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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; Ahyong & O'Meally 2004; Miller & Austin 2006; Ahyong 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 aequilonius* 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).

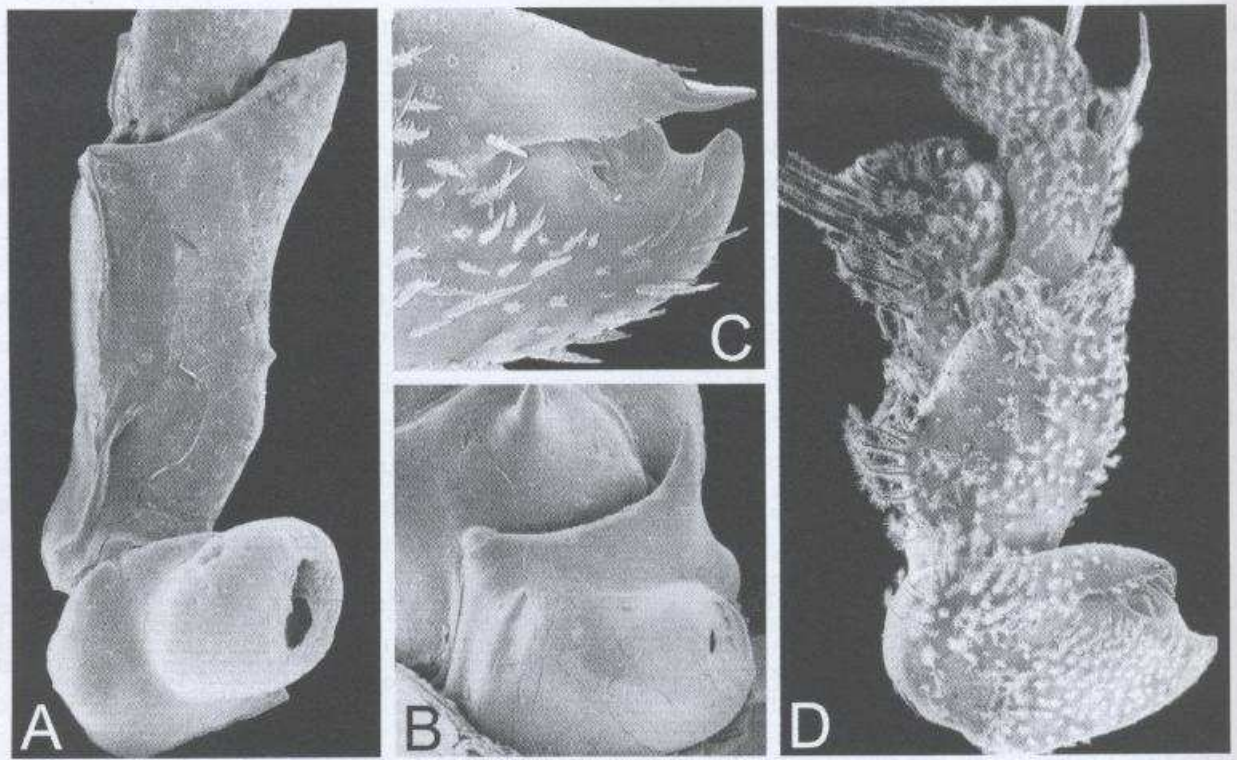


Figure 1. Renal openings, I. The renal opening of a homolid (*Dagnaudus petterdi*) (A) and an astacid (*Paranephrops zealandicus*) (B) showing the plesiomorphic condition of a tube positioned on the proximal part of the 2nd antenna. The beak-like structure around the renal opening is exemplified in a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

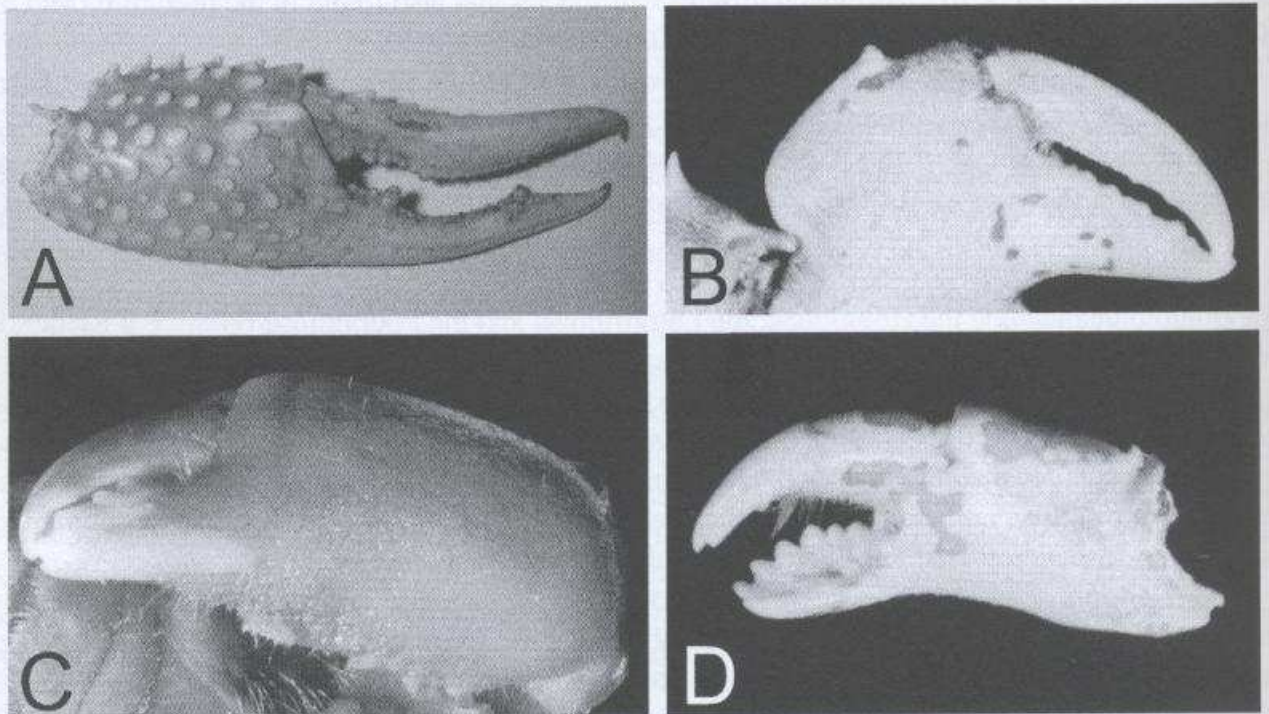


Figure 2. Chelae. (A) Chela of an astacid (*Procambarus clarkii*) and (B) of the raninoid crab *Lyreidus tridentatus* showing the pointed tips of the dactylus and propodus. (C, D): The chelae of a dynomenid (*Dynomene pilumnoides*) (C) and a homolodromiid (*Dicranodromia karubar*) (D) with hollow fingers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

