

Figure 7. The epipods of the 1st maxillipeds. The 1st maxillipeds of (A) the dromiacean *Dynomene pilumnoides*, (B) the raninoid *Lyreidus tridentatus*, (C) the cyclodorippoidean *Tymolus brucei*, and (D) the eubrachiuran *Ovalipes catharus*. The epipod (*) forms a triangular lobe that is elongated and supported by a calcified rod (arrows) in cyclodorippoideans and eubrachiurans. 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 brachiuran relationships based on ossicle patterns of the foregut by Brösing et al. (2007) does not resolve a eubrachiuran–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 Eubrachiura-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.

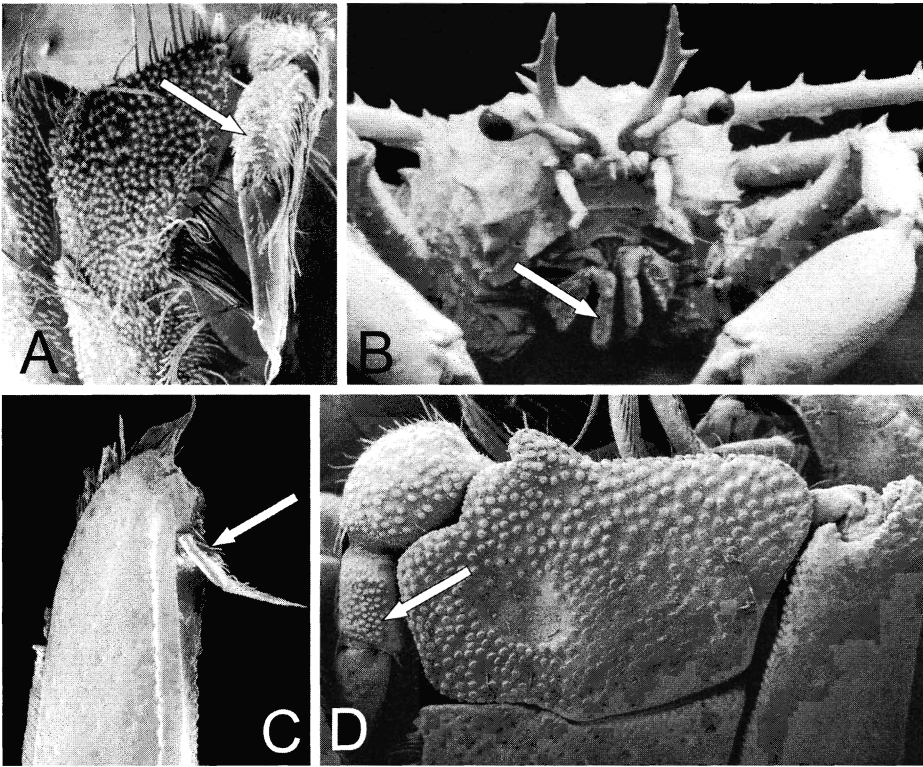


Figure 8. The orientation of the palps (arrows) of the 3rd maxillipeds in (A) the dromiacean *Dynomene pilumnoides*, (B) the homoloid *Dagnaudus petterdi*, (C) the raninoid *Lyreidus tridentatus*, and (D) the eubrachyuran *Xantho poressa*. In C and D the palps lie in one plane with the rest of the maxilliped, 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.

