

The Circulatory System in Malacostraca – Evaluating Character Evolution on the Basis of Differing Phylogenetic Hypotheses

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> Abstract

The circulatory system is one of the major organ systems in Malacostraca. As no consensus on malacostracan phylogeny exists it becomes necessary to evaluate different phylogenetic hypotheses for their impact on circulatory system evolution. Four prevailing hypotheses were therefore used to map different circulatory system characters. The comparison shows that the length of the heart, i.e. the position of the anterior and posterior borders of the heart, changed extensively within malacostracan taxa. However, a general back shift of at least the anterior border from more anterior positions is feasible. A pattern of ostial evolution is not discernable as both an increase and a decrease in the number of pairs of ostia took place. A segmental arrangement is seen as the plesiomorphic condition. Cardiac artery patterns, i.e. the spatial arrangement of cardiac arteries along the heart, changed within malacostracans from a pattern of segmentally arranged arteries to localized patterns. A descending artery, a mostly unpaired artery in the posterior thorax connecting the dorsal and the ventral vessel, evolved only once within Malacostraca. In a second step the general plausibility of the four alternative hypotheses in the explanation of circulatory system characters was evaluated through the calculation of homoplasy indices (HI). A comparison of HI values challenges the only molecular phylogeny compared, while all other morphology-based hypotheses perform almost equally well.

> Key words

Vascular system, heart, morphology, phylogeny.

1. Introduction

Malacostraca is the most species-rich and, due to the fact that it contains the decapods, best-studied crustacean taxon. However, the phylogenetic relationships within this group are far from having been clarified. Indeed, high rank phylogeny is still matter of much dispute (see e.g. the latest combined phylogenetic analysis by JENNER et al. 2009). Almost all possible combinations of higher taxa have been proposed over the years. The few pillars in the context of phylogenetics are the concept that Leptostraca is the sister taxon to the Eumalacostraca (SIEWING 1956; RICHTER & SCHOLTZ 2001; MELAND & WILLASSEN 2007, but see also SCHRAM 1986), that most high rank taxa such as Stomatopoda, Decapoda, Anaspidacea, Euphausiacea, Amphipoda, Tanaidacea, Cumacea and Isopoda are well-founded monophyla, and that there is at least a “core group” of Peracarida (i.e. Amphipoda, Spe-

laeogriphacea, Mictacea, Tanaidacea, Cumacea and Isopoda) that cluster together in most analyses (SIEWING 1956; WATLING et al. 2000; RICHTER & SCHOLTZ 2001; WIRKNER & RICHTER in press). One of the central controversies in malacostracan phylogenetics, however, concerns the mono- vs. polyphyly of the Peracarida (monophyly: e.g. SIEWING 1956; RICHTER & SCHOLTZ 2001; polyphyly: e.g. WATLING et al. 2000; SPEARS et al. 2005).

With the phylogenetic background, a major prerequisite of any evolutionary morphological analysis (e.g. WIRKNER & RICHTER in press), so uncertain, it is difficult to draw any conclusions on the evolution of character complexes or organ systems. Nonetheless, tracing character histories on phylogenetic hypotheses is seen as essential to our understanding of the evolution of morphological traits (e.g. FELSENSTEIN 1985;

HARVEY & PAGEL 1991). Therefore, to be able to gain further insight into the evolution of Malacostraca, it would seem necessary to evaluate different transformation series, i.e. character histories, on different phylogenetic hypotheses. This should enable us to judge and corroborate the plausibility of scenarios of character transformations that are common to competing phylogenetic hypotheses.

Two main methods are available for tracing character histories. These are reconstructing ancestral states based on parsimony, and methods of stochastic reconstruction of ancestral states. While parsimonious tracing tries to minimize the steps between character states on a given phylogeny, stochastic methods were developed to accommodate phylogenetic uncertainty (e.g. BOLLBACK 2006) by either visualizing the probability of the occurrence of character states on the different nodes or by mapping changes that might have occurred between two nodes, i.e. the branches. These stochastic methods rely on models of character evolution for the reconstruction of ancestral states. From my point of view this is problematic as, apart from a few exceptions, no empirical data are available on the evolution of single characters and the use of models of character evolution is therefore highly subjective. More importantly, the generalization that a single model of evolution might fit the diversity of character complexes of a morphological character matrix hardly seems realistic.