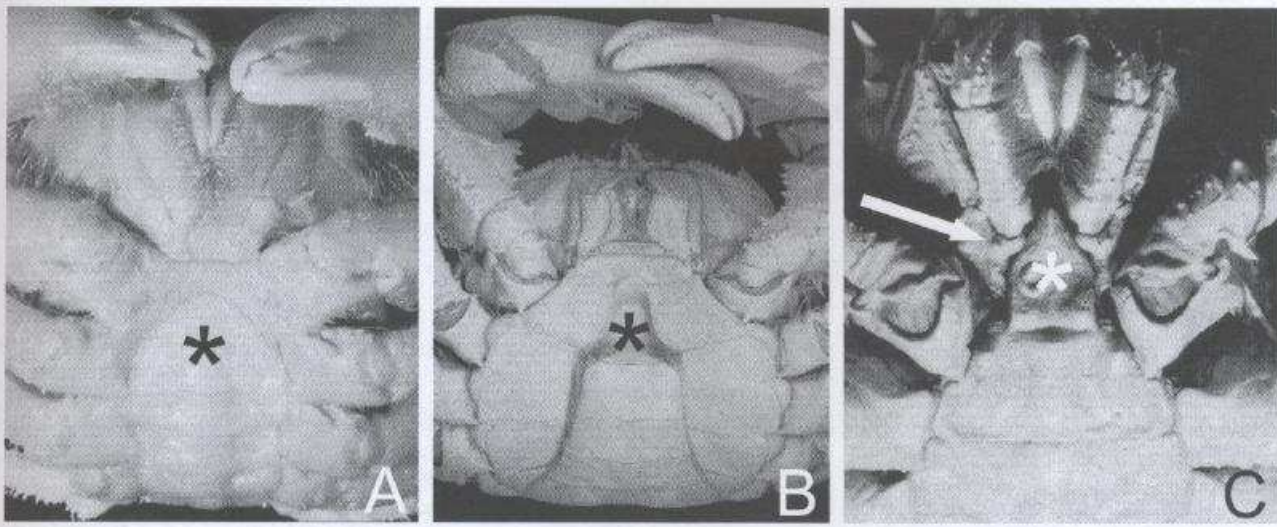


Figure 3. Telson position. (A) The telson of a dynomenid (*Dynomene pilumnoides*), (B) of a eubrachyuran (*Eriocheir sinensis*), and (C) of the homoloid species (*Dagnaudus petterdi*). Telsons marked with (*). The telson in *Dagnaudus* reaches apomorphically between the basal parts of the 3rd maxilliped,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

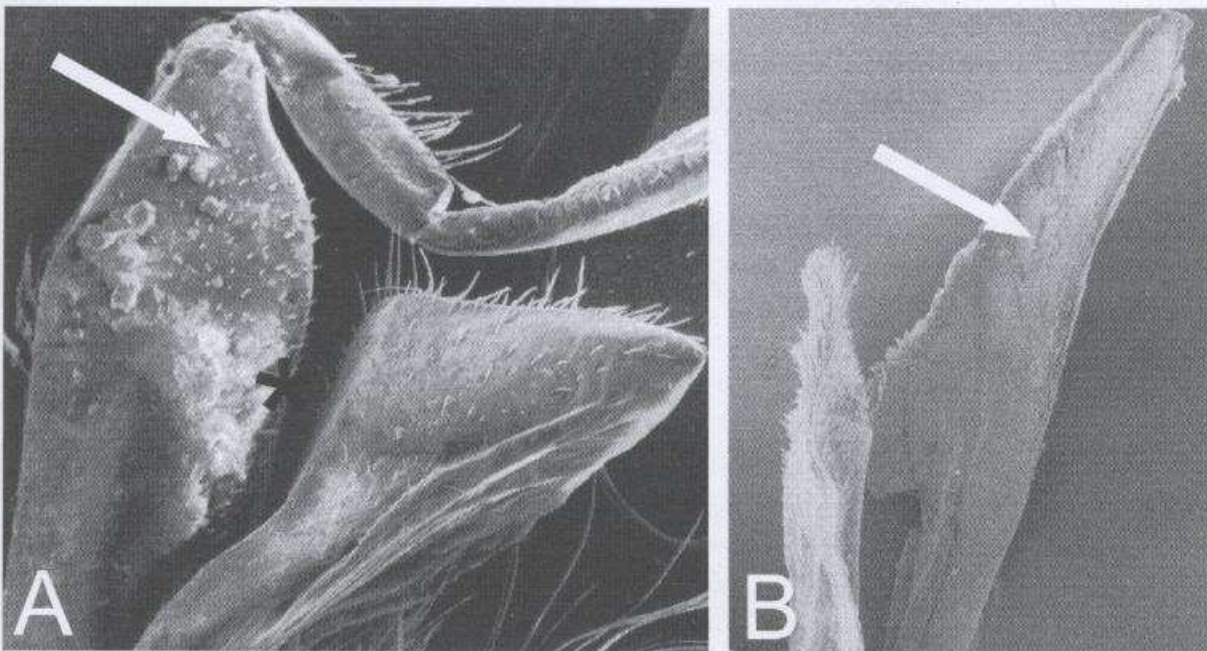


Figure 4. Exopod of the 1st maxilliped. (A) The flat and flagellate exopod of the 1st maxilliped (arrow) of a eubrachyuran (*Prismatopus filholi*) representing the plesiomorphic condition. (B) The apomorphic aflagellate and widened exopod (arrow) in *Lyreidus tridentatus*, a raninoid species.

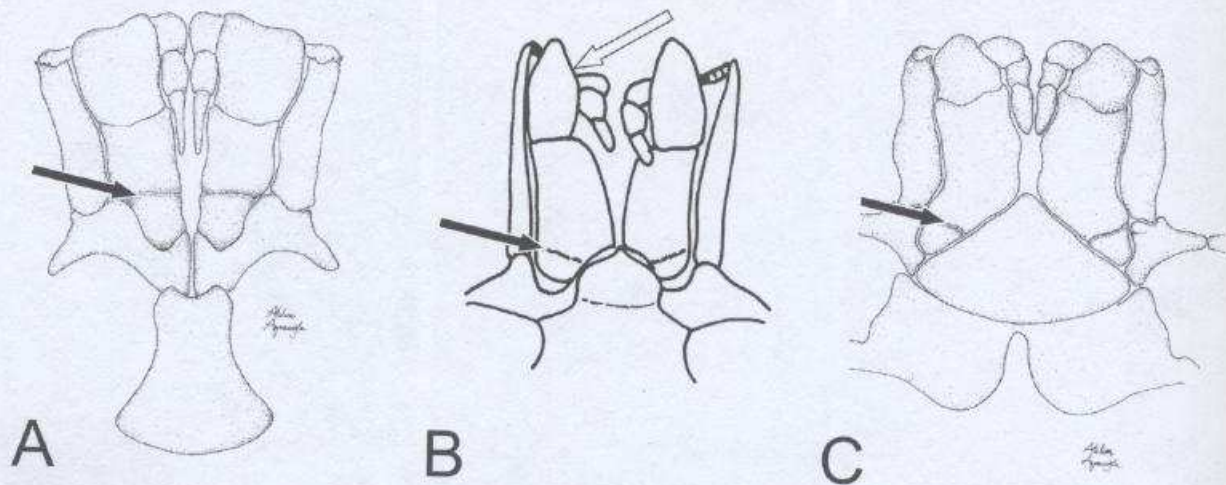


Figure 5. The 3rd maxillipeds of (A) a dromiacean (*Moreiradromia sarraburei*), (B) a cyclodorippoidean (*Cymonomus aequilonius*), and (C) a eubranchyuran (*Nectocarcinus antarcticus*). The black arrows point to the basis-ischium boundary showing that there is a characteristic pattern apomorphically shared by cyclodorippoideans and eubranchyurans. 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 Phyllotymolidae (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 *Eubranchyura*

The Eubranchyura *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 Eubranchyura 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

