

# Uropods of Eumalacostraca (Crustacea s.l.: Malacostraca) and their phylogenetic significance

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## > Abstract

The uropods are the specialised sixth pair of pleopods of eumalacostracan Crustacea. Their quite variable morphology is suggestive of a good potential as a phylogenetic signal. Because uropods have hitherto been neglected in analyses of malacostracan phylogeny, we examined them in 11 representative species of Eumalacostraca and the sixth pleopods of a phyllocarid malacostracan for outgroup comparison. Uropods have apparently evolved in the stem species of Eumalacostraca, possibly being leaf-shaped in the ground-pattern state but already with stabilising carinae along their surface and marginal setae enlarging the effective surface of the rami. Functionally, uropods aid in locomotion and, within the taxon Caridoida, also add to the special tail-flip mechanism. From an original leaf-shaped design in adaptation to different functions and lifestyles uropods may have become rod-shaped, as in Bathynellacea, Cumacea and Amphipoda, but independently so in the first taxon, while this shape might have developed in a common stem species of the latter two, inter alia. Among the taxa that have retained the leaf shape, mysidacean uropods possess a basipod that is drawn out medio-proximally into an outgrowth; Lophogastrida have a triangular median keel there. The uropods of both Euphausiacea and Decapoda also have a latero-distal prolongation, while those of Decapoda are special in bearing a longitudinal median keel on their basipod. All these differences appear to be exclusive to the respective higher taxa, demonstrating the value of uropods, and pleonal structures in general, for phylogenetic considerations.

## > Key words

Pleopods, phylogenetic systematics, morphology, basipod, endopod, exopod, pleon.

## 1. Introduction

Analyses of the systematic relationships within the Malacostraca are numerous, ranging from molecular studies (e.g. SPEARS & ABELE 1999) to morphologically-based analyses considering, for example, the circulatory system (e.g. WIRKNER 2009), the nervous system (e.g. HARZSCH & WALOSZEK 2000), or limb morphology (e.g. MAAS et al. 2009). However, the relationships within Malacostraca have remained unclear and the results are still controversial (e.g. RICHTER & SCHOLTZ 2001; FANENBRUCK et al. 2004; RICHTER et al. 2009; JENNER 2010). Even the broadly accepted hypothesis of a sister-group relationship of Phyllocarida

and Eumalacostraca as the two main subtaxa of Malacostraca (CALMAN 1904 1909; SIEWING 1956), was put into question (e.g. SCHRAM & HOF 1998; KOENEMANN et al. 2009).

Few studies have paid attention to the posterior trunk region, the pleon, and its significance for phylogenetic considerations. One exception is KNOPF et al. (2006), who examined the so-called ‘urosome’ of Thermosbaenacea and Peracarida, which is part of the pleon. However, the pleon is a complex structure. It comprises two major and different elements, the thorax II and the telson (WALOSZEK & MÜLLER 1998). Thorax

II consists of six segments, so-called pleomeres, in Eumalacostraca and an additional seventh, apodous pleomere in Phyllocarida (WALOSSEK & MÜLLER 1998). The telson is the non-segmental caudal end of the trunk, on which the anus is located. In the ground pattern of Malacostraca, the anterior six pleomeres each bear a pair of appendages, the so-called pleopods (terminology introduced by BATE 1856). These pleopods consist of an undivided limb base, or protopod, from which the two rami, the endopod and the exopod, arise (WALOSSEK & MÜLLER 1998). The protopod portion presumably represents the basipod alone, as compared to appendages of thorax I, because neither a coxa nor a 'proximal endite' could be detected with certainty so far (see WALOSSEK & MÜLLER 1990 for description and HAUG et al. 2010a for discussion of this feature and its significance for the early evolution of Crustacea). The situation is somewhat unclear as the extant representatives of the Phyllocarida have vestigial fifth and sixth pleopods lacking structural details, which prevents us from reconstructing their original morphology with certainty.

In the Eumalacostraca, the fifth and sixth pleomeres bear well-developed pleopods, but the sixth pair is modified into what is called uropods. Uropods differ from all other pleopods in their attachment, orientation and shape (BOAS 1883; SARS 1885; GROBBEN 1910). For example, whereas the first five pleopods arise in a central position on their respective pleomere and point ventrally, the uropods arise from the posterior edge of their segment and point straight backwards (BOAS 1883).<sup>1</sup> With respect to their shape, the uropods can be roughly split into two morphotypes: uropods with flat, leaf-shaped rami forming a 'tail fan' together with the telson, and uropods with rod-shaped rami (BOAS 1883). Both morphotypes differ significantly in shape from the anterior pleopods.

Uropods exhibit a broad range of morphological variation and compare well because they always arise from the same pleomere and therefore are easily detected. Although the sixth pleomere of Eumalacostraca is a fusion product of probably three segments, it has been shown that uropods are the appendages of the sixth pleomere alone (SCHOLTZ 1995). However, uropods have not been the focus of a detailed, character-analysing phylogenetic study. One reason for this might be the considerable terminological confusion, not the least of which is attributable to BOWMAN (1971). According to this author, uropods should be

the appendages of the telson, which he interpreted as the most posterior trunk somite (subsequently adopted by e.g. SCHRAM 1986; KNOPF et al. 2006), ignoring the difference between uropods and furcal rami and misinterpreting the non-somitic telson as a segment. Furcal rami are articulated (at least in their ground-pattern state) but only as flap-like outgrowths with marginal setae at the posterior end of the telson, flanking the anus (SCHMINKE 1976; WALOSSEK 1993). Furcal rami are not true limbs and, therefore, not uropods. BOWMAN'S (1971) definition opened up the possibility to apply the term 'uropod' also to non-malacostracan taxa (see e.g. MEISCH 2007) and diluted the usefulness and distinction between the different and non-homologous structures. As a consequence, not only the term uropod became regarded as obscure and ambiguous, diminishing its phylogenetic relevance, but the term furca suffered a similar fate (discussed in detail by WALOSSEK 1993). Despite the terminological confusion several authors indicated that uropods indeed bear characters of phylogenetic interest (see e.g. MAAS & WALOSZEK 2001; HAUG et al. 2010b).

All the problems discussed make uropods even more attractive for study in greater detail, and to be re-evaluated, especially in a phylogenetic context. Therefore, we examined the uropods of 11 eumalacostracan species and the sixth pleopods of one phyllocarid species with the aim to identify structures of phylogenetic significance. Based on the proposed sister-group relationship of Phyllocarida and Eumalacostraca, the phyllocarid species was used for outgroup comparison. We documented the variation existing in uropod design. Based on these data, we evaluate the detected uropodal characters for each taxon in order to reconstruct their putative ground-pattern states. Our phylogenetic approach is to plot these evaluated characters manually on existing phylograms of hypotheses about malacostracan relationships. This is seen as an *a posteriori* test of the proposed phylogeny (REIF 2002; ASSIS 2009; HAUG et al. 2012). By this, we are able to visualise, in the given phylogram, the polarity of characters and evaluate the distribution of the character states for parsimony. This results in a more complete reconstruction of the basic pattern of the Eumalacostraca and in-group taxa with particular emphasis on uropod morphology. From this, we suggest a malacostracan phylogeny explaining character evolution of uropods in a parsimonious way.

<sup>1</sup> In Amphipoda the last three pairs of pleopods are usually all called uropods (GRUNER 1993). Here, however, we strictly refer to uropods as the pair of appendages arising from the posterior edge of the sixth pleomere.

## 2. Material & methods

### 2.1. Material

The sixth pleopods of 12 species selected as representative of phylogenetically diverse malacostracan taxa (Fig. 1; Table 1) were investigated in detail. Of each pair of pleopods only the left one was illustrated, because no differences to that of the right side were observed. Specimens of *Tethysbaena argentarii*, *Allobathynella* sp., *Gammarus roeselii* and *Anaspides tasmaniae* were provided by colleagues (see Acknowledgements); material of all other species was available in the collection of the work group. All specimens were preserved in 70% ethanol, except *Diastylis rathkei*, which was obtained as a dried sample (originally collected by U. Fiedler, Kiel from Kiel Bight in 1990).

### 2.2. Methods

**Documentation:** The specimens and their uropods were documented using scanning electron microscopy (SEM), photography based on light microscopy, and pencil drawings. Preparation for SEM followed the protocol given by MAYER et al. (2008). SEM images were obtained with a Zeiss DSM 962 of the *Central Unit for Electron Microscopy* at the University of Ulm. The SEM images of *T. argentarii* were produced using a JEOL JSM-6335F at the Natural History Museum Copenhagen, Denmark. Photographic images were obtained using the digital microscope camera DCM 500 and the digital camera Canon EOS 450D. The freely available image stacking software 'Combine ZM' was used to improve the depth of focus of the photographic images. For the pencil drawings the specimens were studied under a stereomicroscope (Leica MS 5) and a normal light microscope (Zeiss Axioskop 50). The images were further processed in Adobe Photoshop CS 3.

**Measurements:** Dimensions of length, depth, and width of the uropodal basipod, endopod, and exopod were obtained by measuring from the outermost calcified part towards the opposite side. The measurements of the depth of the basipods was considered to be the major part of the medio-lateral extension. Spines and setae were not included in the measurements. For the length-ratio values for each species the length of the basipod was established as 1.0, and the lengths of endopod and exopod given in relation to this value, rounded to the second decimal place. A transverse su-

ture, being only partial or running throughout from the median to the lateral margin, may divide the exopod into two portions.

**Description:** For the descriptions of the uropods we adopted their classical grouping into leaf-shaped and rod-shaped uropods. We treat each of the species with rod-shaped uropods in alphabetical order followed by the species with leaf-shaped uropods (Table 3). *Nebalia bipes* (Fig. 4), chosen as outgroup taxon, is described last. The terminology applied follows the proposed standard system for Crustacea and arthropods in general by WALOSSEK (1993, 1999) and HAUG et al. (2010a). For definition of carinae on the rami we follow POORE (2004); for setae, i.e. articulated cuticular outgrowths, we follow GARM (2004). Abbreviations are given in Table 2.

**Evaluation:** The species examined were taken as representatives of a malacostracan taxon (Table 1). The detailed examination allowed the detection of morphological characters and their states (Table 3). We are aware of remaining difficulties with categorising morphological states, which cuts potential continua into arbitrary portions and can, therefore, influence the analysis. The categories detected for each species were evaluated by comparison with other extant and fossil representatives of a taxon (Table 3). This was regarded as a validity check for the uropodal character states, i.e. how well our findings represent the ground-pattern state of a taxon in question.

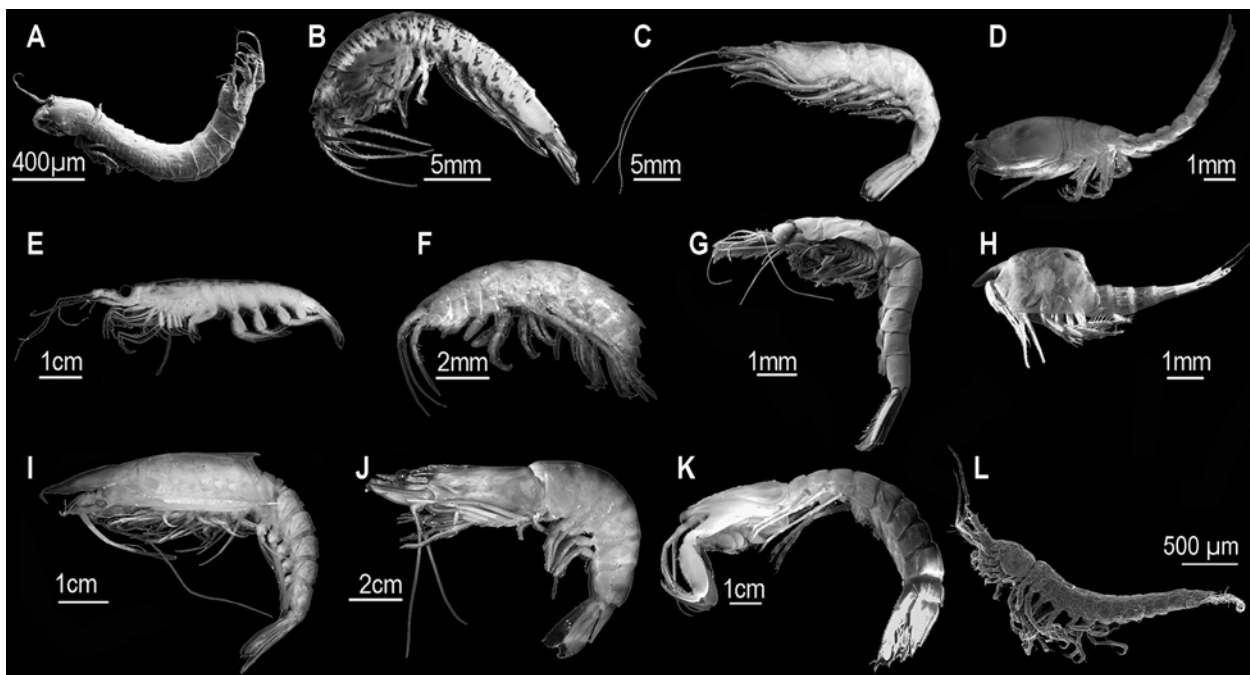
**Mapping:** The uropod characters were examined for phylogenetic significance and their congruence with existing phylogenetic hypotheses. Congruence is measured using parsimony as the criterion, i.e. the number of transformations needed for a particular character along a particular phylogeny. For this test, the character states reconstructed for the ground patterns of the examined taxa were mapped by hand onto the malacostracan phylogeny proposed by SIEWING (1956), and for within Peracarida the phylogenies of RICHTER & SCHOLTZ (2001) and WIRKNER & RICHTER (2010) were additionally used (Fig. 5B,C). After this mapping a critical, *a posteriori* evaluation of the character distribution using the parsimony principle was made (REIF 2002; ASSIS 2009; HAUG et al. 2012; Fig. 7).

## 3. Results

Uropods of the investigated species comprise a proximal portion, the basipod, and two rami, endopod and exopod. They are either rod-shaped or leaf-shaped: rod-like uropods have rather cylindrical rami, whereas

**Table 1.** List of species examined as representatives of particular supra-specific taxa. Column headings: L = length of examined specimens; N = number of examined specimens.