One further point with regard to morphological characters and parsimony has to be made. In a cladistic framework, each character includes homology hypotheses among organisms assigned to the same character state, and hypotheses of transformation which relate the character states of the series to each other (characters as transformation series *sensu* HENNIG 1966). Accordingly, character coding includes hypotheses of the unique evolutionary origin of character states, which fits in exactly with the requirements of cladistic parsimony (manuscript submitted by N. Szucsich and co-workers). The aim of minimizing incompatibilities resulting from homoplasies is thus a logical consequence of the assumptions contained in the input hypotheses (i.e. the homology hypotheses), since homoplasies are the complementary relations to homology hypotheses (FARRIS 1983; KLUGE 1999; MINDELL & MEYER 2001; SZUCSICH & WIRKNER 2007).

The reconstruction of ancestral states on the basis of parsimony is therefore seen as the logical consequence of the input hypotheses, i.e. homology hypotheses, used in the construction of a morphological character matrix.

The circulatory system is one of the major organ systems in Malacostraca. It can be described as an open system as the hemolymph does not stay within the vascular system, i.e. it enters sinuses and lacunae

not structurally connected to the vascular system. Consequently, the hemolymph circulatory system (HCS) can be broken down into three major components: the hemolymph vascular system (HVS), the hemolymph lacunar system (HLS) and the hemolymph itself.

The main component of the HVS is the central pumping structure, the heart. In most crustaceans the heart consists of a single contractile tissue, the myocardium, surrounded by a connective tissue layer. A number of arteries lead off the heart to irrigate the various tissues in different body regions and appendages. Upon leaving the HVS, the hemolymph flows through the body cavity within spaces between the organs. These cavities are called lacunae. However, some structures exist which are not structurally connected with the HVS but which function exclusively by channeling hemolymph. These structures are termed sinuses. Lacunae and sinuses make up the HLS.

To be able to test the evolution of this character complex, six major characters of the circulatory system in Malacostraca are herein surveyed and discussed for malacostracan terminals. I then compare the distribution of character transformations of these characters by mapping them onto different prevailing phylogenetic hypotheses. In a last step, the general plausibility of the alternative hypotheses in explaining circulatory organ evolution is discussed.

2. Material and methods

2.1. Taxon sampling

A total of 28 malacostracan terminals were studied. Table 1 lists the taxa used as terminals for the different phylogenetic hypotheses and cites the literature that was used for the review of the HVS.

2.2. Tracing character evolution

For the reconstruction of ancestral states a nexus file containing the six characters discussed here (see chapter 3) was produced from the original matrix (WIRKNER & RICHTER in press). In Mesquite 2.5 (build j77) (MADISON & MADDISON 2008) the file was loaded and a tree window created. In the trace history function, parsimony reconstruction was chosen (see Introduction for discussion) and only unambiguous changes are shown. For the comparison of different phylogenetic hypotheses, the tree resulting from the analysis by WIRKNER & RICHTER (in press) was changed by swapping the branches. To overcome the problem of different terminals, the POORE (2005) tree and the WATLING et al.

Tab. 1. List of taxa and literature used for the review of the hemolymph vascular system.