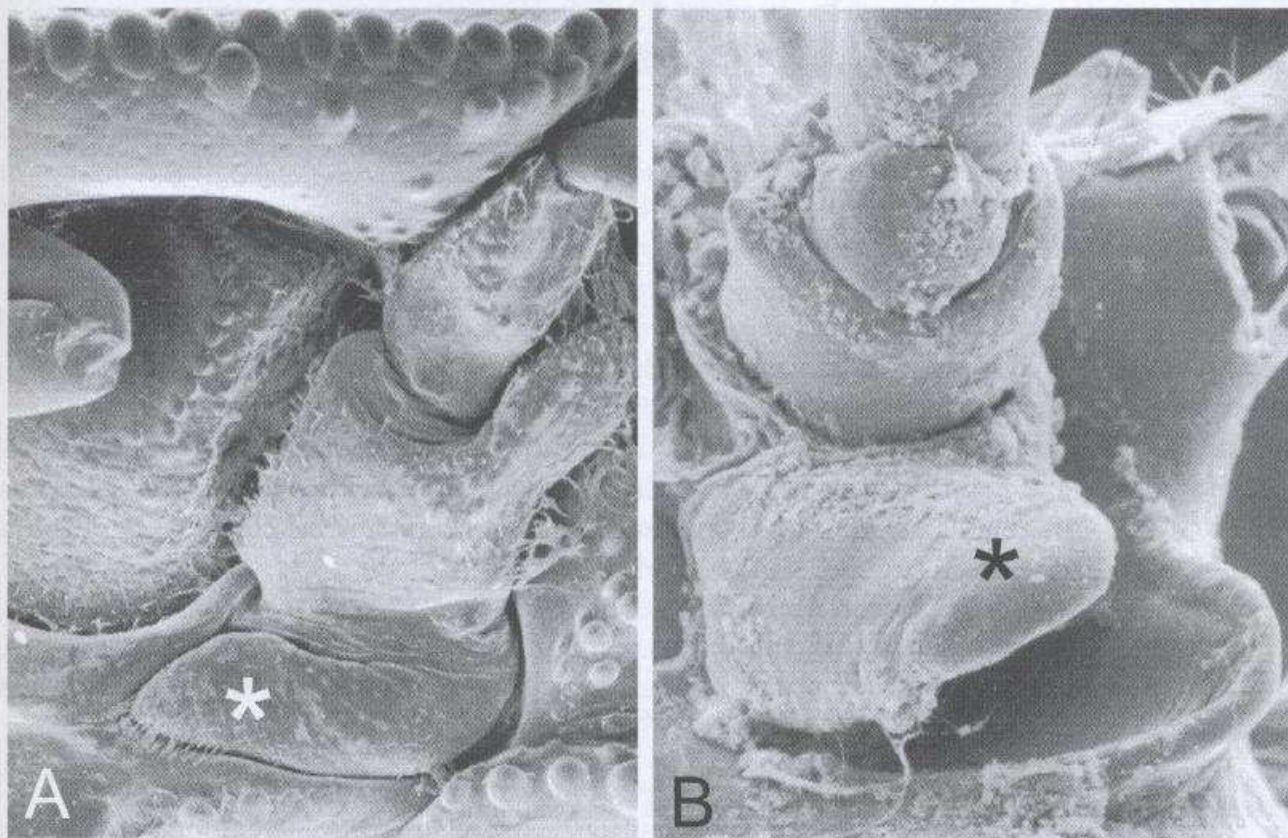


Figure 6. Renal openings, II. The scale-like cover (*) of the renal opening in the eubrachyuran *Hemigrapsus crenulatus* (A) and in the cyclodorippoidea *Krangalangia spinosa* (B). Compare to Figure 1.

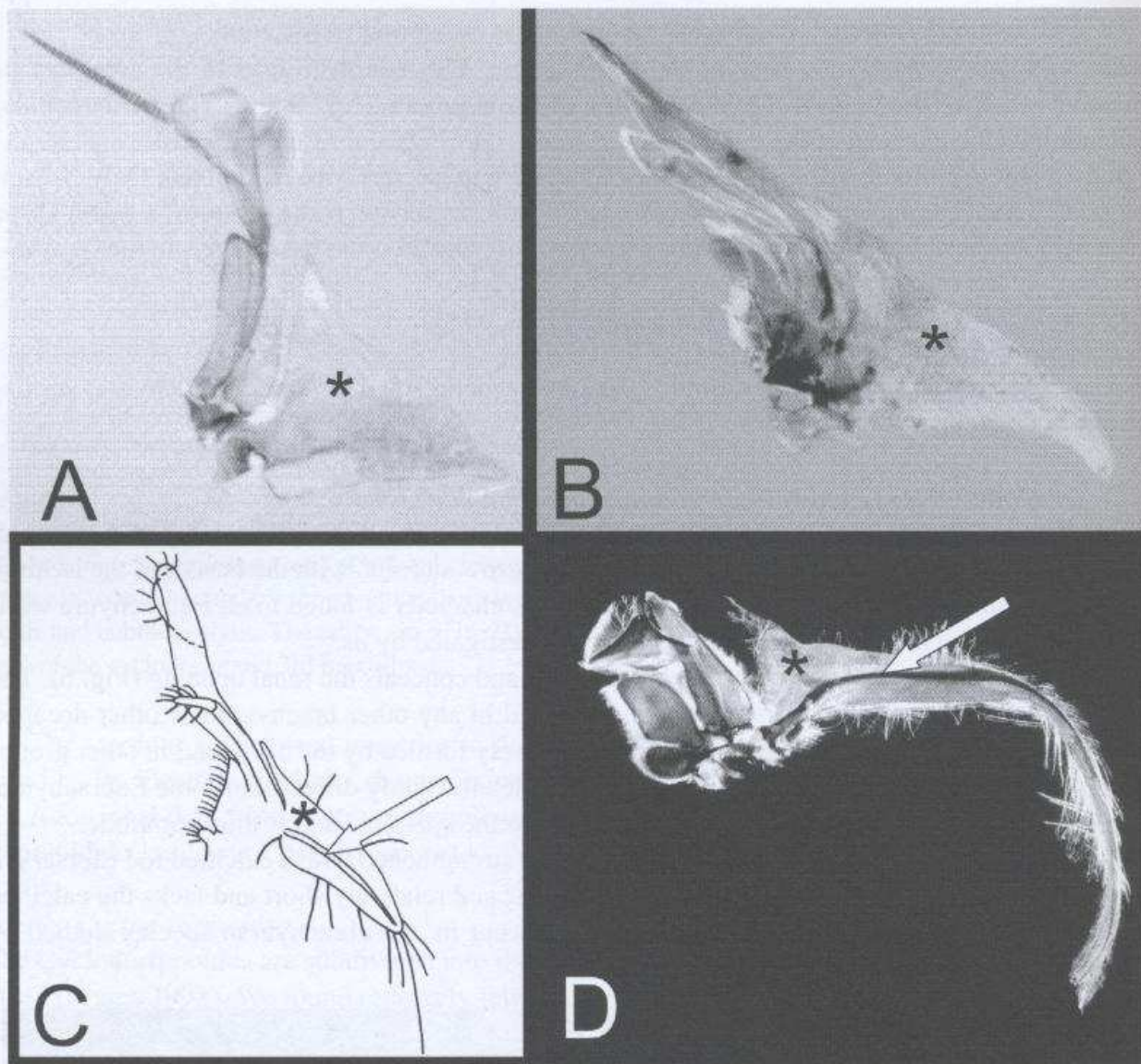


Figure 7. The epipods of the 1st maxillipeds. The 1st maxillipeds of (A) the dromiacean *Dynomene pilumnoides*, (B) the raninoid *Lyreidus tridentatus*, (C) the cyclodorippoid *Tymolus brucei*, and (D) the eubranchyuran *Ovalipes catharus*. The epipod (*) forms a triangular lobe that is elongated and supported by a calcified rod (arrows) in cyclodorippoids and eubranchyurans. At least in the latter two clades, the epipod serves as a gill cleaning brush (flabellum).

us and described in the literature. However, the database is not very large, and further studies are necessary.

A sterno-pleonic cavity is present (see also Guinot & Bouchard 1998) (see Fig. 9D). Plesiomorphically, there is a more or less flat sternum that lacks a corresponding cavity. Again we found no exception, only different degrees of the sharpness of the boundaries of the cavities (see Tavares 1993).

The cladistic analysis of brachyuran relationships based on ossicle patterns of the foregut by Brösing et al. (2007) does not resolve a eubranchyuran–cyclodorippoidean sister group relationship, but a certain affinity of these two taxa plus the Raninoidea, to the exclusion of the Dromiacea and Homoloidea, is also shown.

3.2.2 Synapomorphies of Eubranchyura–Cyclodorippoidea and Raninoidea (character set 7)

The palp of the 3rd maxilliped is inserted and articulates in the plane of the operculum, i.e., it moves in a medial-lateral direction (Fig. 8). In the plesiomorphic condition the palp moves dorso-ventrally, as is seen in all outgroup representatives.