Species	Illustrated specimen	Illustrated uropod	Taxon	L [cm]	N
<i>Allobathynella</i> sp.	Fig. 1A	Fig. 2A,B	Syncarida Packard, 1885 Bathynellacea Chappuis, 1915	0.15	2
<i>Anaspides tasmaniae</i> Thomson, 1894	Fig. 1B	Fig. 3A	Syncarida Packard, 1885 Anaspidacea Calman, 1904	3.2	6
<i>Crangon crangon</i> (Linné, 1758)	Fig. 1C	Fig. 3C	Eucarida Calman, 1904 Decapoda Latreille, 1802 Pleocyemata Burkenroad, 1963 Caridea Dana, 1852	3.0	12
<i>Diastylis rathkei</i> Kröyer, 1841	Fig. 1D	Fig. 2C,D	Peracarida Calman, 1904 Cumacea Kröyer, 1846	1.1	8
<i>Euphausia superba</i> Dana, 1852	Fig. 1E	Fig. 3E	Eucarida Calman, 1904 Euphausiacea Dana, 1852	6.2	17
<i>Gammarus roeselii</i> Gervais, 1835	Fig. 1F	Fig. 2E,F	Peracarida Calman, 1904 Amphipoda Latreille, 1816	1.4	9
<i>Mysis</i> sp.	Fig. 1G	Fig. 3G	Peracarida Calman, 1904 Mysida Haworth, 1825	1.5	17
<i>Nebalia bipes</i> Fabricius, 1789	Fig. 1H	Fig. 4E,F	Phyllocarida Packard, 1879 Leptostraca Claus, 1880	0.6	5
<i>Neognathophausia ingens</i> (Dohrn, 1870)	Fig. 1I	Fig. 3I	Peracarida Calman, 1904 Lophogastrida Sars, 1870	10.5	2
<i>Penaeus monodon</i> Fabricius, 1798	Fig. 1J	Fig. 3K	Eucarida Calman, 1904 Decapoda Latreille, 1802 Dendrobranchiata Bate, 1888	19	4
<i>Squilla mantis</i> (Linné, 1758)	Fig. 1K	Fig. 4A,B	Hoplocarida Calman, 1904 Stomatopoda Latreille, 1817	16	8
<i>Tethysbaena argentarii</i> (Stella, 1951)	Fig. 1L	Fig. 4C,D	Neocarida Ax, 1999 Thermosbaenacea Monod, 1927	0.35	23



**Fig. 1.** Species examined in lateral view (see also Table 1). A, G, L: SEM micrographs; B–F, H–K: photographs, taken with transmitted light. A: *Allobathynella* sp. (Bathynellacea). B: *Anaspides tasmaniae* (Anaspidacea). C: *Crangon crangon* (Decapoda: Pleocyemata). D: *Diastylis rathkei* (Cumacea). E: *Euphausia superba* (Euphausiacea). F: *Gammarus roeselii* (Amphipoda). G: *Mysis* sp. (Mysida). H: *Nebalia bipes* (Phyllocarida) (courtesy of Carolin and Joachim T. Haug). I: *Neognathophausia ingens* (Lophogastrida). J: *Penaeus monodon* (Decapoda: Dendrobranchiata). K: *Squilla mantis* (Hoplocarida: Stomatopoda) (courtesy of Carolin and Joachim T. Haug). L: *Tethysbaena argentarii* (Thermosbaenacea).



leaf-shaped uropods exhibit plane, leaf-like rami (viz. the rami are much less antero-posteriorly extended than medio-laterally). The two uropod shapes are always caused and constituted by extension of the same components. Leaf-shaped uropods constitute a tail fan together with the telson lying in the middle. The endopod and exopod insert distally to the basipod and may rise at the same level, medio-distally (endopod), or latero-proximally (exopod). The basipod of leaf-shaped uropods may exhibit a postero-median depression, a median keel, a latero-distal prolongation, a medio-proximal outgrowth, and/or a basipodal spine. The components may carry various spines and setae, the basipod often is adorned with median spines. Endo- and exopod are either undivided or two-divided and may carry setae medially or marginally, depending on their shape (i.e. broad and leaf-like or rod-shaped). Mainly broad uropodal rami may be stiffened by so-called carinae. These carinae can be broad and flat or slender and sharp.

### 3.1. Species with rod-shaped uropods

#### 3.1.1. *Allobathynella* sp. (Bathynellacea)

Bathynellacea are inter alia characterised by a sixth pleomere and telson being fused to a so-called pleotelson, which, in adults, bears uropods, furcal rami, and the anus (Fig. 1A; SCHMINKE 1982; GRÜNER 1993). The uropods (Fig. 2A,B; Table 3) have a length ratio value of 1:0.58:0.52 and arise from the ventro-lateral surface of the anterior part of the pleotelson. The basipod of the uropods is subcylindrical and its basal surface inserts to the trunk. Twelve cuspidate setae constitute a proximo-distally orientated row on the median surface of the basipod. These setae are subequal in length (ca. 55 µm) and point medially towards the furca. The rami insert at the same level besides each other distally on the basipod. The endopod is undivided and club-shaped. A proximo-distally orientated row of seven cuspidate setae extends along nearly the whole median surface of the endopod. The sturdy proximal seta is the shortest, while the setae become successively larger towards the distal end. They point medio-distally. Another proximo-distal row of simple setae (Fig. 2A) extends along the distal two thirds of the anterior surface of the endopod. These setae vary in length and point antero-distally. The undivided and cone-shaped exopod bears a proximo-distally orientated row of six simple setae. They vary in length and point latero-distally. The three long distal setae are placed on the tip of the exopod and point medio-distally. No carinae are present.

#### 3.1.2. *Diastylis rathkei* (Cumacea)

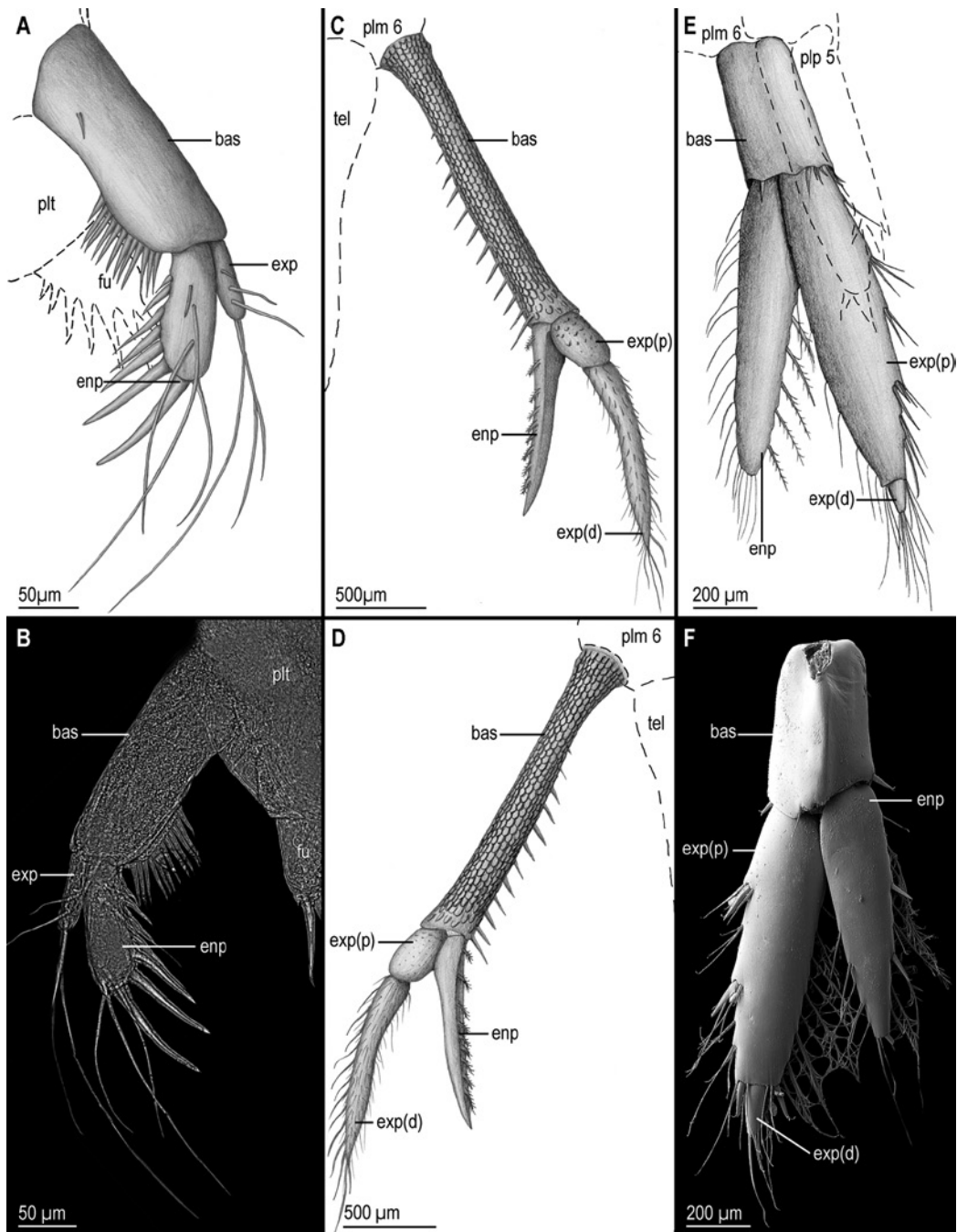
The sixth pleomere is not fused with the cone-shaped telson. The uropods (Fig. 2C,D; Table 3) have a length ratio value of 1:0.66:0.72 and arise postero-laterally from the sixth pleomere. Their basipod is subcylindrical and its basal surface inserts to the trunk. Medially the basipod has a proximo-distally orientated row of 12 cuspidate setae being equal in length (ca. 100 µm) and pointing medially towards the telson. Many regularly arranged scales (ca. 20 µm in diameter) are placed on the basipod. The rami insert at the same level besides each other distally on the basipod. The endopod is undivided and slightly cone-shaped. Its lateral side is depressed along its entire length and the depression is triangular in section. The median surface of the endopod bears a proximo-distally orientated row of eight pappose/ cuspidate setae of subequal length (ca. 50 µm), which point medio-distally. The exopod is divided into two portions: the distal portion is cone-shaped and is clearly set off from the subovoid proximal portion by a constriction. The proximal portion bears scales but lacks setae, whereas the distal portion bears regularly arranged simple setae all around but no scales. No carinae are present.

#### 3.1.3. *Gammarus roeselii* (Amphipoda)

The sixth pleomere is not fused with the telson. The uropods (Fig. 2E,F; Table 3) have a length ratio value of 1:1.39:1.78 and stem ventro-laterally from the posterior surface of the sixth pleomere, directly underneath the telson. The basipod is subcylindrical and its basal surface inserts to the trunk. Its distal margin bears a few simple setae. The rami insert at the same level adjacent to each other, distally on the basipod. The endopod is undivided and cone-shaped. The endopod bears a proximo-distally orientated row of numerous simple setae on the median side, a proximo-distally orientated row of pappose setae on the lateral side, and diffusely spread setae on its tip. The exopod is divided into two portions: the very long proximal portion is subcylindrical, having narrower proximal and distal ends, whereas the short distal portion is cone-shaped. The proximal portion bears two proximo-distally orientated rows of setae, one constituted by regularly arranged, simple setae on the median side, and another one formed by five groups of simple setae on the lateral side. No carinae are present.

**Table 2.** Used abbreviations and their meanings.

Abbreviation	Meaning	Abbreviation	Meaning
bas	basipod	plm	pleomere
bas sp	basipodal spine	plp	pleopod
enp	endopod	plt	pleotelson
exp	exopod	st	sternum
exp(d)/(p)	distal/proximal portion of exopod	tel	telson
fu	furca	urp	uropod



**Fig. 2.** Sixth pleopods (uropods) of various Malacostraca (all rod-shaped). A, C–E: pencil drawings, dashed lines indicate adjacent structures; B: photograph, light microscopy using transmitted light; F: SEM micrograph. Abbreviations see Table 2. A, B: *Allobathynella* sp., anterior (A) and posterior (B) view of left uropod. C, D: *Diastylis rathkei*, anterior (C) and posterior (D) view of left uropod. E, F: *Gammarus roeselii*, anterior (E) and posterior (F) view of left uropod (= ‘uropod 3’ in amphipod terminology; covered *in situ* by pleopod 5 = ‘uropod 2’ in amphipod terminology).

## 3.2. Species with leaf-shaped uropods

All species in this set possess uropods that form a so-called tail fan together with the telson, and the sixth pleomere is never fused to the telson.

### 3.2.1. *Anaspides tasmaniae* (Anaspidacea)

The uropods (Fig. 3A; Table 3) have a length ratio value of 1:4.15:4.44 and arise ventro-laterally from the posterior edge of the sixth pleomere. The basipod (Fig. 3A,B) is subcuboid and its basal surface inserts to the trunk, partially enclosed by the sixth pleomere. The median part of the posterior side of the basipod is deeply depressed (postero-median depression, Fig. 3B, white arrow; Table 3). Numerous cuspidate setae arise from the distal margin of the lateral surface of the basipod. The rami insert at the same level adjacent to each other distally at the basipod. The endopod is undivided and leaf-shaped. It bears two carinae, one on its posterior side and one on its anterior side (Fig. 3A, black star; Table 3). The plumose setae on the median, distal, and lateral margins are shortest proximally and longest distally. The leaf-shaped exopod is incompletely divided into two portions by a transverse suture (Fig. 3A, black arrow), which is limited to the lateral third of the posterior surface of the exopod. One carina lies on the posterior side of the exopod. Seven cuspidate setae arise in a proximo-distally orientated row on the lateral edge of the proximal portion of the exopod between insertion and suture. The plumose setae on the median, distal, and partly lateral margins are shortest proximally and longest distally.

### 3.2.2. *Crangon crangon* (Caridea, Pleocyemata, Decapoda)

The uropods (Fig. 3C, Table 3) have a length ratio value of 1:3.61:3.82 and stem ventro-laterally from the sixth pleomere. The basipod (Fig. 3C,D) is subconical. The median surface of the cone inserts to the trunk and is posteriorly depressed. The distal margin on the basipod possesses a prominent lateral, tipped prolongation (Fig. 3D, white arrowhead). Medially the basipod has a longitudinal, fold-like keel being subrectangular in anterior view (Fig. 3C, black arrowhead). The rami insert at the same level adjacent to each other distally on the basipod. The endopod is undivided and leaf-shaped. It bears three carinae, two on the posterior surface and one anteriorly (Fig. 3C, black stars). The plumose setae on the lateral, distal, and median margins are not equal in length, but shortest proximally and longest distally. The leaf-shaped exopod is com-

pletely divided into two portions by a medio-lateral suture (Fig. 3C, black arrow). It bears two carinae, one on the anterior surface (Fig. 3C, black star) and one on the posterior surface (Table 3). The lateral side shapes a non-articulated, spiky outgrowth bearing two tipped spines both pointing latero-distally. The plumose setae on the lateral, distal, and median margins are shortest proximo-medially and latero-distally distal to the spiky outgrowth.

