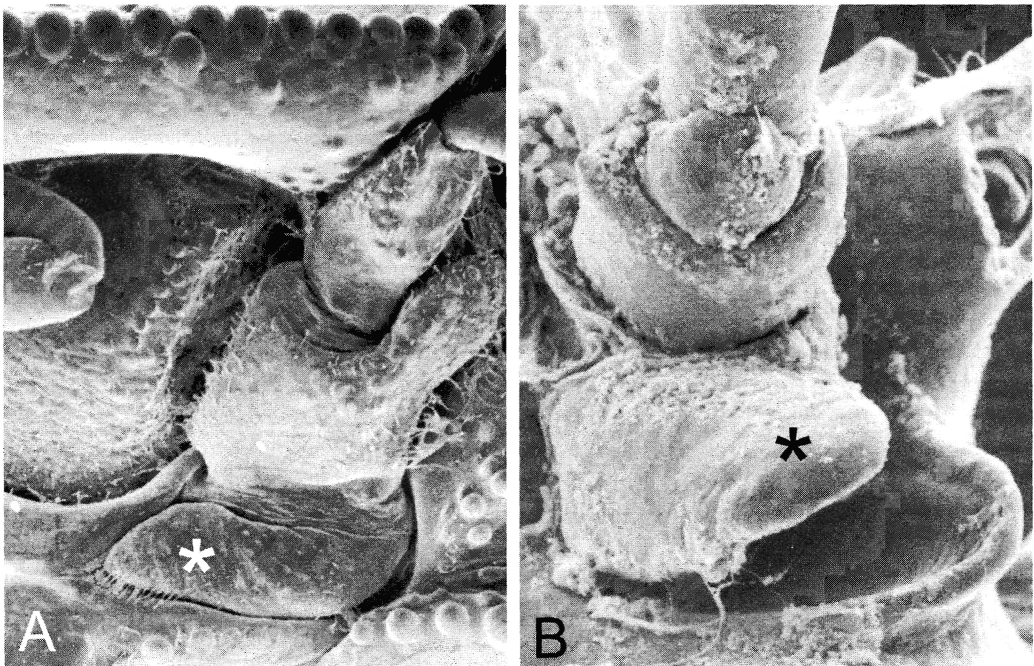


Figure 6. Renal openings, II. The scale-like cover (*) of the renal opening in the eubrachyuran *Hemigrapsus crenulatus* (A) and in the cyclodorippoidea *Krangalugia spinosa* (B). Compare to Figure 1.