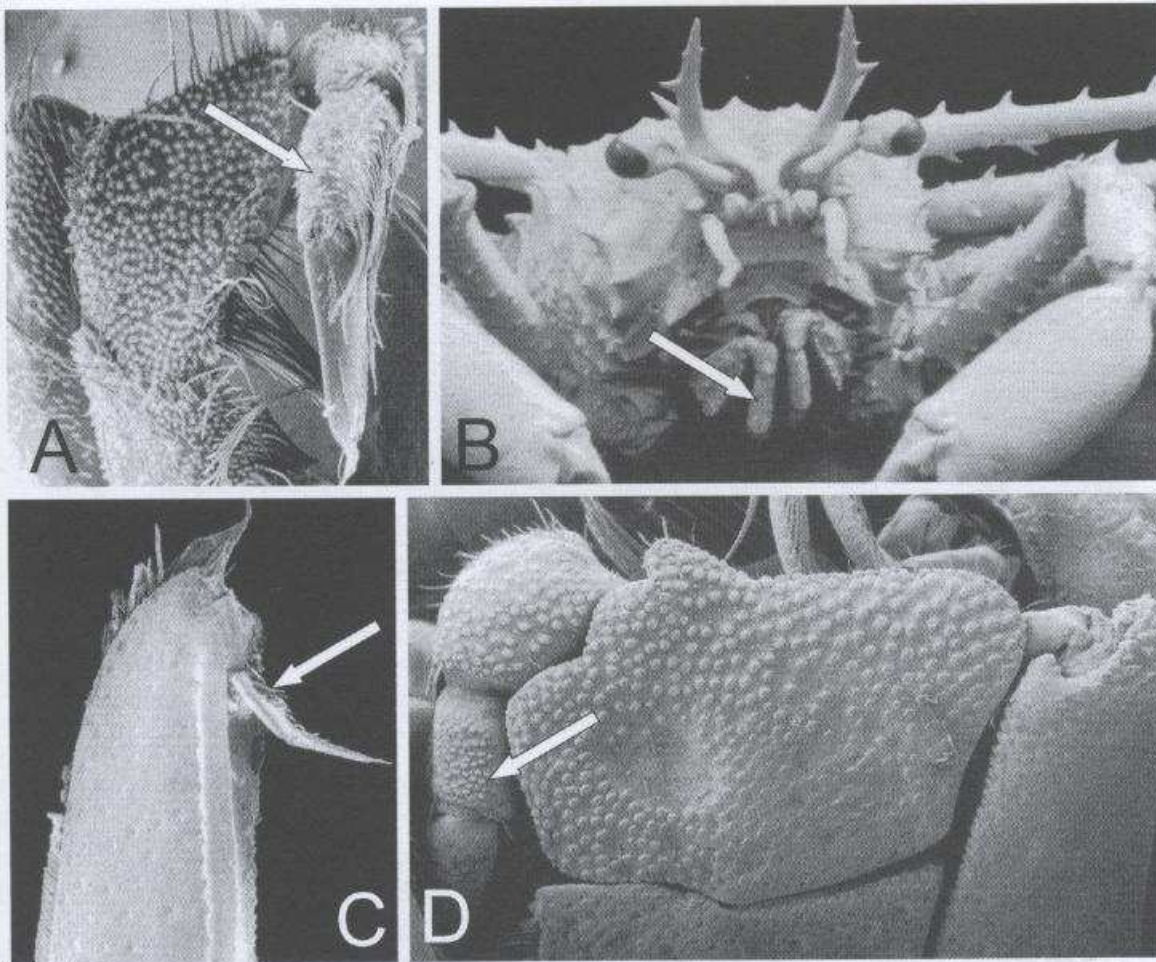


Figure 8. The orientation of the palps (arrows) of the 3rd maxillipeds in (A) the dromiacean *Dynomene pilumnoides*, (B) the homoloid *Dagnaudus petterdi*, (C) the raninoid *Lyreidus tridentatus*, and (D) the eubrachyuran *Xantho poressa*. In C and D the palps lie in one plane with the rest of the maxilliped, whereas in (A) and (B) they are situated at an angle that implies a different plane of movement. This more pediform appearance is the plesiomorphic condition.

The *crista dentata* on the inner margin of the basis-ischium is a plesiomorphic reptant character that is present in the homolodromiids, dromiids, dynomenids, and homolids (except latreilliids), but it has been lost in the ancestor of the cyclodorippids, cymonomids, phyllotymolinids, and raninids, as well as in the Eubrachyura (and independently in latreilliids).

The 3rd maxilliped is truly operculiform. This means that all elements lie in one plane tightly covering the buccal field. The plesiomorphic condition is a pediform third maxilliped. Compared to the condition in crayfish, the 3rd maxilliped of all crabs, including homolodromiids and homoloideans, is slightly flattened (see Scholtz & Richter 1995), and in dromiids and dynomenids it is flattened even more so, resulting in a convergent operculum-like structure. But this is not the same as forming a completely flat and closed field. The condition found in the anomalan porcelain crab *Petrolisthes* and in some thalassinids is only superficially similar, as indicated by the position of the *crista dentata* (see Balss 1940; Scholtz & Richter 1995).

All elements of the sternum form a flat plane, including the episternites (Fig. 9). The plesiomorphic state is that the episternites lie in a dorsal position and the pereopod coxae are withdrawn dorsally.

The coxae of the pereopods are narrow and triangular in ventral view, lacking an anterior lobe (Fig. 9). Homoloidea and Dromiacea as well as the outgroup representatives have a differently shaped coxa.

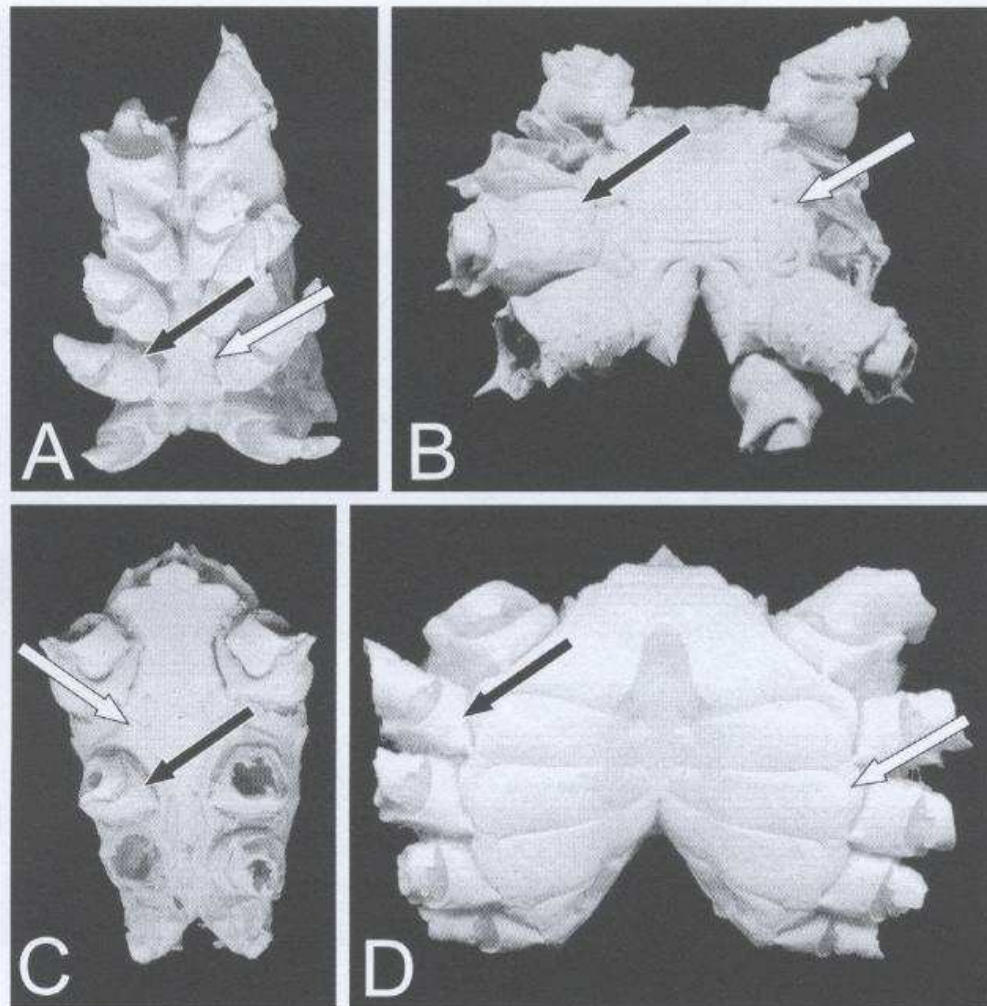


Figure 9. Sternal elements (white arrows) and coxae (black arrows) of (A) the crayfish *Paranephrops zealandicus*, (B) the homoloid *Dagnaudus petterdi*, (C) the raninoid *Lyreidus tridentatus*, and (D) the eubrachiuran *Hemigrapsus crenulatus*. The white arrows point to the lateral elements of the sternal complex, which plesiomorphically are situated in a different level compared to the sternites bearing the sterno-coxal joints (A and B). Apomorphically, all elements lie in the same plane. The coxae are plesiomorphically relatively wide. In the apomorphic condition they are narrow and triangular in ventral view and are pointed to the sterno-coxal joints (C and D).