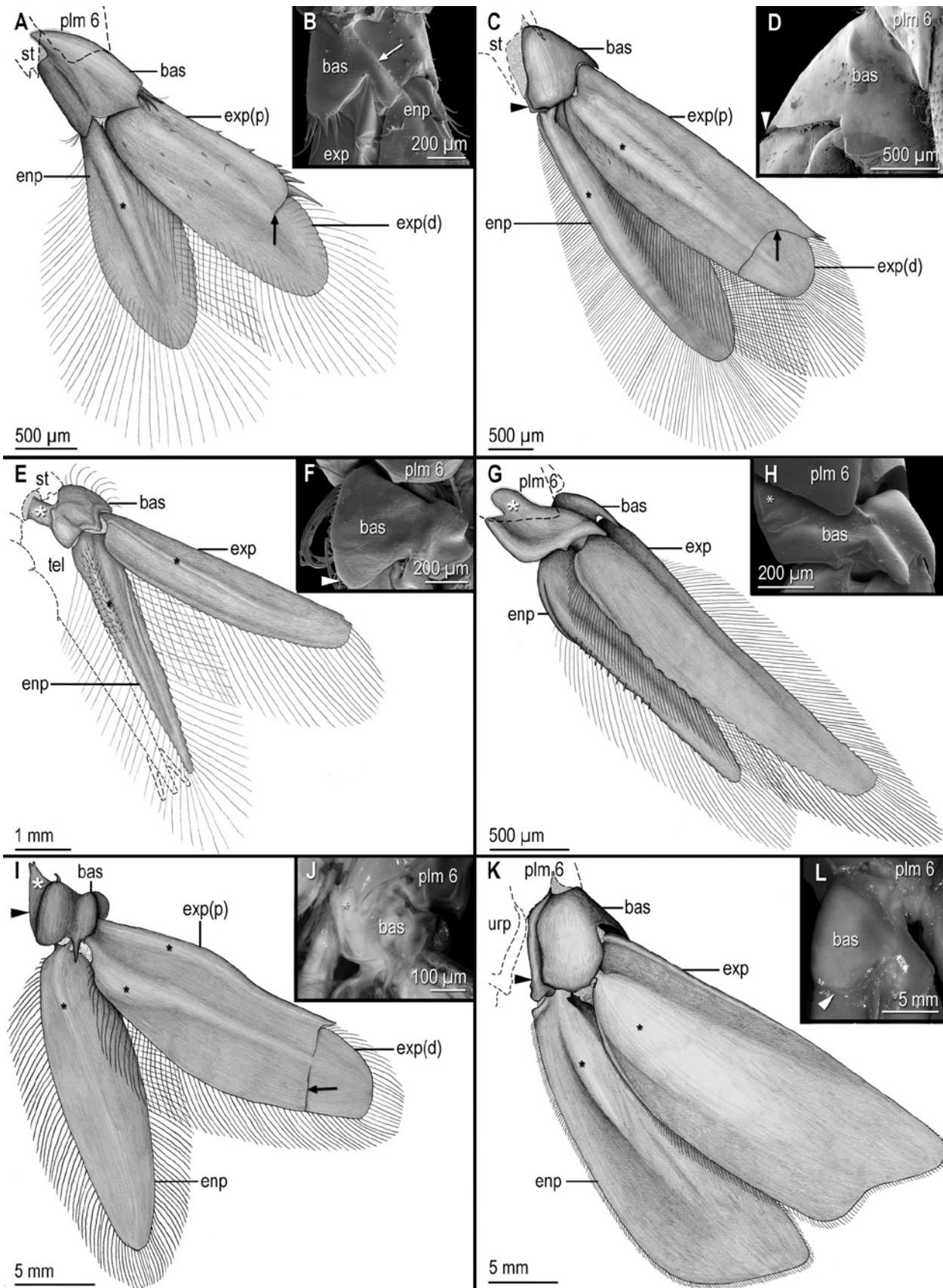
### 3.2.3. *Euphausia superba* (Euphausiacea)

The uropods (Fig. 3E; Table 3) have a length ratio value of 1:9.08:9.54 and arise ventro-terminally from the sixth pleomere. The basipod (Fig. 3E,F) is subconical, being proximally truncate. The truncate part is cylindrically drawn out and inserts with its tip to the trunk (Fig. 3E, white star). This outgrowth is set off laterally. Postero-medially the basipod is slightly depressed (Fig. 3F; Table 3). The posterior side is slightly triangular exhibiting a distal margin forming a so-called prolongation (Fig. 3F, white arrowhead), which is semi-round in lateral view. Numerous plumose setae arise in a proximo-distally orientated row from the lateral surface of the basipod. The rami insert at the same level adjacent to each other distally on the basipod. The endopod is undivided and leaf-shaped. It bears two carinae, one on the anterior surface and one on the posterior surface (Fig. 3E, black star; Table 3). The plumose setae on the lateral, distal, and median margins are not equal in length, but are shortest proximally, the longest being located on the distal end. The exopod is undivided and lanceolate. It bears two carinae, one on the anterior surface and one on the posterior surface (Fig. 3E, black star; Table 3). The median and distal margins of the exopod bear numerous plumose setae, the latero-distal ones being the shortest.

### 3.2.4. *Mysis* sp. (Mysida)

The uropods (Fig. 3G; Table 3) have a length ratio value of 1:5.95:7.46 and stem ventro-laterally from the sixth pleomere. The basipod (Fig. 3G,H) is nearly cuboid and its median surface is drawn out proximally for insertion to the trunk (Fig. 3G,H, white stars). This outgrowth is set off laterally. The sternal plate of the sixth pleomere covers the insertion of the limb. The basipod is postero-medially depressed. On the lateral side of the basipod there is a hook pointing terminally. The rami insert at the same level adjacent to each other distally on the basipod. The endopod is undivided and lanceolate. It bears one carina on the anterior surface. A deep fissure is situated on the lateral side of the endopod. The median side of the endopod bears thirteen





cuspidate setae arranged in a proximo-distally orientated row. Plumose setae arise from its lateral, distal, and median margins. They are not equal in length, but are

shortest proximally, the longest being located on the distal end. The exopod is undivided and leaf-shaped. One carina lies on the posterior surface. The plumose



setae on the lateral, distal, and median margins are not equal in length, but are shortest proximally, the longest being located on the distal end.

### 3.2.5. *Neognathophausia ingens* (Lophogastrida)

The uropods (Fig. 3I; Table 3) have a length ratio value of 1:4.05:4.58 and arise ventro-laterally from the posterior edge of the sixth pleomere. The basipod (Fig. 3I,J) is subconical in shape and postero-medially depressed. Its medio-proximal end is drawn out being triangular in anterior view and having a proximal bifurcation that inserts to the trunk (Fig. 3I,J, white stars; Table 3). This laterally set-off outgrowth extends medio-posteriorly further fading to a median keel, which is triangular in anterior view. A prominent, non-articulated spine arises anteriorly at the distal margin. The rami insert at the same level adjacent to each other distally on the basipod. The endopod is undivided and leaf-shaped; it bears two carinae, one on its posterior surface and one on the anterior surface (Fig. 3I, black star; Table 3). The plumose setae on the lateral, distal, and median margins are not equal in length, but are shortest proximally, the longest being located on the distal end. The leaf-shaped exopod is divided into two portions by a latero-median suture (Fig. 3I, black arrow). It bears three carinae; one carina is at its posterior surface, two extend on the anterior surface (Fig. 3I, black stars; Table 3). The lateral side exhibits a non-articulated, spiky outgrowth pointing latero-distally. The plumose setae on the lateral, distal, and median margins are not equal in length, but are shortest proximally, the longest being located on the distal end.

### 3.2.6. *Penaeus monodon* (Dendrobranchiata, Decapoda)

The uropods (Fig. 3K; Table 3) have a length ratio value of 1:1.96:2.3 and arise ventro-laterally from the sixth pleomere. The basipod (Fig. 3K,L) is subconical and its proximal surface inserts to the trunk. It is postero-medially depressed. The distal margin on

the posterior side of the basipod possesses a prominent lateral prolongation (Fig. 3L, white arrowhead; Table 3), which is rounded in lateral view. Medially the basipod has a longitudinal, fold-like keel being subrectangular in anterior view (Fig. 3K, black arrowhead; Table 3). Neither a medio-proximal outgrowth nor a basipodal spine is present. The rami insert at the same level adjacent to each other distally on the basipod. The endopod is undivided and leaf-shaped. It has two carinae, one on the posterior surface and another broad one on the anterior surface (Fig. 3K, black star; Table 3). The median, distal, and lateral margins exhibit equally short, simple setae. The exopod is undivided and leaf-shaped. It bears two carinae, one lies on the posterior surface, another broad carina runs along its anterior surface (Fig. 3K, black star; Table 3). Short, simple setae arise on the median and distal margins of the exopod.

### 3.2.7. *Squilla mantis* (Stomatopoda, Hoplocarida)

The uropods (Fig. 4A,B; Table 3) have a length ratio value of 1:1.82:2.71 and stem antero-laterally from the trunk in a deep articulation. The basipod is large and has two distinct parts: the main body and the prominent basipodal spine. The main body is cubic in shape. It is postero-dorsally drawn out into a flat basipodal spine, which bends inwards and is distally bifurcate. The endopod inserts on the distal side of the main body of the basipod at an outgrowth; the exopod inserts on the lateral side of the main body of the basipod. The endopod is undivided and machete-shaped. One carina is located on the anterior side of the endopod. The plumose setae on the lateral, distal, and median margins are not equal in length, but are shortest proximally, the longest being located on the distal end. The exopod is divided into two portions: the proximal portion is subcuboidal and the distal portion is leaf-shaped. Posteriorly, the exopod bears one carina, which extends across both portions (Fig. 4B; black stars). Eight cuspidate setae arise from the lateral surface of the proximal portion of the exopod becoming successively larger from proximal to distal. The median surface of the proximal portion of the

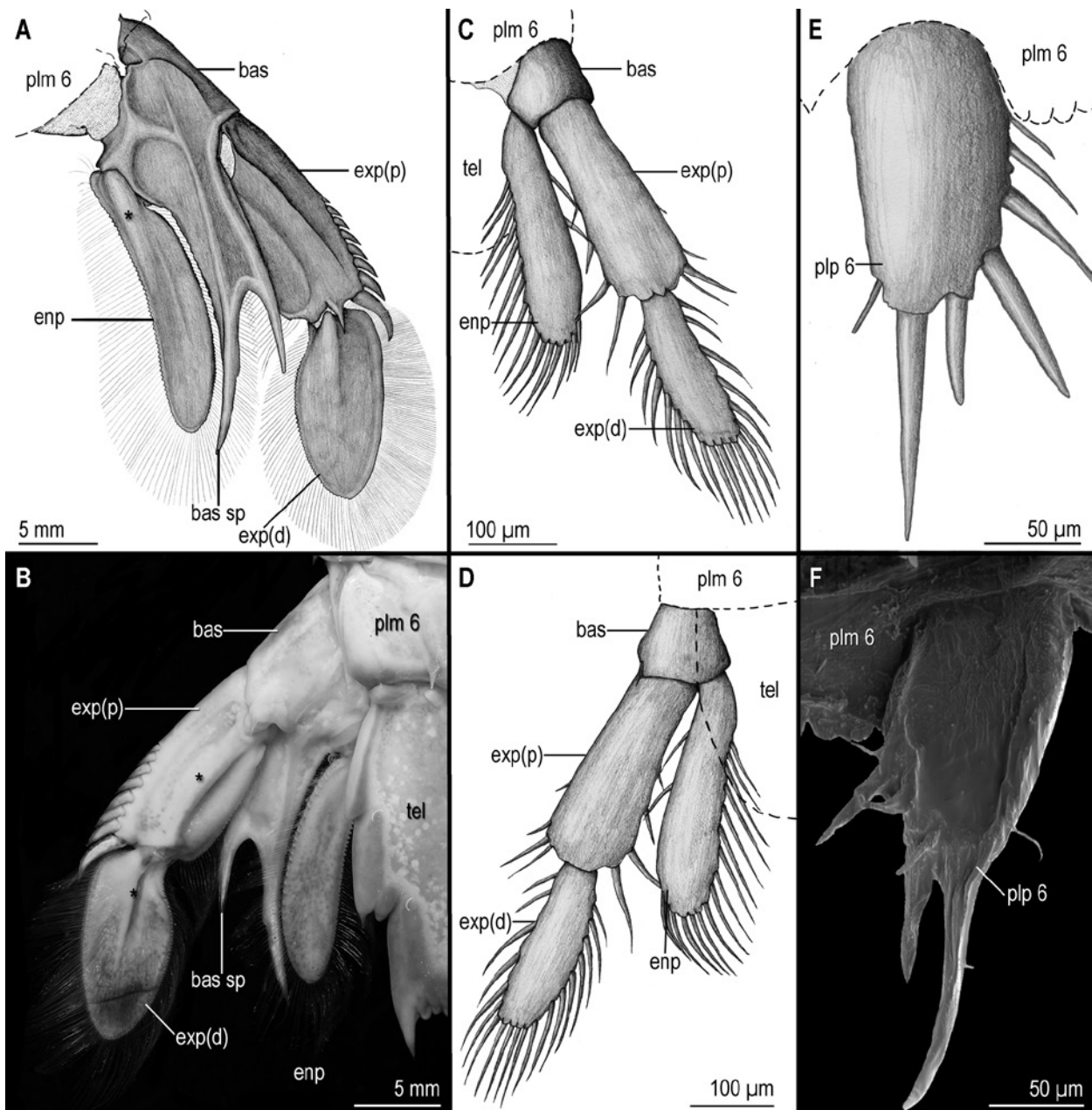
← **Fig. 3.** Sixth pleopods (uropods) of various Malacostraca (all leaf-shaped). A, C, E, G, I, K: pencil drawings, dashed lines indicate adjacent structures; membranous parts are dotted; B, D, F, H: SEM micrographs; J, L: photographs, taken with transmitted light. Black stars emphasise carinae; black arrows indicate sutures; black arrowheads display keels; white stars emphasise medio-proximal prolongations; white arrow emphasises margin of depression; white arrowheads display latero-distal prolongations. Abbreviations see Table 2. **A:** *Anaspides tasmaniae*, anterior view of left uropod. **B:** *A. tasmaniae*, basipod from posterior, telson removed. **C:** *Crangon crangon*, anterior view of left uropod. **D:** *C. crangon*, basipod from posterior. **E:** *Euphausia superba*, anterior view of left uropod. **F:** *E. superba*, basipod from posterior. **G:** *Mysis* sp., anterior view of left uropod. **H:** *Mysis* sp., basipod from anterior. **I:** *Neognathophausia ingens*, anterior view of left uropod. **J:** *N. ingens*, basipod from anterior. **K:** *Penaeus monodon*, anterior view of left uropod. **L:** *P. monodon*, basipod from posterior.

**Table 3.** Characteristics found on (parts of) uropods of all examined eumalacostracan species. Extension equates to length, depth, and width values. Column headings: Part = part of uropod under consideration; Quality = assessed quality of uropod part; remaining headings = species names (partly abbreviated), see Table 1 for full information. Abbreviations: **ant.** = anterior(ly); **dist.** = distal(ly); **exp(d)** = distal portion of exopod; **exp(p)** = proximal portion of exopod; **lat.** = lateral(ly); **lrv** = length ratio value (see Material and Methods); **med.** = median/medially; **post.** = posterior(ly); **prox.** = proximal(ly); **\*** = without basipodal spine.

Part	Quality	<i>Allobathyn.</i>	<i>D. rathkei</i>	<i>G. roeselii</i>	<i>A. tasmaniae</i>	<i>C. crangon</i>	<i>E. superba</i>	<i>Mysis</i> sp.	<i>N. ingens</i>	<i>P. monodon</i>	<i>S. mantis</i>	<i>T. argentarii</i>	
urp	shape	rod-like	rod-like	rod-like	leaf-like	leaf-like	leaf-like	leaf-like	leaf-like	leaf-like	leaf-like	leaf-like	
	oriented	lat.-dist.	lat.-dist.	vent.-lat.	lat.-dist.	lat.-dist.	lat.-dist.	lat.-dist.	lat.-dist.	lat.-dist.	lat.-dist.	lat.-dist.	
	lrv: 1:	0.58: 0.52	0.66: 0.72	1.39: 1.78	4.15: 4.44	3.61: 3.82	9.08: 9.54	5.95: 7.46	4.05: 4.58	1.96: 2.30	1.82: 2.71	3.82: 5.95	
bas urp	shape	cylindrical	cylindrical	subcylindrical	subcuboid with <b>med. depress.</b>	subconical with <b>med. depress., med. keel, lat.-dist. pronon.</b>	subconical with <b>med. depress., lat.-dist. pronon.</b>	subcuboid with <b>med. depress., med. keel, drawn out med.-prox., lat. hook</b>	subconical with <b>med. depress., drawn out med.-prox.</b>	subconical with <b>med. depress., med. keel, lat.-dist. pronon.</b>	subconical with <b>med. depress., med. keel, lat.-dist. pronon.</b>	cubic with prominent basipodal spine	subconical with <b>med. depress.</b>
	silhouette	all sides subrectangular	all sides dumbbell-shaped	all sides rectangular with rounded edges	post., med., and lat. sides subrectangular, ant. side trapezoid	post. and ant. sides subtriangular, med. angular, lat. side rectangular, lat. side rhombic	post. side subtriangular, ant., lat., med. side subrectangular	post. and ant. sides subrectangular, med. angular, lat. side semicircular	post. side right triangular, ant. and med. side rectangular, lat. side subrhombic	post. and ant. side subtriangular, med. side rectangular, lat. side rhombic	post. and ant. sides slightly triangular, med. and lat. sides subtriangular	post. and ant. side subtriangular, med. angular, med. and lat. side rectangular	
	extension	150 µm 60 µm 50 µm	1,155 µm 155 µm 195 µm	590 µm 320 µm 255 µm	755 µm 580 µm 535 µm	1,880 µm 1,765 µm 550 µm	635 µm 730 µm 545 µm	380 µm 715 µm 255 µm	365 µm 235 µm 155 µm	1,105 µm 1,130 µm 770 µm	0.85 cm 0.9 cm 0.45 cm *	80 µm 45 µm 105 µm	80 µm 45 µm 105 µm
enp urp	setation and spination	prox.-dist. row of 12 spines on med. side	prox.-dist. row of 12 spines on med.	setae on dist. margin	setae on dist. margin, post. seta	dendritic setae med. on post. side	prox.-dist. row of pinnate setae on lat. side	not recognised	setae med.	not recognised	single spine at dist. margin of post. side	single seta at lat.-dist. margin of post. side	
	length-ratio to rami	longer	longer	shorter	much shorter	much shorter	much shorter	much shorter	much shorter	much shorter	much shorter	much shorter	
	insertion of rami	at same level	at same level	at same level	at same level	at same level	at same level	at same level	at same level	at same level	exp latero-proximal, enp medio-distal	exp latero-proximal, enp medio-distal	
enp urp	shape	club-shaped	slightly conical	slightly conical	leaf-shaped	leaf-shaped	lanceolate	lanceolate	leaf-shaped	leaf-shaped	machete-shaped	machete-shaped	
	silhouette	all sides rectangular with half circular dist. end	all sides triangular	all sides triangular	ant. and post. sides lanceolate with rounded tip, lat. and med. sides subtriangular	ant. and post. sides oval, lat. and med. sides subtriangular	ant. and post. sides lanceolate, lat. and med. sides subtriangular	all sides lanceolate, side with deep fissure	ant. and post. sides lanceolate with rounded tip, lat. and med. sides subtriangular	ant. and post. side trapezoid, lat. and med. sides subtriangular	ant. and post. sides oval, lat. and med. sides rectangular	ant. and post. sides suboval, lat. and med. sides rectangular	
	extension	90 µm 40 µm 60 µm	760 µm 105 µm 105 µm	820 µm 220 µm 125 µm	3,130 µm 1,045 µm 320 µm	6,790 µm 1,700 µm 335 µm	5,770 µm 800 µm 555 µm	2,260 µm 430 µm 475 µm	1,480 µm 480 µm 250 µm	21.7 mm 9 mm 3.35 mm	1.6 cm 0.2 cm 0.45 cm	280 µm 30 µm 60 µm	280 µm 30 µm 60 µm