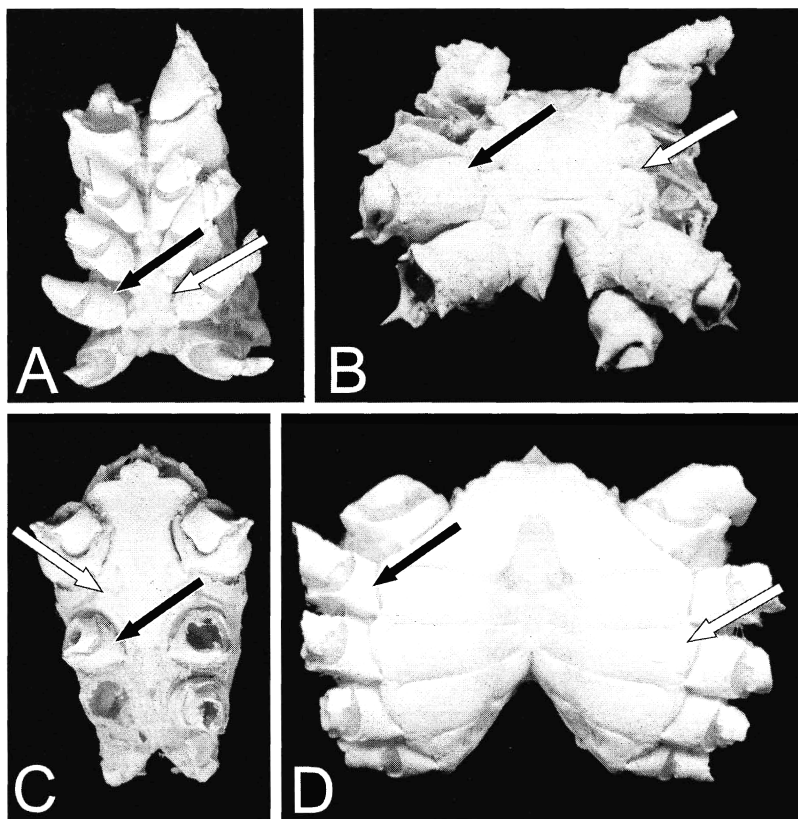


Figure 9. Sternal elements (white arrows) and coxae (black arrows) of (A) the crayfish *Paranephrops zealandicus*, (B) the homoloid *Dagnaudus petterdi*, (C) the raninoid *Lyreidus tridentatus*, and (D) the eubrachiuran *Hemigrapsus crenulatus*. The white arrows point to the lateral elements of the sternal 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).

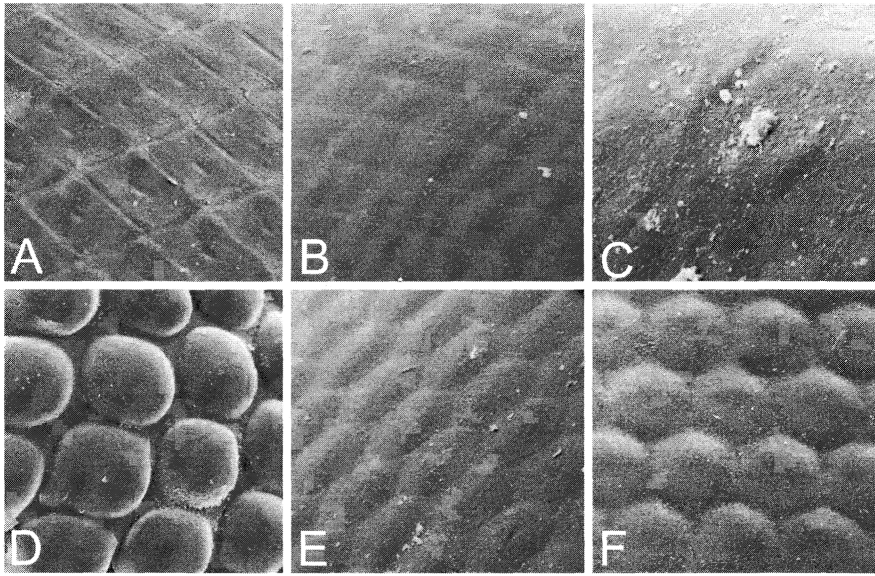


Figure 10. Facets of compound eyes. The crayfish *Paranephrops zealandicus* (A) and the dromiacean *Dynomene pilumnoides* (B) show squared facets, plesiomorphic for reptants, whereas the raninoid *Lyreidus tridentatus* (C), the cyclodorippoidean *Krangalangia spinosa* (D), and the eubrachyurans *Nectocarcinus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

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

The arthropagmal 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; Štević 1995). In contrast to this, Secretan (1998) restricts the word “*sella turcica*” to the situation found in Eubrachyura. We see no fundamental difference between the condition of homoloids, raninoids, and eubrachyurans. In contrast to this, we recognize a distinct difference between the condition found in Dromiaceae and in the other brachyuran crabs. This relates to the fact that the fusion of the arthropagm 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, “*boutonpression*”) 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. Dromiaceae 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 Eubrachyura. 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*