A vertical notch is formed in the epimeral walls of the P1 and P2 segments. A corresponding structure is absent in all other investigated taxa.

An anterior tooth forms a clip for attachment of the carapace to the epimeral wall. A corresponding structure is absent in all other investigated taxa.

The facets of the compound eyes are hexagonal (Fig. 10). This character is found in the Eubrachiura genera *Cancer*, *Ovalipes*, *Nectocarcinus*, and *Hemigrapsus* and appears to be a general feature of eubrachiuran crabs indicating apposition and parabolic superposition eye types (see also Fincham 1980; Nilsson 1983, 1988; Gaten 1998; Richter 2002), the Cyclodorippoidea *Krangalanga* and *Tymolus*, and in the Raninoidea *Lyreidus* and *Ranina* (in contrast to the findings of Gaten 1998, but see Fincham 1980). The cyclodorippid *Cymonomus* has reduced eyes. All representatives of Homoloidea and Dromiacea have square facets, which occur in reflecting superposition eyes. This is apparently the plesiomorphic condition for reptant Decapoda since it occurs in crayfish and lobsters and plesiomorphically in Anomala as is seen in *Petrolisthes* and *Galathea* studied by us (see Fincham 1980; Gaten 1998; Richter 2002; but see also Porter & Cronin this volume).

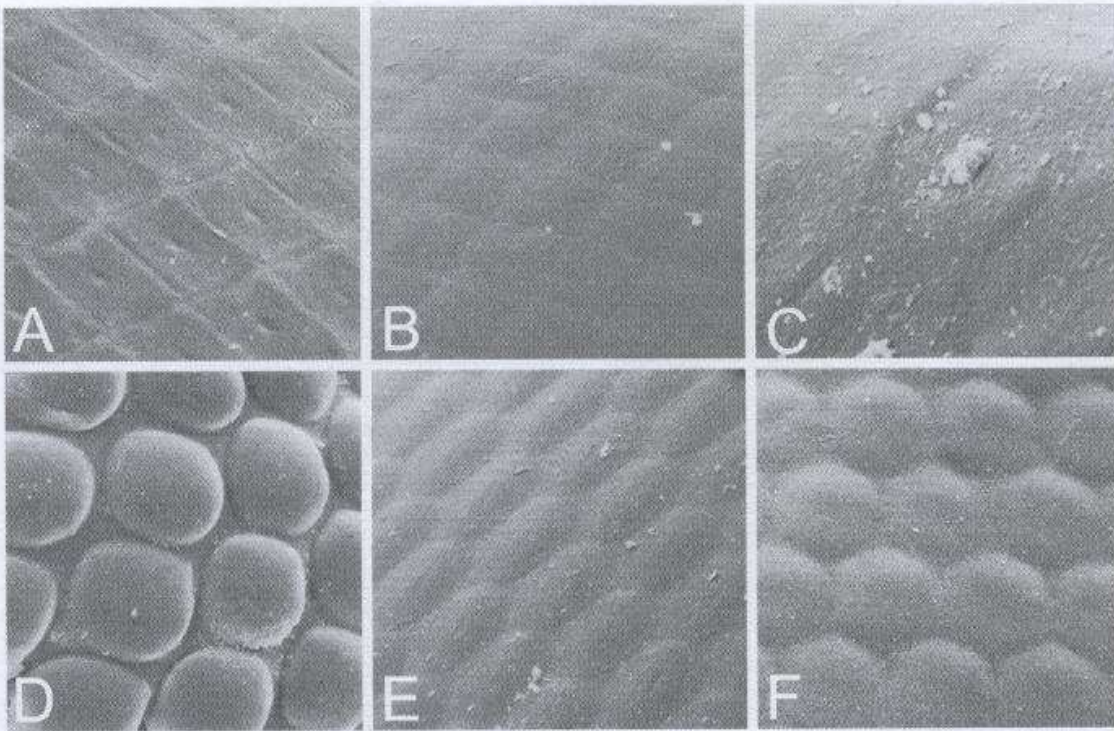


Figure 10. Facets of compound eyes. The crayfish *Paranephrops zealandicus* (A) and the dromiacean *Dynomene pilumnoides* (B) show squared facets, plesiomorphic for reptants, whereas the raninoid *Lyreidus tridentatus* (C), the cyclodorippoidean *Krangalangia spinosa* (D), and the eubrachiurans *Nectocarcinus antarcticus* (E) and *Hemigrapsus crenulatus* (F) possess apomorphic round/hexangular facets.

3.2.3 Synapomorphies of Eubrachiura-Cyclodorippoidea-Raninoidea and Homoloidea (character set 8)

The arthropragmal skeleton of the last thoracic segment is elongated, completely fused in the midline, and forming two anterior wings, i.e. “*sella turcica*” *sensu stricto* (Fig. 11). In the brachyuran literature the term “*sella turcica*” is used in many ways. Some authors consider a “*sella turcica*” as an apomorphy of all Brachyura (e.g., Jamieson et al. 1995; Števc̆ić 1995). In contrast to this, Secretan (1998) restricts the word “*sella turcica*” to the situation found in Eubrachiura. We see no fundamental difference between the condition of homoloids, raninoids, and eubrachiurans. In contrast to this, we recognize a distinct difference between the condition found in Dromiacea and in the other brachyuran crabs. This relates to the fact that the fusion of the arthropragm in dromiaceans is incomplete, leaving a hole in the center (see below). This hole is plesiomorphic because, in the outgroups, the corresponding endoskeletal parts are not medially fused at all (Fig. 11). In several crab lineages the “*sella turcica*” is reduced.

The pleonal retention mechanism involves a pair of cavities (ball-and-socket principle, “*bouton-pression*”) at the posterior margin of the 6th pleon segment (Fig. 12). No uropods are involved. In raninoids this character is present only in the genus *Lyreidus* (Guinot & Bouchard 1998; our study). We consider the presence of this mechanism as plesiomorphic within the Raninoidea, and the absence (loss) is correlated to a more posterior position of the tip of the telson. This seems also the case in Cyclodorippoidea, which lack the ball-and-socket principle. Guinot & Bouchard (1998) discuss the origin of the cavities in the 6th pleon segment from uropods, but this needs confirmation by developmental data.

Uropod vestiges are completely absent. Dromiacea possess small articulated plates at the posterior margin of the 6th pleomere (Guinot & Bouchard 1998; McLay 1999). These are generally interpreted as vestigial uropods. No corresponding structures exist in Homoloidea, Cyclodorippoidea, and Eubrachiura. Hence, the existence of uropods (also vestigial) is the plesiomorphic condition.