Taxon	Species	Source
Stomatopoda	<i>Squilla oratoria</i> (de Haan, 1844)	KOMAI & TUNG (1931)
Leptostraca	<i>Nebalia bipes</i> (O. Fabricius, 1780)	SIEWING (1956)
Decapoda	<i>Melicertus kerathurus</i> (Forskål, 1775)	MAYRAT (1958)
	<i>Palaemonetes vulgaris</i> (Say, 1818)	BRODY & PERKINS (1930)
Anaspidacea	<i>Anaspides tasmaniae</i> Thomson, 1892	SIEWING (1954); SIEWING (1956)
Euphausiacea	<i>Euphausia superba</i> Dana, 1852	ZIMMER (1913)
Thermosbaenacea	<i>Tethysbaena argentarii</i> (Stella, 1951)	WIRKNER & RICHTER (2009)
Lophogastrida	<i>Lophogaster typicus</i> M. Sars, 1857	WIRKNER & RICHTER (2007a)
	<i>Eucopia unguiculata</i> (Willemoes-Suhm, 1875)	SIEWING (1956)
	<i>Neognathophausia ingens</i> (Dohrn, 1870)	BELMAN & CHILDRESS (1976)
Mysida	<i>Boreomysis arctica</i> (Krøyer, 1861)	WIRKNER & RICHTER (2007a)
	<i>Neomysis integer</i> (Leach, 1815)	WIRKNER & RICHTER (2007a)
Amphipoda	<i>Orchestia cavimana</i> Heller, 1865	WIRKNER & RICHTER (2007b)
	<i>Hyalella azteca</i> Saussure, 1858	WIRKNER & RICHTER (2007b)
	<i>Hyperia galba</i> (Montagu, 1813)	WIRKNER & RICHTER (2007b)
	<i>Caprella mutica</i> Schurin, 1935	WIRKNER & RICHTER (2007b)
	<i>Trogloteleupia leleupi</i> Ruffo, 1951	SIEWING (1963)
Spelaeogriphacea	<i>Spelaeogriphus lepidops</i> Gordon, 1957	WIRKNER & RICHTER (2007c)
Mictacea (Mictocarididae)	<i>Mictocaris halope</i> Bowman & Iliffe, 1985	WIRKNER & RICHTER (2007c)
Cumacea	<i>Diastylis rathkei</i> (Krøyer, 1841)	OELZE (1931); WIRKNER & RICHTER (2008)
	<i>Hemilamprops rosea</i> (Norman, 1863)	WIRKNER & RICHTER (2008)
	<i>Leucon nasica</i> (Krøyer, 1841)	WIRKNER & RICHTER (2008)
Tanaidacea	<i>Tanais dulongii</i> (Audouin, 1826)	WIRKNER & RICHTER (2008)
	<i>Aapseudes bermudeus</i> Bacescu, 1980	WIRKNER & RICHTER (2008)
	<i>Neotanais</i> sp.	WIRKNER & RICHTER (2008)
Isopoda	<i>Paramphisopus palustris</i> (Glauert, 1924)	WIRKNER & RICHTER (2003)
	<i>Porcellio scaber</i> Latreille, 1804	WIRKNER & RICHTER (2003)
	<i>Asellus aquaticus</i> (Linnaeus, 1758)	SILEN (1954)

(2000) tree were pruned. As the hypotheses put forward by POORE (2005) and WATLING et al. (2000) are based on a ground pattern approach, their high rank taxa were exchanged for the respective exemplar terminals (e.g. Amphipoda for the five amphipod terminals; see Figs. 2, 3).

2.3. Calculations of homoplasy indices

Homoplasy indices were calculated using the following equation: $HI = 1 - CI$; $CI = m/s$, with m being the minimum steps possible for each character and s being the observed number of steps for each character. The HI values for 22 circulatory system characters as published in WIRKNER & RICHTER (in press) were calculated for each of the alternative hypotheses.

3. Survey of the circulatory organs in Malacostraca

For the evaluation of character histories the following transformation series were chosen as they represent major features of the HVS: the position of the anterior border of the heart, distribution patterns of pairs of ostia, number of pairs of ostia, distribution patterns of lateral cardiac arteries, the occurrence of a descending artery, and the occurrence of a posterior aorta. For detailed conceptualizations of these characters see WIRKNER & RICHTER (in press). In the following, these characters are reviewed and discussed for the malacostracan terminals (see Tab. 1).

3.1. Leptostraca (*Nebalia bipes*)

The anterior border of the heart lies in the anterior cephalothorax, the posterior border is situated in the 4th pleonal segment. With regard to the pattern of ostia, the seven pairs are arranged segmentally in the thorax. The 12 pairs of cardiac arteries are arranged segmentally. A ventral vessel is missing, the heart is extended by a posterior aorta.