Table 3 continued.

	no	no	no	no	2: one post., one ant.	3: two post., one ant.	2: one post., one ant.	1: one post.	2: one post., one ant.	2: one post., one ant.	1: one ant.	no
<i>carinae, position</i>	no	no	no	no	2: one post., one ant.	3: two post., one ant.	2: one post., one ant.	1: one post.	2: one post., one ant.	2: one post., one ant.	1: one ant.	no
<i>setation and spination</i>	prox.-dist. row of seven spines med. and five ant.	prox.-dist. row of nine spines med.	prox.-dist. rows of setae on med. and lat. sides, setae also at peak	prox.-dist. rows of setae on med. and lat. sides, setae also at peak	setae partly on med., dist., and lat. margins	setae med.-prox., partly on lat., med., and dist. margins	setae on carinae, partly on med., dist., and lat. margins	dendritic setae lat.-prox., setae on med., dist., and lat. margins, prox.-dist. 13 spines med.	setae partly on med., dist., and lat. margins	setae partly on med., dist., and lat. margins	pinnate setae partly on med., dist., and lat. margins	16 spines med.-dist.; two lat.
<b>exp</b>												
<b>urp</b>												
<i>shape</i>	slightly cone-shaped	digitiform, bipartite	digitiform, bipartite	digitiform, bipartite	leaf-shaped	leaf-shaped	leaf-shaped	leaf-shaped	leaf-shaped	leaf-shaped	digitiform, bipartite	digitiform, bipartite
<i>silhouette</i>	all sides triangular with rounded tip	all sides triangular with rounded tip	all sides subtriangular	all sides subtriangular	ant. and post. sides lanceolate with rounded tip, lat. and med. sides subtriangular	ant. and post. sides lanceolate with rounded tip, lat. and med. sides rhombic	ant. and post. sides lanceolate, lat. and med. sides subtriangular	ant. and post. sides lanceolate, lat. and med. sides subtriangular	ant. and post. sides lanceolate, lat. and med. sides subtriangular	ant. and post. sides trapezoid, edges rounded, lat. and med. sides subtriangular	ant. and post. sides rectangular with dist. added oval, med. and lat. sides slightly rectangular	ant. and post. sides rectangular with dist. added oval, med. and lat. sides slightly rectangular
<i>extension</i>	45 µm 25 µm 20 µm	830 µm 85 µm 115 µm	1,050 µm 245 µm 170 µm	3,350 µm 1,370 µm 190 µm	7,190 µm 2,055 µm 355 µm	6,060 µm 950 µm 400 µm	2,835 µm 475 µm 380 µm	1,670 µm 410 µm 225 µm	25.4 mm 9.8 mm 3.6 mm	2.3 cm 0.7 cm 0.25 cm	410 µm 35 µm 95 µm	
<i>carinae, position</i>	no	no	no	1: one post.	2: one post., one ant.	3: two post., one ant.	1: one post.	3: one post., two ant.	2: one post., one ant.	1: one ant. on both portions	no	no
<i>setation and spination</i>	prox.-dist. row of six setae post.	setae all over	prox.-dist. rows of setae on med. and lat. sides	setae partly on med., dist., and lat. margins, prox.-dist. row of spines on lat. edge	irregularly arranged setae ant., setae on med., dist., and lat. margins	parts of med. and dist. margin with setae	setae on med., dist., and lat. margins	setae partly on med., dist., and lat. margins	setae on med. and dist. margins	eight lat. spines, setae on med. and dist. margins	expl): four spines med., four lat., expl): 19 spines med., dist., lat.	
<i>relation to emp</i>	shorter	longer	longer	longer	longer	longer	longer	longer	longer	longer	longer	longer
<i>division</i>	no	yes	yes	partly	yes	no	no	yes	yes	yes	yes	yes



**Fig. 4.** Sixth pleopods of three species. A, C–E: pencil drawings, dashed lines indicate adjacent structures; membranous parts are dotted; B: photograph, taken with transmitted light; F: SEM micrograph. Abbreviations see Table 2. A, B: *Squilla mantis*, anterior (A) and posterior (B) view of left uropod. C, D: *Tethysbaena argentarii*, anterior (C) and posterior (D) view of left uropod. E, F: *Nebalia bipes*, anterior (E) and posterior (F) view of left pleopod 6.

exopod bears plumose setae. The plumose setae on the lateral, distal, and median margins of the distal portion are not equal in length, but are shortest proximally, the longest being located on the distal end.

### 3.2.8. *Tethysbaena argentarii* (Thermosbaenacea)

The uropods (Fig. 4C,D, Table 3) have a length ratio value of 1 : 3.82 : 5.95 and arise postero-laterally from the sixth pleomere. The basipod is subconical and its proximal surface inserts to the trunk. A single simple

seta arises on the latero-distal margin. The endopod inserts on the median side; the exopod inserts on the distal side of the basipod. The endopod is undivided and machete-shaped. 16 densely set, cuspidate setae arise from its median and distal margins; two additional cuspidate setae are located on the lateral margin. The exopod is divided into two portions: the proximal portion is club-shaped; the distal portion is leaf-shaped. Four cuspidate setae arise from the median margin and four from the lateral margin of the proximal portion. 19 cuspidate setae arise from the median, distal, and lateral margins of the distal portion.



### 3.3. *Nebalia bipes* (Phyllocarida)

The sixth pleopods are not differentiated into ‘uropods’ (Fig. 4E,F; as in all other leptostracan phyllocarids), are lentiform and originate postero-ventrally from the sixth pleomere. They are undivided and no differentiation in basipod, endopod, or exopod can be detected, therefore no length ratio value can be given. No carinae are present. The lateral and distal surface of the sixth pleopod is armed with six cuspidate setae.

## 4. Discussion

In the following we evaluate the morphometric and morphological aspects of the uropods and their substructures in relation to their presence in malacostracan taxa and discuss the putative ground-pattern states for the stem species of Malacostraca and those of selected subtaxa.

### 4.1. Shape of uropods

#### 4.1.1. Evaluation

The two known morphotypes of uropods (BOAS 1883), rod-shaped and leaf-shaped, are also recognised in the species investigated. In rod-shaped uropods the basipod is long compared to the rami. By contrast, leaf-shaped uropods consist of a stout basipod and the rami are longer than the basipod. We found a numerical correlation with the length-ratio value of basipod and rami: rod-shaped uropods have a length-ratio value of 1:( $<1.5$ ):( $<2.0$ ), leaf-shaped uropods have 1:( $>1.5$ ):( $>2.0$ ). This categorisation was not tested statistically.

**Rod-shaped uropods:** In general, Bathynellacea, represented by *Allobathynella* sp. (Fig. 2A,B), have rod-shaped uropods (e.g. *Bathynella natans* Vejdvosky, 1882; CALMAN 1917; CHO & HUMPHREYS 2010). Bathynellacea are not known from the fossil record. We assume the ground-pattern state for the uropods of Bathynellacea to be rod-shaped (Table 4).

*D. rathkei* has rod-shaped uropods (Fig. 2C,D), like other extant (e.g. *Ceratocuma horridum* Calman, 1905; CALMAN 1905) and fossil (e.g. Jurassic †*Palaeocuma hessi* Bachmeyer, 1960; BACHMEYER 1960)

cumaceans, none of them contradicting our length-ratio categorisation. We assume the ground-pattern state for the uropods of Cumacea to be rod-shaped (Table 4).

*G. roeselii* has rod-shaped uropods, which seems to be the general shape in extant gammarids (e.g. *Alicella gigantea* Chevreux, 1899; BARNARD & INGRAM 1986) as well as fossil species (e.g. Eocene †*Niphargus* sp.; JAZDZEWSKI & KUPRYJANOWICZ 2010), none of them contradicts our length-ratio categorisation. A gammarid habitus most likely represents the ground-pattern condition for Amphipoda (DAHL 1977; WIRKNER & RICHTER 2007), contrasting other amphipod in-groups, such as Hyperiidea, Ingolfiellidea, and Caprellidea. The latter two taxa seem to be highly derived in various aspects of their morphology, which led us to assume a ground-pattern state for the uropods of Amphipoda to be rod-shaped (Table 4), as developed in *G. roeselii* (Fig. 2E,F).

**Leaf-shaped uropods:** *A. tasmaniae* served as representative for Anaspidacea, comprising the extant taxa Anaspididae, Koonungidae, Psammaspididae, and Stygocarididae (cf. GRUNER 1993). Anaspididae and Koonungidae possess leaf-shaped uropods being consistent with our length-ratio categorisation, while Psammaspididae and Stygocarididae have rod-shaped uropods (GRUNER 1993). Leaf-shaped uropods are also found in fossil representatives of the Anaspidacea (e.g. SCHRAM 1984 for many taxa; example: the Carboniferous †*Palaeocaris typus* Meek & Worthen, 1865; see also PERRIER et al. 2006). We assume the ground-pattern state for the uropods of Anaspidacea to be leaf-shaped (Table 4).

Caridean decapod species have, like *C. crangon*, leaf-shaped uropods (see e.g. RICE 1967 for many examples). The same applies to fossil representatives of Caridea (e.g. the Oligocene †*Propalaeomon osborniensis* Woods, 1925; MOORE & McCORMICK 1969b). All examples considered correspond to our length-ratio categorisation. This is why we assume the ground-pattern state for the uropods of Caridea to be leaf-shaped (Table 4).

*E. superba* (Fig. 3E) and other extant Euphausiacea have leaf-shaped uropods (e.g. SARS 1885). Fossil Euphausiacea are not known. All examples considered are concordant to our length-ratio categorisation. Therefore we assume leaf-shaped uropods in the ground pattern of Euphausiacea (Table 4).

*Mysis* sp. represents Mysida, and *N. ingens* exemplifies Lophogastrida. Both species have leaf-shaped uropods (Fig. 3G,I). The two taxa Mysida and Lophogastrida are often united as Mysidacea (e.g. RICHTER & SCHOLTZ 2001). Other representatives of these two taxa also possess leaf-shaped uropods, including fossil representatives, e.g. the Trias-

sic lophogastrid †*Schimperella acanthocercus* Taylor, Schram & Yan-Bin, 2001 (TAYLOR et al. 2001). All examples are concordant to our length-ratio categorisation, consequently we assume leaf-shaped uropods in the ground pattern of Mysidacea. Note that the fissure present at the median side of the endopod of *Mysis* sp. (Fig. 3G) is interpreted to serve the statocyst, which is located in the uropods of Mysidae (ESPEEL 1985) and does not represent the ground-pattern state of all Mysida.

*P. monodon* has leaf-shaped uropods (Fig. 3K) like other dendrobranchiate decapod species of the two sister taxa Penaeoidea and Sergestoidea (see e.g. PEREZ FARFANTE 1977 including many examples). The same holds true for fossil dendrobranchiates, e.g. *Penaeus speciosus* occurring in the upper Cretaceous (MOORE & McCORMICK 1969b). None of the examples contradicts our length-ratio categorisation. This is why we assume the ground-pattern state for uropods of Dendrobranchiata to be leaf-shaped (Table 4).

*S. mantis* has leaf-shaped uropods (Fig. 4A,B) with a length-ratio value of 1:1.82:2.71 (Table 2). However, this measurement did not include the prominent basipodal spine, which would have changed the value considerably. Nevertheless, assuming leaf-shaped uropods with a comparably short basipod as the ground-pattern condition for Hoplocarida seems plausible if considering the fossil record of this taxon: The †Aeschronectida, sister taxon to the Stomatopoda, which includes various extinct groups and all living taxa (see HAUG et al. 2010b for a recent analysis), have leaf-shaped uropods with a stout basipod lacking a spine (e.g. the Carboniferous †*Kallidectes richardsoni* Schram, 1969; SCHRAM 1969). The spine evolved within the Stomatopoda (see 4.6.). Taking into account that †Aeschronectida have a leaf-shaped uropod in the sense of our categorisation, we assume the ground-pattern state for the uropods of Hoplocarida also to be leaf-shaped (Table 4).

*T. argentarii* has leaf-shaped uropods (Fig. 4C,D). However, the variability of uropodal shape is high among Thermosbaenacea, including both rod- and leaf-shaped uropods (WAGNER 1994). No fossil Thermosbaenacea are known. WAGNER (1994: pp. 297f) states the ground-pattern condition of the uropods of Thermosbaenacea to be 'flattened', most likely a synonymous expression for our term 'leaf-shaped'. Accordingly we assume the ground-pattern state for the uropods of Thermosbaenacea to be leaf-shaped (Table 4).