The gills are of the phyllobranchiate type (Fig. 13). The plesiomorphic condition is trichobranchiate gills, as seen in crayfish, lobsters, and *Anomala/Anomura* (Balss 1940). (*Petrolisthes*

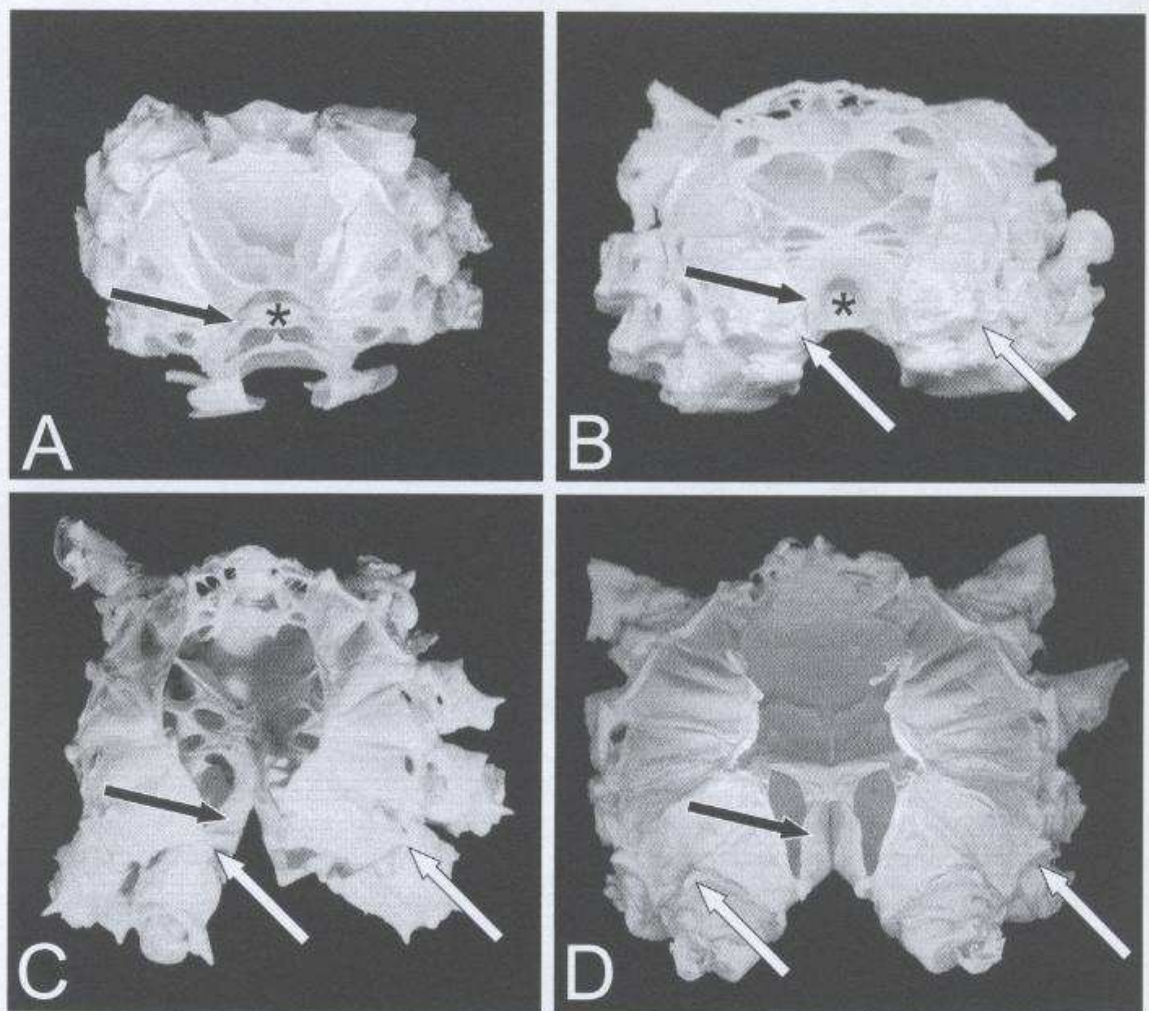


Figure 11. The endoskeleton. (A) The anomalan *Petrolisthes elongatus*. (B) The dromiacean *Dynamene pilumnoides*. (C) The homoloidean *Dagnaudus petterdi*. (D) The eubranchyuran *Ovalipes catharus*. The black arrows point to the arthropod of the last thoracic segment. In (A) they form small dorsally projecting lobes. In (B) to (D) they project anteriorly and fuse with more anterior endosternal elements. The asterisk (*) marks the open area between the two arthropod lobes. This hole is still present in the Dromiacea (B), but closed in the Homoloidea (C) and in all other Brachyura. The white arrows mark the little process at the epimeral walls of the 4th and 5th pereopodal segments that form a clip-on mechanism with the carapace margin.

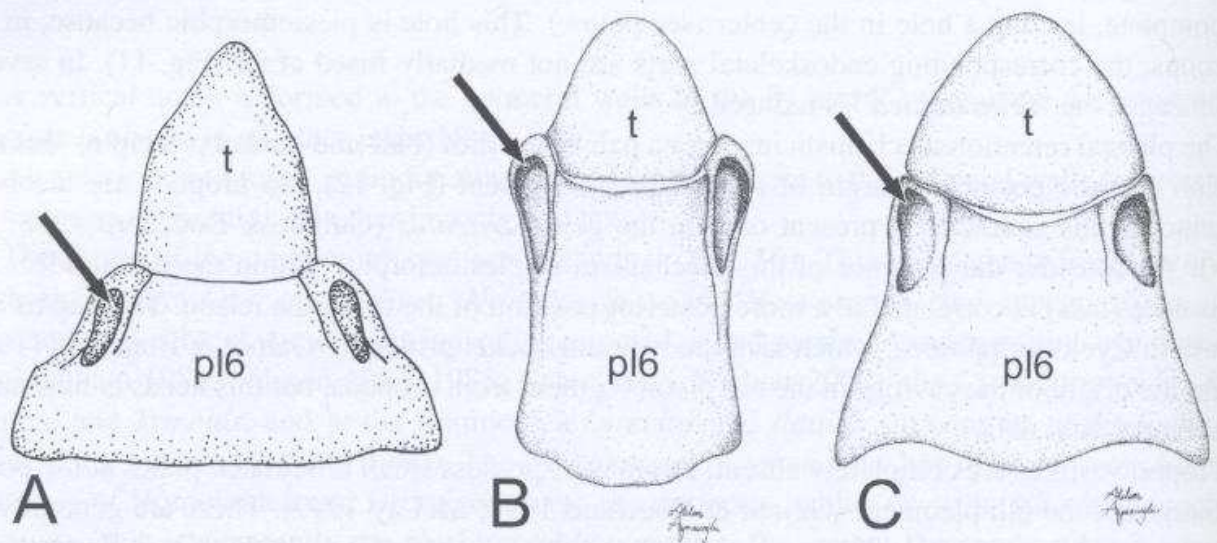


Figure 12. Pleon retention structures. The 6th pleomere is equipped with sockets at the posterior margin in representatives of homoloids (*Dagnaudus petterdi*) (A), raninoids (*Lyreidus tridentatus*) (B), and eubranchyurans (*Medorippe lanata*) (C).

