

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 dynamenid (*Dynomene 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 Dromiaceae (*Hypoconcha arcuata*). (E–G): Phyllobranchiate gills of the homoloid *Dagnaudus petterdi* (E), the raninoid *Lyreidus tridentatus* (F), and the eubrachiuran *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, Eubrachiura) (Figs. 13E–G) and are a clear case of convergence.

3.2.4 Synapomorphies of Eubrachiura-Cyclodorippoidea-Raninoidea-Homoloidea and Dromiaceae = 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 arthropod 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 arthropods 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; Števcíć 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.

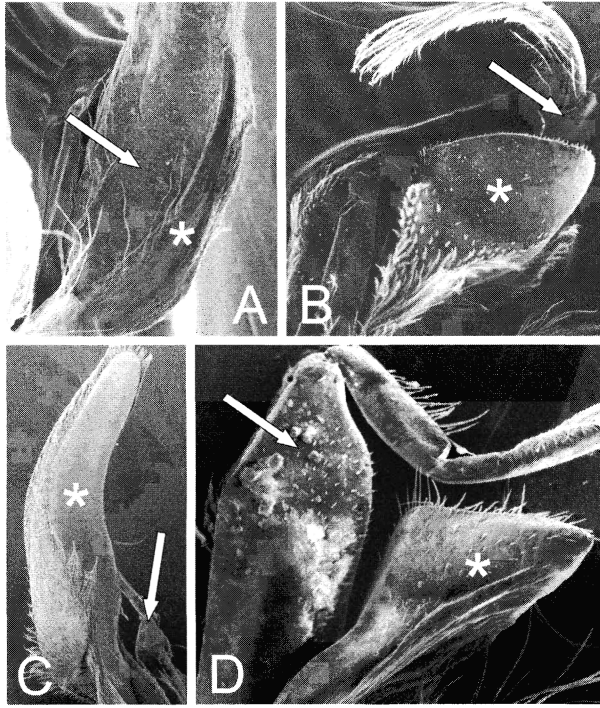


Figure 14. The endopods of the 1st maxillipeds (*) of the crayfish *Paranephrops zealandicus* (A), the dromiacean *Dynomene pilumnoides* (B), and the eubranchyurans *Medorippe lanata* (C) and *Pristatopus filholi* (D). In all brachyuran crabs the endopod shows a characteristic bend, which is absent in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

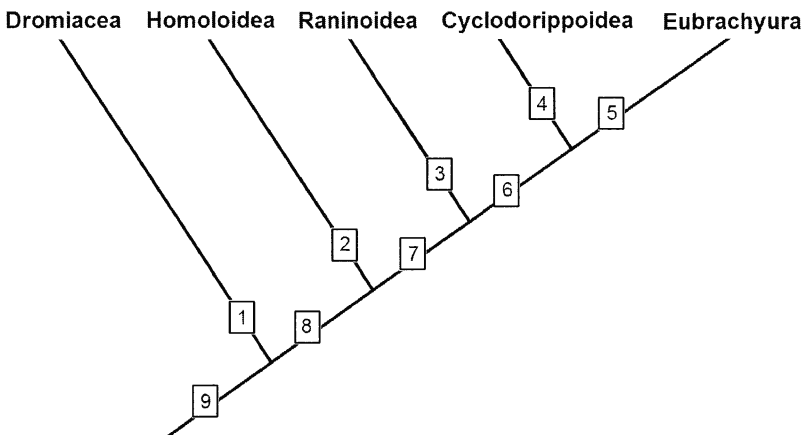


Figure 15. The cladogram of Brachyura resulting from our morphological analysis. Each branch is supported by at least one apomorphy. The numbers refer to the apomorphic character sets mentioned in the text.

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 cyclodorippoids 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 dromiaceans, 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; Ah Yong 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 cyclodorippoids, 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 Raninioidea 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 Raninioidea 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 arthrodial 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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