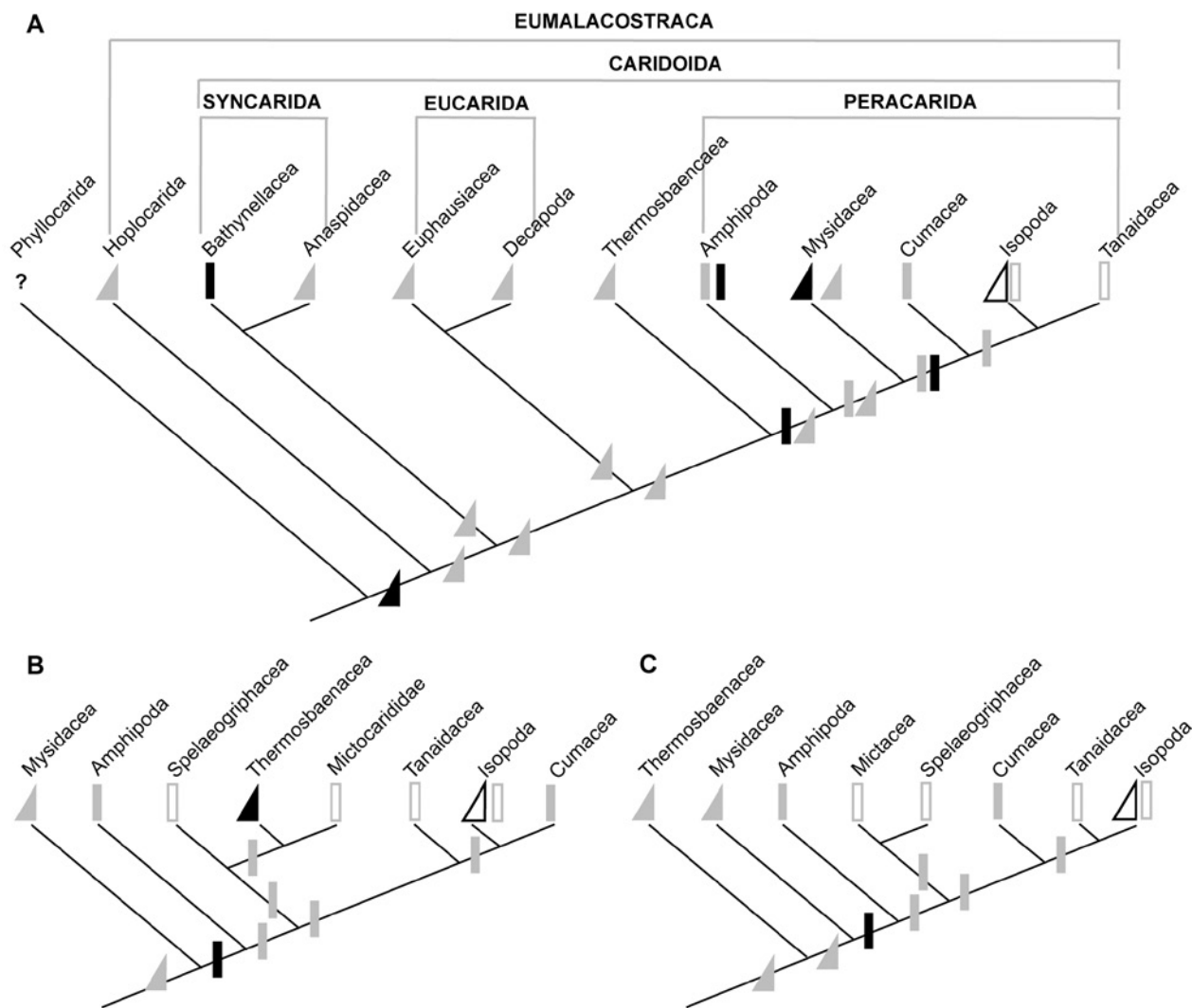
**Condition in outgroup:** *N. bipes* is a special case. Its sixth pleopod consists of a single portion (Fig. 4E,F), preventing the application of a length-ratio category. It is unknown which part(s) of the appendage (basipod, endopod, or exopod) this single portion corresponds

to. Embryonic research on *Nebalia longicornis* Thomson, 1879 also only revealed a uniform anlage of unclear assignment to any of the limb portions (OLESEN & WALOSSEK 2000). Living leptostracan phyllocarid species with a sixth pleopod comprised of two portions (see e.g. *Speonebalia cannoni* Bowman, Yager & Iliffe, 1985; BOWMAN et al. 1985) do exist, but with these taxa it is also unknown to which portions the two parts belong. The fossil record of Phyllocarida is even more problematic since these forms, for example the Silurian †*Cinerocaris magnifica* Briggs, Sutton, Siveter & Siveter, 2004, and the Devonian †*Nahecaris stuerzi* Jaekel, 1921, from which limbs are preserved, are not only much larger than any of the living taxa, but also lack a sixth pair of pleopods (BERGSTRÖM et al. 1987; BRIGGS et al. 2004). These differing conditions of Recent and fossil representatives prevent a reconstruction of a ground-pattern state of the sixth pleopod for Phyllocarida (including all other characters associated with the sixth pleopod). This is indicated by a question mark in figures 5 and 6.

#### 4.1.2. Mapping

Based on the distribution of leaf-shaped uropods among eumalacostracans we conclude that leaf-shaped uropods represent the ground-pattern condition for Eumalacostraca (Fig. 7, GPC 2), a condition retained in Anaspidacea, Eucarida, and the stem species of Neocarida (see below). Contrasting the central insertion of pleopods 1–5 on their pleomeres, eumalacostracan uropods and the sixth pleopods of Phyllocarida both arise from the posterior edge of the sixth pleomere. Therefore, this character is assumed to be plesiomorphic for Phyllocarida and Eumalacostraca (Fig. 7, GPC 1). The limb was surely biramous, but whether the sixth pleopod was leaf-shaped in the ground pattern of Malacostraca remains unclear. We propose that the lack of the sixth pleopod in fossil Phyllocarida resulted from the reduction of a regular pleopod, rather than from an already reduced uropod. This may also be supported by the presence of an additional apodous segment anterior to the conical telson with furcal rami.

We assume that leaf-shaped uropods functioned in locomotion in the eumalacostracan stem species. Then rod-shaped uropods would be derived. The caridoid escape reaction plays an important role in eumalacostracan locomotion (HESSLER 1983). It is reported for almost all species examined with leaf-shaped uropods. These animals swim more or less freely in the pelagic to semi-pelagic realm (see e.g. SILVEY & WILSON 1979; MACMILLIAN et al. 1981; GRUNER 1993; HEITLER et al. 2000; OLESEN et al. 2006). This life style seems to demand for a fast escape mechanism as realised by the caridoid escape reaction (caridoid facies of HESSLER



**Fig. 5.** Results of mapping the shape of uropods. Mysidacea is the taxon name of sister taxa Mysida + Lophogastrida. Legend: triangle = leaf-shaped uropods; rectangle = rod-shaped uropods; grey = plesiomorphic conditions; black = autapomorphic conditions; filled symbol = examined in this study; hollow symbol = data reconstructed from literature. **A:** Phylogeny based on SIEWING (1956). Mictacea and Spelaeogriphacea were not known that time. Two possible mapping scenarios are given for within Peracarida; left and right symbols correspond to one or the other way of interpretation. **B:** Phylogeny of Peracarida including Thermosbaenacea based on WIRKNER & RICHTER (2010). Mictocarididae correspond to Mictacea. **C:** Phylogeny of Neocarida based on RICHTER & SCHOLTZ (2001) exhibiting the most parsimonious distribution of uropod characters.

1983), which is achieved by the leaf-shaped uropods arranged with the telson in a so-called tailfan. However, leaf-shaped uropods do not necessarily occur in combination with this reaction. An example is *S. mantis* (Fig. 1K; Hoplocarida), which has a tail fan but not a caridoid escape reaction. HEITLER et al. (2000) concluded that *S. mantis* – as perhaps all stomatopods – has more ‘primitive’ (better, plesiomorphic) escape behaviours (the so-called limb-flick response, the intermediate response, and the maximal response) than the tail-flip mechanism developed in Eucarida and Syncarida. The somersaulting of *Nannosquilla decemspinosa* Rathbun, 1910 (CALDWELL 1979) appears similarly non-caridoid. As uropods do not act in a caridoid escape reaction in any extant stomatopod (Verunipel-

tata, HAUG et al. 2010b), they fulfil other, mainly behavioural functions, but also play a role in locomotion (VERRILL 1923; GRUNER 1993). Verunipeltatan species swim by using their pleopods whereby the uropods function as rudder. Yet, Verunipeltata are, in general, benthic and move over the bottom (GRUNER 1993). Leaf-shaped uropods in Hoplocarida are well documented from their fossil record (e.g. SCHRAM 1969; JENNER et al. 1998; SCHRAM 2007). The most parsimonious interpretation is that the stem species of Eumalacostraca autapomorphically possessed leaf-shaped uropods (Fig. 7, GPC 2) but (still) lacked the caridoid escape reaction, which evolved – based on a specific muscle arrangement in the pleon (DANIEL 1932) – in the evolutionary lineage of Caridoida (Fig. 7, GPC 3).

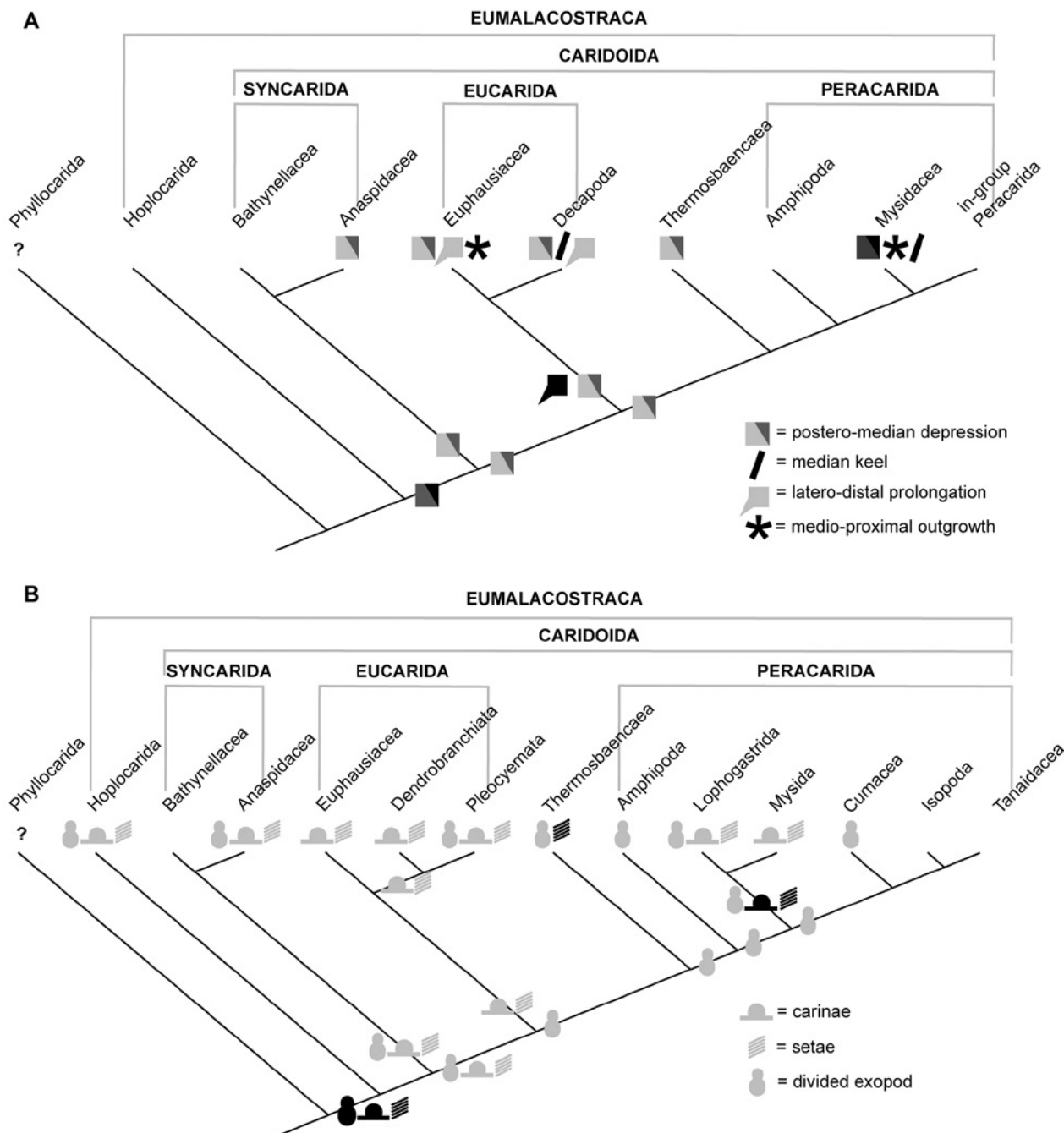
Rod-shaped uropods are interpreted as the derived condition, which evolved convergently in e.g. Bathynellacea, Cumacea, and Amphipoda due to adaptation to different environmental conditions (likewise in the non-examined peracarid taxa Mictacea, Spelaeogriphacea, Tanaidacea, and Isopoda, and the anaspidacean taxa Psammaspididae and Stygocarididae). We assume that the rod-shape in Bathynellacea is an (autapomorphic) adaptation (Fig. 7, GPC 4) to their interstitial lifestyle (NOODT 1964; SCHMINKE 1981) because it is more suitable than leaf-shape when moving between sand grains (the same applies to Psammaspididae and Stygocarididae also having an interstitial lifestyle). A caridoid escape reaction has not been reported for Bathynellacea and its lack has been interpreted as an adaptation to their interstitial lifestyle (CALMAN 1917; NOODT 1964). According to SIEWING'S (1956) phylogeny this would mean an autapomorphic change of leaf-shaped uropods to rod-shaped ones in the ground pattern of caridoid Bathynellacea combined with a likewise autapomorphic secondary loss of the caridoid escape reaction (Fig. 7, GPC 4). According to the phylogeny of WILLS et al. (2009: fig. 4), who considered Bathynellacea as a sister taxon to Eumalacostraca, a lack of the caridoid escape mechanism would be primary for Bathynellacea. This lack would also be a primary condition for Phyllocarida, the next outgroup (Fig. 7, dashed lines). Because Phyllocarida lack uropods, the presence of uropods would be an autapomorphy of the stem species of Bathynellacea + all other Eumalacostraca taking the phylogeny of WILLS et al. (2009) as a basis. Then Syncarida would be non-monophyletic. Based on our analysis, a definite conclusion, i.e. which phylogeny is more likely, cannot be made.

For Cumacea and Amphipoda the situation is different. A caridoid escape reaction has neither been reported for Cumacea nor for Amphipoda (RICHTER & SCHOLTZ 2001). However, Cumacea swim with the exopods of their thoracopods aided by ventral flexion of the pleon (GRUNER 1993). The uropods seem to play a minor role and are rather used for grooming. For cleaning the whole pleon is flexed ventrally allowing the uropods to reach anterior structures (e.g. shield, thoracopods; DIXON 1944). In this context, uropod features of *D. rathkei* (e.g. scaly surface, median spine crests, and the exopod fitting perfectly into a groove of the endopod if moved medially, so the rami can probably serve as a pincer, Fig. 2C,D) are interpreted to be adaptations to this function. In gammaridean amphipods, the uropods are used for a special lateral locomotion for which the uropods are temporarily hooked to the substrate (DAHL 1977; VOGEL 1985). The rod-like shape of the uropods of *G. roeselii* (Fig. 2E,F) and numerous spines and setae attached to it are construed as adaptations to this special swimming mechanism.

Among Peracarida, uropods are leaf-shaped in Mysida, Lophogastrida, some Isopoda, and the possible out-group Thermosbaenacea, but rod-shaped in Amphipoda, Cumacea, Tanaidacea, Mictacea, Spelaeogriphacea, and some Isopoda. According to SIEWING (1956) Thermosbaenacea are the sister taxon to Peracarida including Amphipoda as sister taxon to Mysidacea + (Cumacea + (Isopoda + Tanaidacea)) (Fig. 5A). Mictacea and Spelaeogriphacea were not included in SIEWING'S (1956) study since discovered in the 1980's. Two possible scenarios can be discussed: In both cases, Thermosbaenacea have retained a leaf-shaped uropod and the caridoid escape reaction from the stem species of Caridoida (see above). (1) The common stem species of the peracaridan taxa has acquired rod-shaped uropods and lost the caridoid escape reaction (Fig. 5A, black rectangle) as present in Amphipoda. Mysidacea (Mysida + Lophogastrida) have made a 'step back' and evolved leaf-shaped uropods (Fig. 5A, black triangle) and the caridoid escape reaction. The remaining in-groups (Cumacea + (Isopoda + Tanaidacea)) retained the rod-shaped uropods and lack of the caridoid escape reaction. This would imply that Amphipoda and the stem species of Cumacea + (Isopoda + Tanaidacea) lost the caridoid escape mechanism independently from each other. Moreover, Mysidacea would have re-evolved two features present in the ground pattern of Caridoida. (2) The peracaridan stem species has plesiomorphically retained leaf-shaped uropods (Fig. 5, grey triangle), Amphipoda evolved rod-shaped uropods as an autapomorphy (Fig. 5, black rectangle), the common stem species of Mysidacea + (Cumacea + (Isopoda + Tanaidacea)) retained leaf-shaped uropods (Fig. 5, grey triangle), and the stem species of Cumacea + in-groups has rod-shaped uropods as an autapomorphy. However, the reconstruction of the ground-pattern states of the various nodes within SIEWING'S (1956) phylogeny of Peracarida is ambiguous. Mapping uropod shape to SIEWING'S (1956) phylogeny of Peracarida requires a number of transformation events between rod-shaped and leaf-shaped, rather than the minimum of only one such transformation. This means it fails our phylogenetic test (REIF 2002; ASSIS 2009; HAUG et al. 2012).