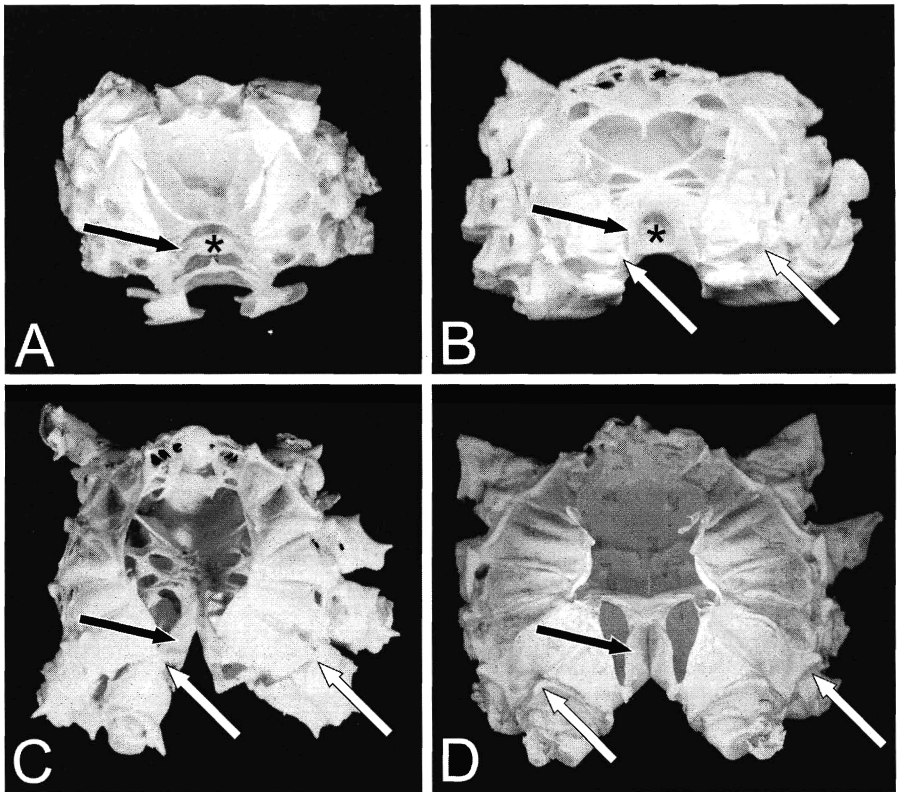


Figure 11. The endoskeleton. (A) The anomalan *Petrolisthes elongatus*. (B) The dromiacean *Dynomene pilumnoides*. (C) The homoloidean *Dagnaudus petterdi*. (D) The eubrachiuran *Ovalipes catharus*. The black arrows point to the arthropragm of the last thoracic segment. In (A) they form small dorsally 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 arthropragm 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.

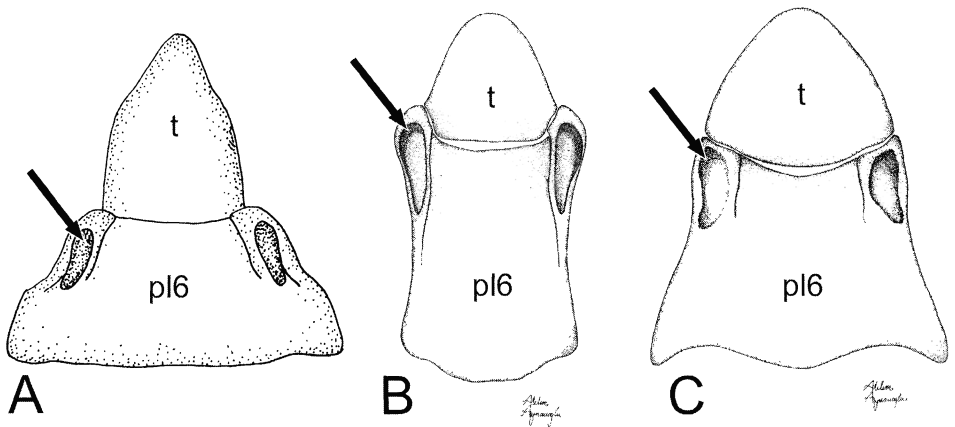


Figure 12. Pleon retention structures. The 6th pleomere is equipped with sockets at the posterior margin in representatives of homoloids (*Dagnaudus petterdi*) (A), raninoids (*Lyreidus tridentatus*) (B), and eubrachiurans (*Medorippe lanata*) (C).