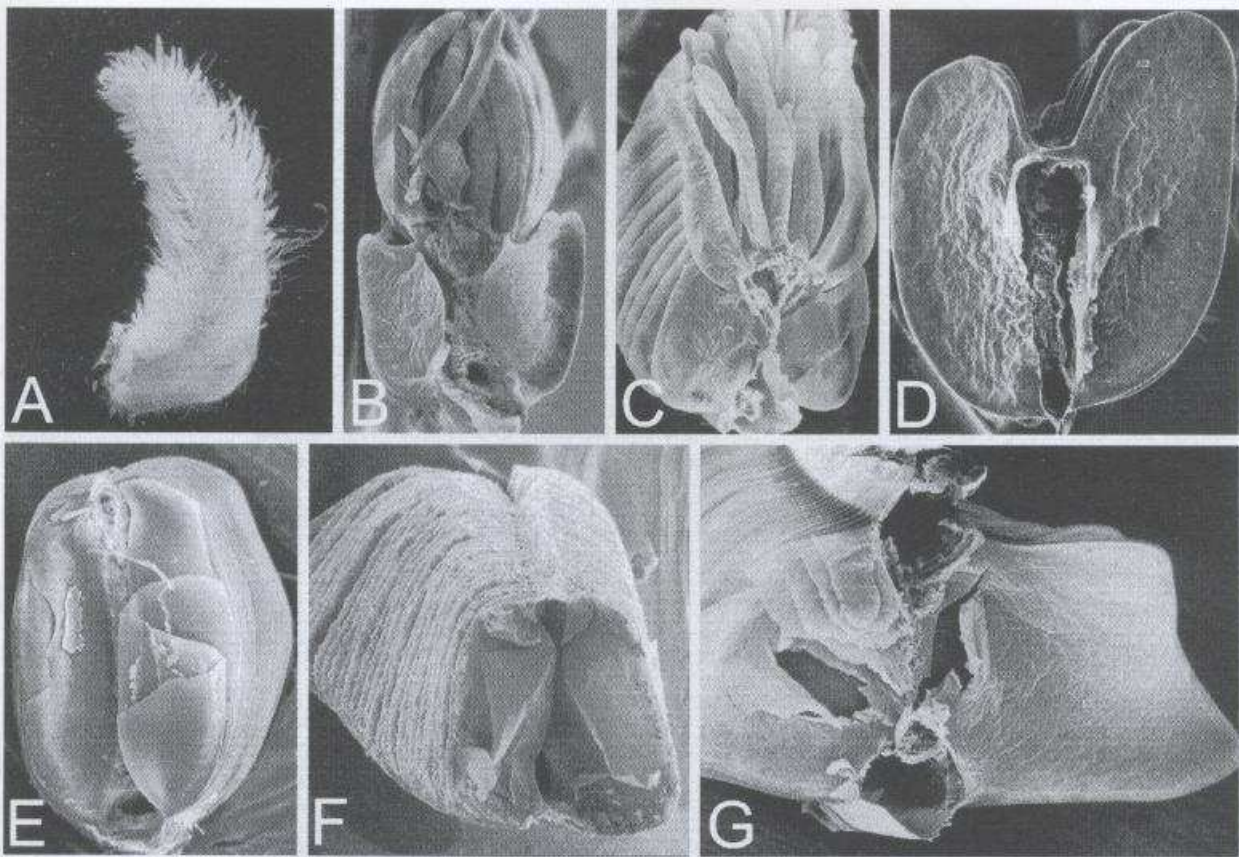


Figure 13. Gill structures. The plesiomorphic trichobranchiate gills of a freshwater crayfish (A) and of two species of dromiaceans, a homolodromiid (*Dicranodromia karubar*) (B) and a dynomenid (*Dynamene pilumnoides*) (C), the latter with a kind of intermediate gill type between trichobranchiate and phyllobranchiate gills (cross-section). (D) The heart-shaped special type of phyllobranchiate gills that evolved within Dromiacea (*Hypoconcha arcuata*). (E–G): Phyllobranchiate gills of the homoloid *Dagnaudus petterdi* (E), the raninoid *Lyreidus tridentatus* (F), and the eubranchyuran *Hemigrapsus crenulatus* (G).

and *Galathea* are examples of convergent evolution towards phyllobranchiate gills in anomalans). Interestingly enough, dromiaceans show patterns of transition between trichobranchiate and phyllobranchiate gills (see Bouvier 1896) (Figs. 13B–D). The latter occur, in particular, in the Dromiidae. These are differently shaped from the phyllobranchiate gills of the remainder of the crabs (Homoloidea, Cyclodorippoidea, Eubranchyura) (Figs. 13E–G) and are a clear case of convergence.

3.2.4 Synapomorphies of Eubranchyura-Cyclodorippoidea-Raninoidea-Homoloidea and Dromiacea = apomorphies of Brachyura (character set 9)

The endopod of the 1st maxilliped is characteristically shaped with a rectangular bend to form the bottom of a tunnel for the breathing current (Fig. 14). The endopods of the 1st maxilliped in other reptants are flat.

The carapace is locked posteriorly by projections of the epimeral walls of the segments of pereopods 4 and 5 (Fig. 11). Corresponding structures were not found in outgroup species, not even in the very crab-like *Petrolisthes* (Fig. 11A).

The arthropodagms of the last thoracic segment are elongated, incompletely fused medially, and forming two anterior wings (primitive “*sella turcica*” with hole) (see Fig. 9). The outgroups show short and separated arthropodagms of the last thoracic segment.

There are a number of other morphological characters indicating the monophyly of the Brachyura (see Scholtz & Richter 1995; Jamieson et al. 1995; Štević 1995; Schram 2001; Dixon et al. 2003; Brösing et al. 2007).

Fig. 15 presents an overview of the phylogenetic relationships of Brachyura resulting from our morphological analysis. The numbers refer to the character sets mentioned in the text.

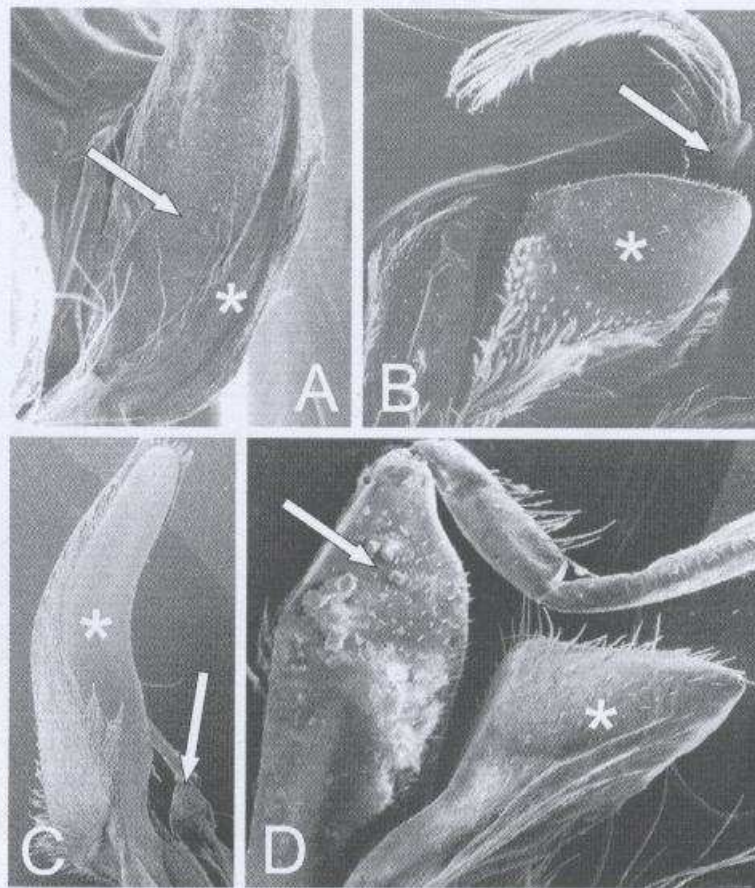


Figure 14. The endopods of the 1st maxillipeds (*) of the crayfish *Paranephrops zealandicus* (A), the dromiacean *Dynamene pilumnoides* (B), and the eubrachyurans *Medorippe lanata* (C) and *Pristatopus filholi* (D). In all brachyuran crabs the endopod shows a characteristic bend, which is absent in the flat crayfish endopod. The arrows mark the exopods.

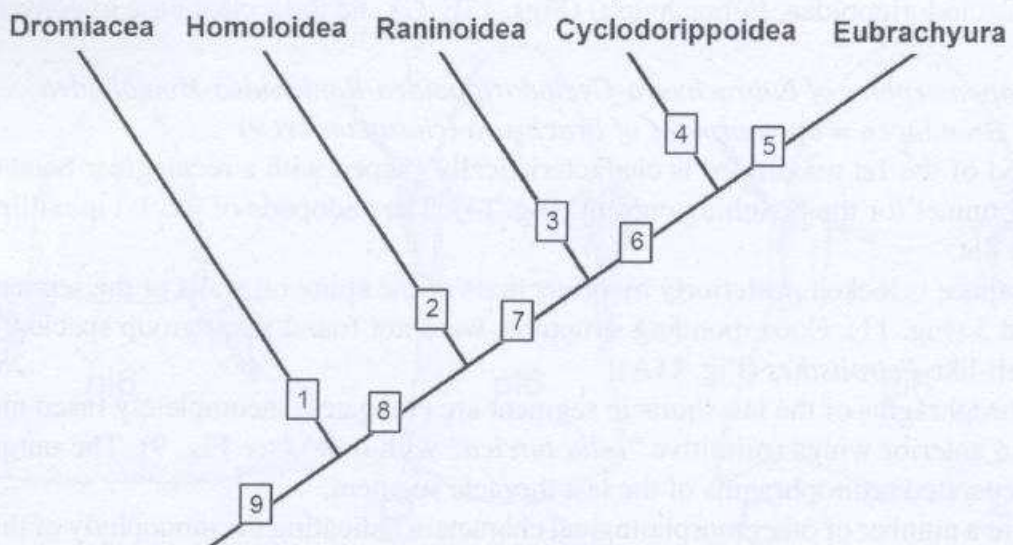


Figure 15. The cladogram of Brachyura resulting from our morphological analysis. Each branch is supported by at least one apomorphy. The numbers refer to the apomorphic character sets mentioned in the text.