Mapping uropod shape onto the phylogeny of WIRKNER & RICHTER (2010: fig. 2) suggests the following interpretation: Mysidacea are shown as the sister taxon of Amphipoda + remaining Peracarida (Fig. 5B). Mysidacea would have retained the leaf-shaped uropods in combination with the caridoid escape reaction (Fig. 5B, grey triangles). The stem species of Amphipoda and the remaining Peracarida would have evolved rod-shaped uropods (Fig. 5B, black rectangle) and lost the caridoid escape reaction. However, since the Amphipoda + remaining Peracarida taxa of WIRKNER & RICHTER (2010) include Thermosbaenacea, they





**Fig. 6.** Results of mapping characters of basipod and rami on SIEWING'S (1956) phylogeny. Black indicates autapomorphies. **A:** Mapping of basipodal characters postero-median depression, median keel, latero-distal prolongation, medio-proximal outgrowth, and basipodal spine. Note that all characters are only applicable to leaf-shaped uropods. Mysidacea is the taxon name of the assumed sister taxa Mysida + Lophogastrida; median keel as autapomorphy only valid for Lophogastrida. **B:** Mapping of the characters carinae on endopod and exopod, setae on endopod and exopod (of leaf shaped uropods; see text section 4.1), and division of exopod. Note that setae of Thermosbaenacea are modified and therefore black. Isopoda and Tanaidacea were not examined.

would have made a 'step back' to leaf-shaped uropods (Fig. 5B, black triangle) and the caridoid escape reaction. The reconstruction of the ground-pattern states of the various nodes in WIRKNER & RICHTER'S (2010) phylogeny of Peracarida is not parsimonious either.

According to the phylogenetic study of Peracarida by RICHTER & SCHOLTZ (2001), Amphipoda + Mancoida [= (Mictacea + Spelaeogriphacea) + Cumacea

+ (Tanaidacea + Isopoda)] (Fig. 5C) all exhibit a simple pleon musculature and lack a tail fan escape reaction (RICHTER & SCHOLTZ 2001: characters 59 and 60, fig. 7). This allows apomorphic rod-shaped uropods, like in Cumacea and Amphipoda (this paper), Mictacea (e.g. BOWMAN & ILIFFE 1985), Spelaeogriphacea (e.g. GORDON 1957) and Tanaidacea (e.g. SARS 1899), for the ground pattern of this taxon (Fig. 2C–F; Fig.

5C, black rectangle), combined with a loss of the caridoid escape reaction (Fig. 7, GPC 10). However, within Isopoda leaf-shaped uropods occur along with rod-shaped ones (e.g. MOORE & MCCORMICK 1969a; WÄGELE 1989; WILSON 1996). This is an autapomorphic ‘step back’ according to all peracaridan phylogenies discussed herein. However, this ‘step-back’ assumption demanded according to RICHTER & SCHOLTZ (2001) is more parsimonious than the one presumed for Thermosbaenacea with the phylogeny of WIRKNER & RICHTER (2010), as no secondary development of the caridoid escape reaction has to be assumed here. However, controversial opinions on the phylogenetic relevance of uropod shape in Isopoda exist: WÄGELE (1994: p. 93) acts based on the assumption that leaf-shaped uropods are part of the ground pattern of Isopoda (retained from the peracaridan stem species) whereas WILSON (1996: p. 12) names styliform uropods as the ancestral state for Isopoda.

According to the phylogeny of SIEWING’S (1956) and RICHTER & SCHOLTZ’S (2001), Thermosbaenacea are the sister taxon to the remaining Peracarida (= Neocarida). This implies that they plesiomorphically retained the leaf shape of uropods from the ground pattern of Eumalacostraca and the caridoid escape reaction from the stem species of Caridoida. The uropods of *T. argentarii* are leaf-shaped (Fig. 4C,D), however, they differ from the leaf-shaped uropods of the other examined eumalacostracan species in the length of the rami relative to the basipod (Table 2). Furthermore, numerous spines are attached to the rami (Fig. 4C,D), a condition found only in other thermosbaenacean species (see WAGNER 1994). These two morphological characteristics can be interpreted as an autapomorphic adaptation of Thermosbaenacea to a semi-pelagic life style (Fig. 7, GPC 7).

## 4.2. Postero-medial depression on basipod

### 4.2.1. Evaluation

A postero-medial depression is present in all species examined possessing leaf-shaped uropods (see Fig. 3A, white arrow for *A. tasmaniae*) except for *S. mantis*. We suppose this depression facilitates formation of the tail fan as it provides space for the telson lying between the two uropods. This seems to apply to species whose uropods arise in a ventro-lateral position on the sixth pleomere, i.e. *A. tasmaniae*, *C. crangon*, *E. superba*, *Mysis* sp., *N. ingens*, and *P. monodon*. The uropod of *S. mantis* arises in a more lateral position. But this does not seem to reflect the ground-pattern condition of Hoplocarida considering reconstructions

of basal representatives such as †*K. richardsoni* (†Aeschronectida) (SCHRAM 1969) which have ventro-laterally arising uropods. The presence of a postero-medial depression on the basipod of †*K. richardsoni* is not documented. However, literature data on covered structures, as is the condition of the postero-medial depression (which is hidden by the telson), is lacking. This also applies to taxa with rod-shaped uropods. We assume a postero-medial depression for the ground patterns of Anaspidacea, Caridea, Dendrobranchiata, Euphausiacea, and Thermosbaenacea (Table 4).

### 4.2.2. Mapping

Similar to the general shape of the uropod, we also find problems concerning the character of a postero-medial depression on the basipod within Peracarida. According to SIEWING’S (1956) phylogeny, Mysidacea would have made a ‘step back’ to leaf-shaped uropods including a postero-medial depression (Fig. 6A). This non-parsimonious assumption is avoided in the phylogeny of RICHTER & SCHOLTZ (2001). Because a postero-medial depression is neither known for Recent Hoplocarida (e.g. *S. mantis*) nor fossil representatives (see e.g. JENNER et al. 1998; SCHRAM 2007), we state this character to be an autapomorphy of Caridoida (Fig. 7, GPC 3).

## 4.3. Median keel on basipod

### 4.3.1. Evaluation

The median keel is found exclusively in species with leaf-shaped uropods, namely *C. crangon*, *P. monodon*, and *N. ingens* (Fig. 3C,K,I, black arrowheads). Although literature data on such a keel is lacking, we assume this keel to be part of the ground patterns of Caridea, Dendrobranchiata, and Lophogastrida (Table 4). However, the keels found in *C. crangon*, *P. monodon*, and *N. ingens* differ in morphology: they are of uniform height throughout (thus ribbon-like in profile) in *C. crangon* and *P. monodon* (Fig. 3C,K, black arrowheads), but much higher proximally than distally (thus triangular in profile) in *N. ingens* (Fig. 3I, black arrowhead).

### 4.3.2. Mapping

The median keel is found only in Decapoda and Lophogastrida. Due to the lack of this keel in Euphausiacea and other neocaridan taxa we interpret the keel

in Lophogastrida as convergence. This is underpinned by the different morphology of the keels. Therefore, a ribbon-like median keel on the basipod is assumed to be an autapomorphy in the ground pattern of Decapoda (Fig. 7, GPC 6), and a triangular one is interpreted as an autapomorphy of Lophogastrida (Fig. 7, GPC 9).

#### 4.4. Latero-distal prolongation on basipod

##### 4.4.1. Evaluation

A latero-distal prolongation occurs in *C. crangon*, *E. superba*, and *P. monodon* (Fig. 3D,F,L; white arrowheads), thus only in species with leaf-shaped uropods. Even these three species display different conditions of the prolongation: tipped in *C. crangon* (Fig. 3D, white arrowhead), more rounded in *E. superba* (Fig. 3F, white arrowhead), and very rounded in *P. monodon* (Fig. 3L, white arrowhead). The variability is even more significant considering literature data: tipped prolongations are also found in Dendrobranchiata (e.g. *Penaeus setiferus* (Linné, 1758): GRUNER 1993) and Euphausiacea (e.g. *Bentheuphausia* sp.: MOORE & McCORMICK 1969a) and rounded ones in Caridea (e.g. *Pandalus montagui* Leach, 1814: GRUNER 1993). The variability of this character is high among fossil representatives of Caridea and Dendrobranchiata (MOORE & McCORMICK 1969b). In all examined specimens this latero-distal prolongation hampers full lateral spreading of the exopod, a fact not traceable for fossils. Because of this functional equality in Recent species, we consider absence or presence of a latero-distal prolongation and not its various shapes. We presume latero-distal prolongations for the ground patterns of Caridea, Euphausiacea, and Dendrobranchiata (Table 4).

##### 4.4.2. Mapping

A latero-distal prolongation at the basipod is only present in eucaridan taxa (Fig. 6A). This is why we suppose it to be an autapomorphy in the ground pattern of Eucarida (Fig. 7, GPC 5). This assumption is supported by the presence of the latero-distal prolongation of the basipod in the uropods of *Amphionides reynaudii* (Milne Edwards, 1832) (WILLIAMSON 1973), being most likely the sister species to Decapoda. Again, such a prolongation is neither found in *A. tasmaniae*, nor in *Mysis* sp., *N. ingens*, *S. mantis*, or in *T. argentarii* (Figs. 3, 4A–D).

#### 4.5. Medio-proximal outgrowths at the basipod

##### 4.5.1. Evaluation

Such laterally set off outgrowths are found in species with leaf-shaped uropods only. They occur in *E. superba*, *Mysis* sp., and *N. ingens* (Fig. 3E,G,I, white stars). In *N. ingens*, the outgrowth fades into the median keel. A medio-proximal outgrowth is visible in other euphausiacean species (SARS 1885) but not documented for Mysidacea. Nothing is known about this structure in fossil representatives of these taxa. Taking our results as a basis, we assume a medio-proximal outgrowth for the respective ground patterns of Euphausiacea and Mysidacea (Table 4).

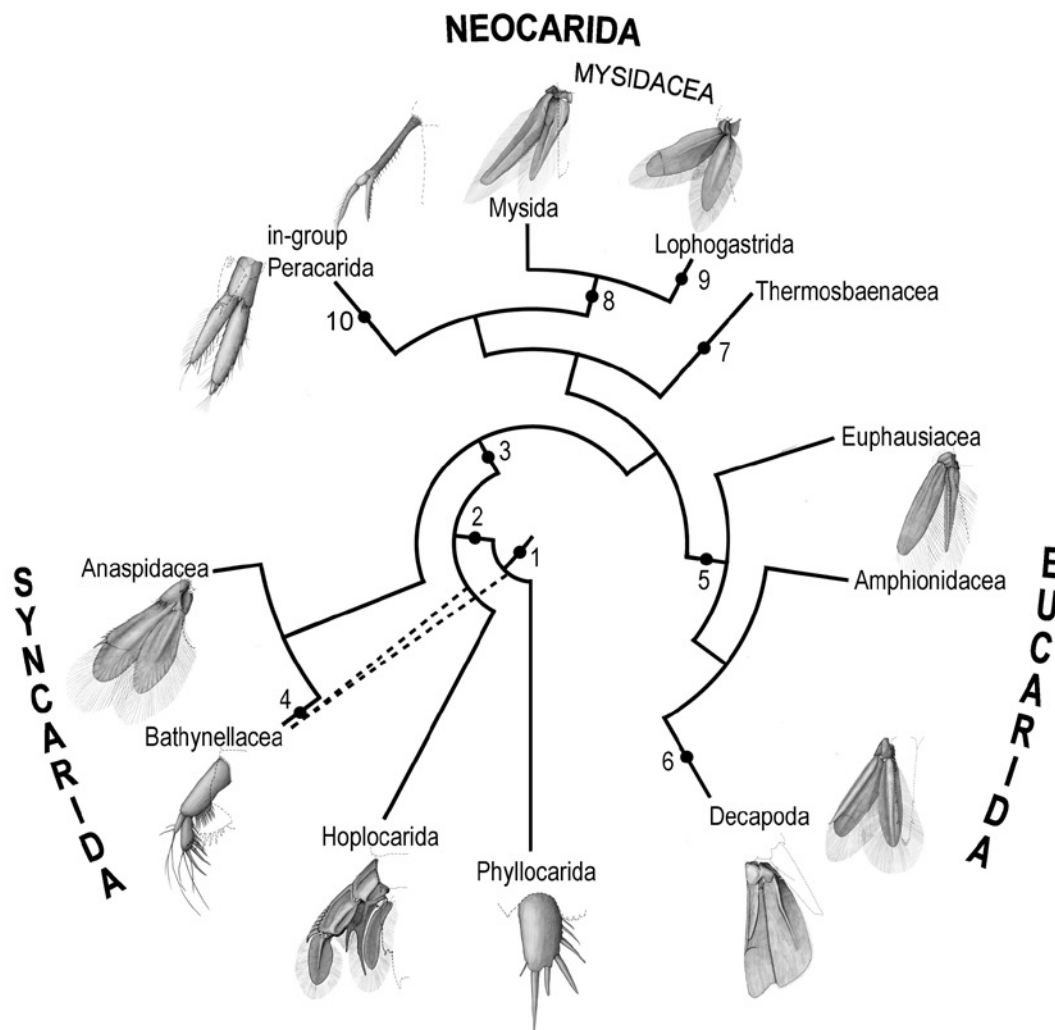
##### 4.5.2. Mapping

We conclude a medio-proximal outgrowth on the basipod to be an autapomorphy in the ground pattern of Mysidacea (Fig. 6A, black star; Fig. 7, GPC 8). Such an outgrowth is not present in the outgroup Thermosbaenacea, represented by *T. argentarii*. Consequently, Euphausiacea would have evolved a similar medio-proximal outgrowth independently. This interpretation is supported by the morphology of the medio-proximal outgrowths, being cylindrical in *E. superba* and triangular in anterior view in *Mysis* sp. and *N. ingens*. Alternatively, one may consider this as a symplesiomorphic character of Mysida, Lophogastrida, and Euphausiacea, and, hence, as a possible ground-pattern element of a common stem species (consequently, Thermosbaenacea would have lost this character). More data has to be accumulated before it can be decided if the medio-proximal outgrowths are retained from a common stem species of Mysidacea and Euphausiacea or have evolved convergently in these taxa.

#### 4.6. Basipodal spine

##### 4.6.1. Evaluation

A basipodal spine is exclusively found in *S. mantis* (Fig. 4A,B). No other species examined exhibits such a structure. Such a basipodal spine can be found in all Recent Stomatopoda (see e.g. AHYONG 2001). The morphological variations and states are enormous (for



**Fig. 7.** Ring phylogram of malacostracan taxa displaying most parsimonious arrangement of uropod characters. Slightly changed hypothesis of SIEWING (1956). Images are pencil drawings of posterior side of uropods. Black dots represent evolutionary ground-pattern conditions (GPC) of the sixth pleopod. For reconstruction see text section 4. Dashed lines indicate other possible positions of Bathynellacea within Malacostraca. GPC 1: The sixth pleopod of Malacostraca inserts on the posterior edge of the sixth pleomere. GPC 2: Eumalacostraca have a leaf-shaped uropod, stabilised by carinae on the rami and having a surface being enlarged by setae arising from the edges of the rami. GPC 3: The basipod of Caridoida is postero-medially depressed giving space for the telson in tail-fan formation. The caridoid escape reaction is developed. GPC 4: Bathynellacea abandoned the caridoid escape mechanism and have rod-shaped uropods. GPC 5: All Eucarida have a latero-distal prolongation at the basipod. GPC 6: Decapoda possess a longitudinal median keel on the anterior side of the uropodal basipod. GPC 7: Neocaridan Thermosbaenacea exhibit cuspidate setae rather than plumose setae to enlarge the surface of the rami. GPC 8: Mysidacea (Mysida + Lophogastrida) have a basipod being medio-proximally drawn out on the anterior side. GPC 9: Lophogastrida have a triangular median keel at the basipod. GPC 10: The in-group Peracarida consists of Amphipoda, Cumacea, Mictacea, Spelaeogriphacea, Tanaidacea, and Isopoda; they all have lost the caridoid escape reaction and possess rod-shaped uropods.

details see AHYONG 2001). The Carboniferous †*Daidal acanthocercus* (Jenner, Hof & Schram, 1998) and †*Gorgonophontes peleron* Schram, 1984 (both ‘†Archaeostomatopoda’ Schram, 1969, here in quotation marks because being most likely non-monophyletic, see HAUG et al. 2010b) have regular, leaf-shaped uropods with small, presumably initial basipodal spines (JENNER et al. 1998; SCHRAM 2007). But no such spine is reported e.g. for †*K. richardsoni* (†Aeschronectida) (SCHRAM 1969). Hence, the prominent basipodal

spine seems to be a structure occurring only in modern Hoplocarida and cannot be assumed to be part of their ground pattern (Table 4).

#### 4.6.2. Mapping

As a basipodal spine does not represent the ground-pattern state of Hoplocarida, mapping was not addressed.



**Table 4.** Characters and their condition as reconstructed for the respective taxa. Taken as a basis for mapping. Column headings list characters. Abbreviations: bassp = basipodal spine; carin = carinae on endopod and exopod; depr = postero-medial depression on basipod; ex div = division of the exopod; keel = median keel on basipod; leaf = leaf-shaped uropod; outgr = medio-proximal outgrowth on basipod; prol = latero-distal prolongation of the basipod; rod = rod-shaped uropod; setae = setae surrounding the margins of uropodal rami; + = applies to taxon; – = does not apply to taxon.

	leaf	rod	depr	keel	prol	outgr	bassp	carin	setae	ex div
Hoplocarida	+	–	–	–	–	–	–	+	+	+
Bathynellacea	–	+	–	–	–	–	–	–	–	–
Anaspidacea	+	–	+	–	–	–	–	+	+	+
Euphausiacea	+	–	+	–	+	+	–	+	+	–
Dendrobranchiata	+	–	+	+	+	–	–	+	+	–
Caridea	+	–	+	+	+	–	–	+	+	+
Thermosbaenacea	+	–	+	–	–	–	–	–	+	+
Amphipoda	–	+	–	–	–	–	–	–	–	+
Mysida	+	–	+	–	–	+	–	+	+	–
Lophogastrida	+	–	+	–	–	+	–	+	+	+
Cumacea	–	+	–	–	–	–	–	–	–	+

## 4.7. Carinae on endopod and exopod

### 4.7.1. Evaluation

Carinae (cf. POORE 2004) on the uropodal rami are found exclusively in species with leaf-shaped uropods except for *T. argentarii*. The morphological variations occurring among carinae is broad: Sharply set-off and slender carinae are present in *E. superba* (Fig. 3E, black star) contrasting smoothly set-off and broad carinae in *P. monodon* (Fig. 3K, black star). All kinds of carinae are present in other species of the represented taxa (for Anaspidacea see e.g. SWAIN et al. 1971; for Euphausiacea see e.g. SARS 1885; for various Decapoda and Mysidacea see e.g. GRUNER 1993; for Hoplocarida see e.g. AHYONG 2001). Intermediate states exist, also in the fossil record (see e.g. †*Palaeocaris secretanae* Schram, 1984 (PERRIER et al. 2006); MOORE & McCORMICK 1969b). We suppose that carinae stabilise the rami of leaf-shaped uropods to withstand the water pressure occurring during uropod movement. We assume carinae for the ground patterns of Anaspidacea, Caridea, Euphausiacea, Mysidacea, Dendrobranchiata, and Hoplocarida respectively (Table 4).

### 4.7.2. Mapping

Mapping this character (Fig. 6B) reveals that carinae occur in Hoplocarida, Anaspidacea, Eucarida, and Mysidacea. The most parsimonious explanation for the distribution of this character among Eumalacostraca is that stabilising carinae on the rami of leaf-shaped uropods are developed together with leaf-shaped uropods

in the stem species of Eumalacostraca (Fig. 7, GPC 2). Assuming this, we suggest the following ground-pattern conditions and changes from the one found in Eumalacostraca for the following taxa: Thermosbaenacea have lost the carinae of their leaf-shaped uropods. Again, for Peracarida we refer to the phylogeny of RICHTER & SCHOLTZ (2001) allowing the assumption that the stem species of Amphipoda and Mancoida lost the carinae together with the leaf shape of uropods (see above).

## 4.8. Setae on endopod and exopod

### 4.8.1. Evaluation

Setae arise from all rami of all examined uropods. In leaf-shaped uropods, many setae are attached to the lateral, distal, and median margins (Fig. 3). This condition is found in general in Anaspidacea (e.g. PERRIER et al. 2006), Caridea (e.g. RICE 1967), Euphausiacea (e.g. SARS 1885), Mysida (e.g. SARS 1885), Lophogastrida (e.g. SARS 1885), Dendrobranchiata (e.g. PEREZ FARFANTE 1977), and Hoplocarida, recent (e.g. AHYONG 2001) and fossil (e.g. JENNER et al. 1998 for Carboniferous †*Daidal acanthocercus* (Jenner, Hof & Schram, 1998)) (Table 4). These marginal setae of leaf-shaped uropods vary in form (cuspidate or plumose) and length. We assume all of them enlarge the effective surface of the uropodal rami, an assumption that only applies to taxa with leaf-shaped uropods. Consequently, the following ‘setae on endopod and exopod’ only applies to taxa with leaf-shaped uropods.

#### 4.8.2. Mapping

Setation is present at the uropodal rami of Anaspidaea, Eucarida, Mysidacea, and Hoplocarida. This is why we conclude that setae of leaf-shaped uropods evolved together with the plane shape. Consequently, it would be an autapomorphic feature of Eumalacostraca (Fig. 7, GPC 2). Accordingly, Thermosbaenacea, Bathynellacea, and the stem species of Amphipoda + Mancoida would have changed this condition (Fig. 7, GPC 7).

#### 4.9. Division of the exopod

##### 4.9.1. Evaluation

Divided exopods are present in species with rod-shaped and leaf-shaped uropods. In species with rod-shaped uropods the exopod is divided in *D. rathkei* and *G. roeselii* (Fig. 2C–F) and undivided in *Allobathynella* sp. (Fig. 2A,B). In general Bathynellacea have undivided uropodal exopods (see e.g. CALMAN 1917; NOODT 1964; SCHMINKE 1972, 1979, 1980, 1988). The exopod is always divided in Cumacea, fossil and Recent ones (see e.g. BACHMEYER 1960; SIEWING 1952), which is why we assume divided exopods for the ground pattern of Cumacea. In Amphipoda both divided (e.g. MOORE & McCORMICK 1969a) and undivided exopods (e.g. BARNARD & INGRAM 1986) occur, and the ground-pattern condition is unresolved. We take our examined species as a basis and hypothesise a divided exopod for the ground pattern of Amphipoda.

In species exhibiting leaf-shaped uropods, we find divided exopods in *A. tasmaniae* (Fig. 3A; black arrow), *C. crangon* (Fig. 3C; black arrow), *N. ingens* (Fig. 3I; black arrow), *S. mantis* (Fig. 4A,B), and *T. argentarii* (Fig. 4C,D). Functionally, a divided exopod is interpreted to allow the distal portion of the exopod to flex ventrally in a dorsal movement of the pleon and diminish water resistance during this movement compared to a stiff, undivided exopod. Nothing is known about alternative mechanism to reduce the water resistance during uropod movement. However, undivided and divided exopods exist in fossil and extant species of Anaspidaea, Caridea, Lophogastrida, Hoplocarida, and Thermosbaenacea (see e.g. GRUNER 1993).

##### 4.9.2. Mapping

For the most part, no consistency within the taxa could be recognised concerning division of the exopod (see

above) and therefore the mapping is probably not representative (Fig. 6B). However, MAAS & WALOSZEK (2001) state a divided uropodal exopod to be a ground-pattern condition of Eumalacostraca. Consequently, undivided exopods are then secondary changes. Accordingly, an undivided exopod in Bathynellacea is an autapomorphic character for this taxon.

#### 4.10. Phylogenetic significance of uropods

The distribution of uropodal characters among Eumalacostraca implies the following assumptions for the ground-pattern conditions (GPC) of several eumalacostracan taxa:

- The malacostracan stem species had a pair of sixth pleopods arising from the posterior margin of the sixth pleomere (Fig. 7, GPC 1).
- Autapomorphies of the eumalacostracan ground pattern are leaf-shaped uropods with stabilising carinae on the rami, which also possess setation to enlarge their effective surface (Fig. 7, GPC 2). These uropods form a tail fan together with the telson.
- The stem species of Caridoida evolved a medio-proximal depression on the uropodal basipod giving space for the telson (Fig. 7, GPC 3). Additionally the caridoid escape reaction – together with a re-arrangement of pleon musculature – evolved.
- Bathynellacea acquired a rod-like shape of the uropods and lost the caridoid escape reaction (Fig. 7, GPC 4; both being adaptations to their interstitial life style), and the exopod became undivided.
- An autapomorphic character for Eucarida is a latero-distal prolongation at the uropodal basipod (Fig. 7, GPC 5).
- Decapoda acquired a longitudinal median keel on the uropodal basipod (Fig. 7, GPC 6).
- Autapomorphic features of Thermosbaenacea are uropod rami that are enlarged by spines and have a smaller proximo-distal and medio-lateral extension relative to the basipod than leaf-shaped uropods of other taxa (Fig. 7, GPC 7).
- Mysidacea (Mysida + Lophogastrida) acquired a uropodal basipod being drawn out medio-proximally (Fig. 7, GPC 8).
- Lophogastrida acquired a triangular median keel on the basipod of their uropods (Fig. 7, GPC 9).
- In Peracarida, the Amphipoda + Mancoida taxon acquired a rod-like shape of the uropods and lost the caridoid escape reaction (Fig. 7, GPC 10).

Although many questions concerning uropod morphology and malacostracan phylogeny are unresolved, uropodal characters contribute to phylogenetic questions significantly.

## 5. Outlook

Data on uropod morphology are still lacking for some taxa and has to be added. This may give additional evidence to test the results and interpretations of our study. As uropods have revealed their potential to contribute to the ongoing discussion on malacostracan evolution, the whole pleon as a functional unit is regarded as similarly promising for drawing phylogenetic conclusions. Future morphological studies should focus on the character-complex pleon. It bears multiple features, all of which have the potential to serve as a phylogenetic signal. Examples are external characters such as 1) shape, composition, and articulation of pleopods; 2) shape, composition, and articulation of pleomeres including the situation of their sternites; 3) shape of the telson including position of the anus and fusion with pleomeres. Furthermore, anatomical features like the arrangement of muscles can also be considered. In the course of this a re-evaluation of the caridoid escape reaction should be evaluated, as there seem to exist several different types.

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## 7. References

- AHYONG S.T. 2001. Revision of the Australian Stomatopod Crustacea. – Records of the Australian Museum, Supplement **26**: 12–326.
- ASSIS L.C.S. 2009. Coherence, correspondence, and the renaissance of morphology in phylogenetic systematics. – *Cladistics* **25**: 528–544.
- BACHMEYER F. 1960. Eine fossile Cumaceenart (Crustacea: Malacostraca) aus dem Callovien von La Voulte-sur-Rhone (Ardeche). – *Berichte der Schweizerischen Paläontologischen Gesellschaft* **53**: 422–426.
- BARNARD J.L., INGRAM C.L. 1986. The supergiant amphipod *Alicella gigantea* chevreux from the North Pacific gyre. – *Journal of Crustacean Biology* **6**(4): 825–839.
- BATE C.S. 1856. On the British Edriophthalma. Part I. The Amphipoda. – Report of the twenty-fifth Meeting of the British Association for the Advancement of Science; held at Glasgow in September 1855: 18–62 pp. + pls.
- BERGSTRÖM J., BRIGGS D.E.G., DAHL E., ROLFE W.D.I., STÜRMER W. 1987. *Nahecaris stuertzi*, a phyllocarid crustacean from the Lower Devonian Hunsrück Slate. – *Paläontologische Zeitschrift* **61**(3/4): 273–298.
- BOAS J.E.V. 1883. Studien über die Verwandtschaftsbeziehungen der Malakostraken. – *Morphologisches Jahrbuch* **8**: 488–579.
- BOWMAN T.E. 1971. The case of the nonubiquitous telson and the fraudulent furca. – *Crustaceana* **21**: 165–175.
- BOWMAN T.E., ILIFFE T.M. 1985. *Mictocaris halope*, a new unusual peracaridan crustacean from marine caves on Bermuda. – *Journal of Crustacean Biology* **5**(1): 58–73.
- BOWMAN T.E., YAGER J., ILIFFE T.M. 1985. *Speonebalia cannoni*, n. gen. sp. from the Caicos Islands, the first hypogean leptostracan (Nebaliacea: Nebaliidae). – *Proceedings of the Biological Society of Washington* **98**(2): 439–446.
- BRIGGS D.E.G., SUTTON M.D., SIVETER DA.J., SIVETER DE.J. 2004. A new phyllocarid (Crustacea: Malacostraca) from the Silurian Fossil-Lagerstätte of Herefordshire, UK. – *Proceedings of the Royal Society of London B* **271**: 131–138.
- CALDWELL R.L. 1979. A unique form of locomotion in a stomatopod – backward somersaulting. – *Nature* **282**: 71–73.
- CALMAN W.T. 1904. On the classification of the Crustacea Malacostraca. – *The Annals and Magazine of Natural History, including Zoology, Botany, and Geology* **7**(13): 144–158.
- CALMAN W.T. 1905. The Cumacea of the Siboga Expedition. – *Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch Gebied* **36**: 1–23.
- CALMAN W.T. 1909. Part VII. Appendiculata. 3<sup>rd</sup> vol. Crustacea. A Treatise on Zoology. – Adam and Charles Black, London. 136 pp.