4 DISCUSSION

4.1 Paraphyly of Podotremata

When Guinot erected the taxon Podotremata in the late 1970s, she used the coxal gonopores of both sexes as the constituting character for this group (Guinot 1977, 1978, 1979a). This was part of a comprehensive approach to a new subdivision of the entire Brachyura based on the position and differentiation of gonopores and the associated organs such as the spermathecae. Gordon had already proposed a similar approach in 1963, but she suggested excluding all peditreme representatives from the Brachyura, proposing that only sternitreme groups should constitute the true crabs. The major part of crabs, the Eubrachyura (*sensu de Saint Laurent 1980*), is convincingly supported by an apomorphic sternal position of the genital openings in females in combination with a spermatheca connected to the oviduct and internal fertilization. In contrast to this, the coxal position of gonopores of the Podotremata is a clear plesiomorphy since a corresponding condition is found in all other decapods and in the vast majority of Malacostraca to which the Decapoda and thus the Brachyura belong. The absence of an apomorphic character does not necessarily disprove monophyly of the group under consideration, but it at least casts doubt about its validity. Accordingly, Guinot herself discusses this issue critically (1979b). Cladistic studies mainly based on sperm ultrastructure and on some other characters seemingly support the monophyly of Podotremata (Jamieson 1994; Jamieson et al. 1995). Moreover, Tavares (2003) and Guinot & Quenette (2005) discuss the type of external sperm receptacles (here we follow the terminology of Guinot & Quenette 2005, who discriminate between a seminal receptacle as seen in eubrachyurans and the spermathecae as seen in podotrematans) occurring in a characteristic pattern in podotrematan crabs as a putative apomorphy. However, the sperm data are not very convincing. The only three sperm characters in favor of Podotremata are (i) a depressed acrosome, (ii) a predominantly horizontal zonation of the acrosome, and (iii) a bilaterally symmetrical capitate perforatorial head (Jamieson 1994; Jamieson et al. 1995). The first two characters are probably not independent of each other, and whether the conditions seen in raninoids and cyclodorippoidea have to be scored as depressed and horizontally zoned is at least disputable (see the figures in Jamieson 1994; Jamieson et al. 1995). The third character occurs only in some species of the dromiacea, and even Jamieson et al. (1995) doubt its relevance. The polarization of the spermathecal character is problematic because comparable structures do not occur in anomalans or astacids, and the eubrachyuran condition might be derived from that found in podotrematan groups. In contrast to these investigations, two molecular studies dealing with this topic have so far resolved podotrematans as paraphyletic or even polyphyletic with respect to the Eubrachyura (Spears et al. 1992; Ahyong et al. 2007). This is also suggested in a recent study using the ossicle pattern of the foregut of brachyuran crabs (Brösing et al. 2007). The molecular study by Tsang et al. (2008) is somewhat ambiguous. The only depicted tree (Tsang et al. 2008: fig 2) based on sequence data of two nuclear protein coding genes resolves Podotremata as monophyletic, but in the discussion the authors state that a tree based on just one gene shows paraphyletic podotrematans. Furthermore, their taxon sampling did not include Cyclodorippoidea, the putative sister group of Eubrachyura, which might have led to a different result.

The major podotrematan groups Dromiacea, Homoloidea, Raninoidea, and Cyclodorippoidea are all monophyletic in our analysis. However, not all groups are equally well supported. In particular, for the Homoloidea and Cyclodorippoidea more characters are needed to unambiguously support these clades. The Dromiacea do not include the Homoloidea as some authors suggest (Boas 1880; Borradaile 1907). Thus, they form the Dromiacea *sensu stricto* of Guinot (1978, 1979a). There are no apomorphies to support the separate Homolodromioidea superfamily proposed by Ng et al. (2008). A proposed group composed of the homoloids, raninoids, and cyclodorippoidea, the Archaeobrachyura (Guinot 1978), finds no support from our data. We can clearly show that the Podotremata is a paraphyletic assemblage. This is revealed not only by the result that the Cyclodorippoidea is the

sister group to the Eubrachyura, but also by the general topology and character distribution found by us. For example, the fact that some characters of the Homoloidea and Raninoidea are shared with the rest of the crabs, but not with the dromiaceans, renders the Podotremata paraphyletic. Our suggestion of internal brachyuran relationships is also supported by larval data. Williamson (1974) and, in particular, Rice (1980, 1981a, 1983) stress the similarities of homolid and raninoid zoea and megalopa larvae to those of eubrachyurans to the exclusion of dromiaceans. Moreover, several characteristics of raninoid zoeae (e.g., the overall appearance, the ventrally directed rostrum, and the dorsal and paired lateral spines on the carapace) and megalopae (reduced uropods) indicate a closer relationship to Eubrachyura than to homoloids (Rice 1980, 1981a, 1981b, 1983). Little is known about the larval development of Cyclodorippoidea, but the description of megalopa larvae lacking uropods, as is the case in Eubrachyura, corroborates our conclusion of a sister group relationship between Eubrachyura and Cyclodorippoidea (Rice 1981b).

Our tree is largely congruent with that of the most recent study of brachyuran phylogeny by Ah Yong et al. (2007). The only difference is that these authors found a close relationship between dromiids, dynomenids, and homoloids, which all form a common clade, the Dromiacea *sensu lato*. Morphologically, we did not observe any character supporting such a group, and it is also not resolved in other molecular studies on Brachyura phylogeny (Tsang et al. 2008).

4.2 Brachyuran monophyly

Although a number of carcinologists suggested that the Brachyura form a natural group or monophyletic taxon (e.g., Boas 1880; Borradaile 1907; Guinot 1978), the monophyly has been doubted by several authors based on different levels of evidence such as adult morphology, larval characters, or molecular data (Milne Edwards 1837; Gordon 1963; Williamson 1974; Rice 1980, 1981a, 1983; Spears et al. 1992). In particular, the Raninoidea and the Dromiacea have been excluded from brachyurans due to their adult morphology and the anomuran-like larvae. However, in phylogenetic systematics the exclusion of taxa is only relevant if they can be related to other taxa based on shared apomorphies. In their molecular phylogeny of the Brachyura, Spears et al. (1992) found that the dromiacean representative *Hypoconcha arcuata* clusters with hermit crabs. Accordingly, these authors suggested that dromiaceans should be excluded from Brachyura. In contrast to this view, Scholtz & Richter (1995) and Jamieson et al. (1995) listed a number of characters supporting a monophyletic Brachyura. Here we found several additional characters supporting the Brachyura as monophyletic. These characters include the shape of the endopod of the first maxilliped and the fusion of the arthrodistal membranes of the last thoracic segments forming anteriorly directed wings. What is more, our reinvestigation of *Hypoconcha arcuata* reveals that in addition to brachyuran characters, this species shows all apomorphies of the Dromiacea. These apomorphies are nested within the brachyuran characters. Hence, there is no doubt that *Hypoconcha* is a brachyuran and, in particular, a dromiacean. Our results concur with those of the molecular analysis of Ah Yong et al. (2007) and the morphological analyses of Jamieson et al. (1995) and Brösing et al. (2007).

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