- CALMAN W.T. 1917. Notes on the morphology of *Bathynella* and some allied Crustacea. – *Journal of the Microscopical Society* **62**: 489–514.
- CHO J.-L., HUMPHREYS W.F. 2010. Ten new species of the genus *Brevisomabathynella* Cho, Park and Ranga Reddy, 2006 (Malacostraca, Bathynellacea, Parabathynellidae) from Western Australia. – *Journal of Natural History* **44**(17/18): 993–1079.
- DAHL E. 1977. The amphipod functional model and its bearing upon systematics and phylogeny. – *Zoologica Scripta* **6**: 221–228.
- DANIEL R.J. 1932. Comparative study of the abdominal musculature in Malacostraca. Part II. The superficial and main ventral muscles, dorsal muscles and lateral muscles, and their continuation into the thorax. – *Proceedings and Transactions of the Liverpool Biological Society* **46**: 45–107.
- DIXON A.Y. 1944. Notes on certain aspects of the biology of *Cumopsis goodsir* (Van Beneden) and some other cumaceans in relation to their environment. – *Journal of the Marine Biological Association of the United Kingdom* **26**: 61–71.
- ESPEEL M. 1985. Fine structure of the statocyst of the mysid shrimp *Neomysis integer* Crustacea, Mysidacea. – *Journal of Morphology* **186**(2): 149–166.
- FANENBRUCK M., HARZSCH S., WÄGELE J.H. 2004. The brain of the Remipedia (Crustacea) and an alternative hypothesis on their phylogenetic relationships. – *Proceedings of the National Academy of Sciences USA* **101**(11): 3868–3873.
- GARM A. 2004. Revising the definition of the crustacean seta and setal classification systems based on examinations of the mouthpart setae of seven species of decapods. – *Zoological Journal of the Linnean Society* **142**: 233–252.
- GORDON I. 1957. On *Spelaeogriphus*, a new cavernicolous crustacean from South Africa. – *Bulletin of the British Museum (Natural History)* **5**(2): 31–47.
- GROBEN K. 1910. *Lehrbuch der Zoologie*, 2. Auflage. – N.G. Elwert'sche Verlagsbuchhandlung, Marburg. 418–491 pp.
- GRUNER H.-E. 1993. *Lehrbuch der Speziellen Zoologie. Band I: Wirbellose Tiere. 4. Teil: Arthropoda (ohne Insecta)*. 4. Auflage. – Gustav Fischer Verlag, Jena, Stuttgart, New York. 1279 pp.
- HARZSCH S., WALOSZEK D. 2000. Serotonin-immunoreactive neurons in the ventral nerve cord of Crustacea: a character to study aspects of arthropod phylogeny. – *Arthropod Structure & Development* **29**: 307–322.
- HAUG J.T., MAAS A., WALOSZEK D. 2010a. †*Henningsmoenicaris scutula*, †*Sandtorpia vestrogothiensis* gen. et sp. nov. and heterochronic effects in early crustacean evolution. – *Transactions of the Royal Society of Edinburgh* **100**: 311–351.
- HAUG J.T., HAUG C., MAAS A., KUTSCHERA V., WALOSZEK D. 2010b. Evolution of mantis shrimps (Stomatopoda, Malacostraca) in the light of new Mesozoic fossils. – *BMC Evolutionary Biology* **10**: 290.
- HAUG J.T., WALOSZEK D., MAAS A., LIU Y., HAUG C. 2012. Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. – *Palaeontology* **55**(2): 369–399.
- HEITLER W.J., FRASER K., FERRERO E.A. 2000. Escape behaviour in the stomatopod crustacean *Squilla mantis*, and the evolution of the caridoid escape reaction. – *Journal of Experimental Biology* **203**: 183–192.
- HESSLER R.R. 1983. A defense of the caridoid facies: wherein the early evolution of the Eumalacostraca is discussed. Pp. 145–164 in: SCHRAM F.R. (ed.), *Crustacean Phylogeny – Crustacean Issues*. – A.A. Balkema, Rotterdam.
- JAZDZEWSKI K., KUPRYJANIWICZ J. 2010. One more fossil niphargid (Malacostraca: Amphipoda) from baltic amber. – *Journal of Crustacean Biology* **30**(3): 413–416.
- JENNER R.A. 2010. Higher-level crustacean phylogeny: Consensus and conflicting hypotheses. – *Arthropod Structure & Development* **39**: 143–153.
- JENNER R.A., HOF C.H.J., SCHRAM F. 1998. Palaeo- and Archaeostomatopods (Hoplocarida: Crustacea) from the Bear Gulch Limestone, Mississippian (Namurian), of central Montana. – *Contributions to Zoology* **67**(3): 155–186.
- KNOFF F., KOENEMANN S., SCHRAM F.R., WOLFF C. 2006. The urosome of the Pan- and Peracarida. – *Contributions to Zoology* **75**(1/2): 1–21.
- KOENEMANN S., JENNER R.A., HOENEMANN M., STEMME T., VON REUMONT B.M. 2009. Arthropod phylogeny revisited, with a focus on crustacean relationships. – *Arthropod Structure & Development* **39**: 88–110.
- MAAS A., HAUG C., HAUG J.T., OLESEN J., ZHANG X., WALOSZEK D. 2009. Early crustacean evolution and the appearance of epipodites and gills. – *Arthropod Systematics & Phylogeny* **67**(2): 255–273.
- MAAS A., WALOSZEK D. 2001. Larval development of *Euphausia superba* Dana, 1852 and a phylogenetic analysis of the Euphausiacea. – *Hydrobiologia* **448**: 143–169.
- MACMILLAN D.L., SILVEY G.E., WILSON I.S. 1981. Coordination of the movements of the appendages on the Tasmanian mountain shrimp *Anaspides tasmaniae* (Thomson) (Syn-carida: Anaspididae). – *Proceedings of the Royal Society of London B* **212**: 213–231.
- MAYER G., MAIER G., MAAS A., WALOSZEK D. 2008. Mouthparts of the Ponto-Caspian invader *Dikerogammarus villosus* (Amphipoda: Pontogammaridae). – *Journal of Crustacean Biology* **28**(1): 1–15.
- MEISCH C. 2007. On the origin of the putative furca of the Ostracoda (Crustacea). – *Hydrobiologia* **585**: 181–200.
- MOORE R.C., MCCORMICK H.L. 1969a. *Treatise on Invertebrate Paleontology, part R, Arthropoda* 4(1). – Geological Society of America & University of Kansas Press, Lawrence.
- MOORE R.C., MCCORMICK H.L. 1969b. *Treatise on Invertebrate Paleontology, part R, Arthropoda* 4(2). – Geological Society of America & University of Kansas Press, Lawrence.
- NOODT W. 1964. *Natürliches System und Biogeographie der Syn-carida (Crustacea, Malacostraca)*. – *Gewässer und Abwässer* **37/38**: 76–186.
- OLESEN J., WALOSZEK D. 2000. Limb ontogeny and trunk segmentation in *Nebalia* species (Crustacea, Malacostraca, Lepidostrecha). – *Zoomorphology* **120**: 47–64.



- OLESEN J., PARNAS S.T., PETERSEN J.F. 2006. Tail flip and escape response of *Tethysbaena argentarii* (Malacostraca: Thermosbaenacea). – *Journal of Crustacean Biology* **26**(3): 429–432.
- PEREZ FARFANTE I. 1977. American solenocerid shrimps of the genera *Hymenopenaeus*, *Haliporoides*, *Pleoticus*, *Hadropenaeus* new genus, and *Mesopenaeus* new genus. – *Fishery Bulletin* **75**(1): 261–346.
- PERRIER V., VANNIER J., RACHEBOEUF P.R., CHARBONNIER S., CHABARD D., SOTTY D. 2006. Syncarid crustaceans from the Monteceau Lagerstätte (Upper Carboniferous, France). – *Palaeontology* **49**(3): 647–672.
- POORE G. 2004. Marine Decapod Crustacea of Southern Australia. A Guide to Identification with a Chapter on Stomatopoda by Shane Ahyong. – Museum of Victoria Melbourne. 574 pp.
- REIF W.-E. 2002. Evolution of organ systems: phylogeny, function and reciprocal illumination. – *Senckenbergiana Lethaea* **82**: 357–366.
- RICE A.L. 1967. Crustacea (pelagic adults). Order: Decapoda V. Caridea. Families: Pasiphaeidae, Oplophoridae, Hippolytidae and Pandalidae. – *Zooplankton* **112**: 2–7.
- RICHTER S., MØLLER O.S., WIRKNER C.S. 2009. Advances in Crustacean Phylogenetics. – *Arthropod Systematics & Phylogeny* **67**(2): 275–286.
- RICHTER S., SCHOLTZ G. 2001. Phylogenetic analysis of the Malacostraca (Crustacea). – *Journal of Zoological Systematics and Evolutionary Research* **39**: 113–136.
- SARS G.O. 1885. The Voyage of H.M.S. Challenger: Report on the Schizopoda collected by H.M.S. Challenger during the years 1873–1876. Reports on the Scientific Results of the Voyage of H.M.S. Challenger. – *Zoological Challenger Expedition* **37**: 1–228.
- SARS G.O. 1899. An account of the Crustacea of Norway. Vol. II. Isopoda. – Christiania, Bergen.
- SCHMINKE H.K. 1972. *Hexabathynella halophila* gen. n., sp. n. und die Frage nach der marinen Abkunft der Bathynellacea. – *Marine Biology* **15**: 282–287.
- SCHMINKE H.K. 1974. *Psammaspides williamsi* gen. n., sp. n., ein Vertreter einer neuen Familie mesopsammaler Anaspidea (Crustacea, Syncarida). – *Zoologica Scripta* **3**: 177–183.
- SCHMINKE H.K. 1976. The ubiquitous telson and the deceptive furca. – *Crustaceana* **30**(3): 293–300.
- SCHMINKE H.K. 1979. Eine neue Gattung der Familie Parabathynellidae (Bathynellacea, Syncarida) aus dem nördlichen Südamerika. – *Bijdragen tot de Dierkunde* **49**(1): 97–101.
- SCHMINKE H.K. 1980. *Agnathobathynella ecclesi* gen. n., sp. n. aus Malawi und die Formenvielfalt der Familie Bathynellidae (Crustacea, Bathynellacea). – *Bijdragen tot de Dierkunde* **50**(1): 145–154.
- SCHMINKE H.K. 1981. Adaptation of Bathynellacea (Crustacea, Syncarida) to life in the interstitial (“Zoea Theory”). – *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **66**(4): 575–637.
- SCHMINKE H.K. 1982. Syncarida. Pp. 233–237 in: PARKER S.P. (ed.), *Synopsis and Classification of Living Organisms*, Vol. 2. – McGraw-Hill, New York.
- SCHMINKE H.K. 1988. A new genus and species of Syncarida (Crustacea: Malacostraca) from Borneo. – *Journal of Natural History* **22**: 631–637.
- SCHOLTZ G. 1995. Expression of the *engrailed* gene reveals nine putative segment-anlagen in the embryonic pleon of the freshwater crayfish *Cherax destructor* (Crustacea, Malacostraca, Decapoda). – *The Biological Bulletin* **188**: 157–165.
- SCHOLTZ G., RICHTER S. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). – *Zoological Journal of the Linnean Society* **113**: 289–328.
- SCHRAM F.R. 1969. Some middle Pennsylvanian Hoplocarida (Crustacea) and their phylogenetic significance. – *Fieldiana Geology* **12**(14): 235–310.
- SCHRAM F.R. 1984. Fossil Syncarida. – *Transactions of the San Diego Society of Natural History* **20**(13): 189–246.
- SCHRAM F.R. 1986. Crustacea. – Oxford University Press. 605 pp.
- SCHRAM F.R. 2007. Palaeozoic proto-mantis shrimp revisited. – *Journal of Paleontology* **81**(5): 895–916.
- SCHRAM F.R., HOF C.H.J. 1998. Fossils and the interrelationships of major Crustacean groups. Pp. 233–302 in: EDGE-COMBE G.D. (ed.), *Arthropod Fossils and Phylogeny*. – Columbia University Press, New York.
- SIEWING R. 1952. Morphologische Untersuchungen an Cumaceen. – *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* **72**: 552–559.
- SIEWING R. 1956. Untersuchungen zur Morphologie der Malacostraca (Crustacea). – *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* **75**: 39–176.
- SILVEY G.E., WILSON I.S. 1979. Structure and function of the lateral giant neurone of the primitive crustacean *Anaspides tasmaniae*. – *Journal of Experimental Biology* **78**: 121–136.
- SPEARS T., ABELE L.G. 1999. Phylogenetic relationships of crustaceans with foliaceous limbs: an 18S rDNA study of Branchiopoda, Cephalocarida, and Phyllocarida. – *Journal of Crustacean Biology* **19**(4): 825–843.
- STOCK J.H. 1967. A revision of the European species of the *Gammarus locusta*-group (Crustacea, Amphipoda). – *Zoologische Verhandlungen* **90**: 4–56.
- STOCK J.H. 1968. A revision of the European species of the *Echinogammarus pungens*-group (Crustacea, Amphipoda). – *Beaufortia* **16**(211): 13–78.
- SWAIN R., WILSON I.S., ONG J.E. 1971. A new species of *Allanaspides* from south-western Tasmania. – *Crustaceana* **21**: 196–202.
- TAYLOR R.S., SCHRAM F.R., YAN-BIN S. 2001. A new Upper Middle Triassic shrimp (Crustacea: Lophogastrida) from Guizhou, China, with discussion regarding other fossil “mysidaceans”. – *Journal of Paleontology* **75**(2): 310–318.
- VERRILL A.E. 1923. Crustacea of Bermuda. Schizopoda, Cumacea, Stomatopoda and Phyllocarida. – *Transactions of the Connecticut Academy of Arts and Sciences*. 211 pp.

- VOGEL F. 1985. Das Schwimmen der Talitridae (Crustacea, Amphipoda): Funktionsmorphologie, Phänomenologie und Energetik. – *Helgoländer Meeresuntersuchungen* **39**: 303–339.
- WÄGELE J.-W. 1989. Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. – *Zoologica* **47**(140): 1–262.
- WÄGELE J.-W. 1994. Review of methodological problems of ‘computer cladistics’ exemplified with a case study on isopod phylogeny (Crustacea: Isopoda). – *Zeitschrift für Zoologische Systematik und Evolutionsforschung* **32**: 81–107.
- WAGNER H.P. 1994. A monographic review of the Thermosbaenacea (Crustacea: Peracarida). – *Zoologische Verhandlungen* **291**: 1–338.
- WALOSSEK D. 1993. The Upper Cambrian *Rehbachella kinnekullensis* and the phylogeny of Branchiopoda and Crustacea. – *Fossils & Strata* **32**: 1–202, pls. 1–34. Oslo.
- WALOSSEK D. 1999. On the Cambrian diversity of Crustacea. Pp. 3–27 in: SCHRAM F.R., VON VAUPEL KLEIN J.C. (eds.), *Crustaceans and the Biodiversity Crisis, Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998*. – Brill Academic Publishers, Leiden.
- WALOSSEK D., MÜLLER K.J. 1990. Upper Cambrian stem-lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus*. – *Lethaia* **23**: 409–427.
- WALOSSEK D., MÜLLER K.J. 1998. Cambrian ‘Orsten’-type arthropods and the phylogeny of Crustacea. Pp. 141–155 in: FORTEY R.R., THOMAS R. (eds.), *Symposium on Relationships of Major Arthropod Taxa*. – Chapman & Hall, London.
- WILLIAMSON D.I. 1973. *Amphionides reynaudii* (H. Milne Edwards), representative of a proposed new order of Eucarid-ian Malacostraca. – *Crustaceana* **25**: 35–50.
- WILLS M.A., JENNER R.A., NI DHUBHGHAILL C. 2009. Eumalacostracan evolution: Conflict between three sources of data. – *Arthropod Systematics & Phylogeny* **67**(1): 71–90.
- WILSON G.D.F. 1996. Of uropods and isopod crustacean trees: a comparison of ‘groundpattern’ and cladistic methods. – *Vie et Milieu* **46**(2): 139–153.
- WIRKNER C.S. 2009. The circulatory system in Malacostraca – evaluating character evolution on the basis of differing phylogenetic hypotheses. – *Arthropod Systematics & Phylogeny* **67**(1): 57–70.
- WIRKNER C.S., RICHTER S. 2007. Comparative analysis of the circulatory system in Amphipoda (Malacostraca, Crustacea). – *Acta Zoologica* **88**: 159–171.
- WIRKNER C.S., RICHTER S. 2010. Evolutionary morphology of the circulatory system in Peracarida (Malacostraca; Crustacea). – *Cladistics* **26**: 143–167.