3.2. Stomatopoda (*Squilla oratoria*)

The anterior border of the heart lies in the maxillary region (the border of the last cephalic and 1st thoracic segments), the posterior border in the 5th pleonal segment. In the adult, the heart is equipped with 13 pairs of ostia, coded therefore as a segmental arrangement. The pleon is supplied via lateral cardiac arteries. 15 pairs of arteries branch off the heart. The first pair (anterior lateral arteries, ALA) supplies the anterior cephalothorax, the remaining 14 can be identified as segmental arteries. The latter supply the organs in the trunk and the corresponding legs. The dorsal and ventral vessels are connected via nine shunts that connect from the lateral cardiac arteries to the ventral vessel. A descending artery (as present in some other malacostracans, see below) is not present. The ventral vessel only supplies the ventral nerve cord, while the ventral vessel in Decapoda, Anaspidacea, Euphausiacea and Mysidacea supplies the thoracopods (see below).

3.3. Dendrobranchiata (*Melicertus kerathurus*)

Like all other decapods, *M. kerathurus* possesses a globular heart which lies at the posterior border of the carapace. As a result, its anterior border cannot be assessed, while its posterior border is coded as lying in the 8th thoracic segment. The heart is equipped with five pairs of ostia, two pairs dorsally, two pairs laterally and one pair latero-ventrally. A posterior aorta supplies the pleon with hemolymph via lateral arteries. Three unpaired arteries emanate from the heart: the anterior aorta, the posterior aorta and the descending artery. In addition, two pairs of arteries branch off the anterior part of the heart. These are the anterior lateral arteries (ALA), which supply the musculature of the mandibles and the two pairs of antennae, and the hepatic arteries, which supply the midgut gland. This pattern of cardiac arteries is assigned its own state. The descending artery splits into an anterior and a posterior branch underneath the ventral nerve cord, thus forming a subneural ventral artery, which supplies the thoracopods through lateral branches.

3.4. Pleocyemata (*Palaemonetes vulgaris*)

As in *M. kerathurus*, the position of the anterior border of the heart is difficult to ascertain. The posterior border lies in the 8th thoracic segment. BRODY & PERKINS (1930) make no statements on the ostia, but according to BALSS et al. (1940) and MAYRAT (1958) five pairs occur in Caridea. The same pattern of cardiac arteries, descending artery and ventral vessel occur as in *M. kerathurus*.

3.5. Anaspidacea (*Anaspides tasmaniae*)

The anterior border of the heart lies in the anterior part of the 1st thoracic segment. The heart extends through the whole trunk and its posterior border is situated in the 5th pleonal segment. According to SIEWING (1956) the single pair of ostia is situated in the 3rd thoracic segment. One pair of lateral cardiac arteries occurs in the first and the last thoracic segment respectively. In the pleon, five further pairs exist. In the 8th thoracic segment a descending artery leads down to the ventral side and splits just above the ventral nerve cord into an anterior and a posterior branch. While the posterior branch pierces the ventral nerve cord to run ventrally of it into the pleon, the anterior branch runs above the nerve cord. The thoracopod-supplying lateral arteries branching off the descending artery still run underneath the connectives into the corresponding leg, however. The heart is extended by a posterior aorta, which has no lateral branches.

3.6. Euphausiacea (*Euphausia superba*)

Euphausia superba possesses a globular heart located in the posterior part of the thorax. No clear statement can be made about its anterior border, but its posterior border is situated in the 8th thoracic segment. The heart is equipped with two pairs of ostia which are positioned laterally in the heart wall. Ten arteries branch off the heart, the unpaired anterior aorta and two pairs of arteries from the anterior part, and the unpaired descending artery and two pairs of arteries from the posterior part. Of the latter pairs of arteries, one supplies the pleon and the pleopods. The descending artery splits above the ventral nerve cord. An unpaired posterior aorta is not present (see posterior aorta chapter 4.5. below).

3.7. Lophogastrida (*Lophogaster typicus*, *Eucopia unguiculata*, *Neognathophausia ingens*)

In Lophogastrida the anterior border of the heart lies in the anterior part of the cephalothorax and is therefore assigned to the first thoracic segment. The heart extends through the whole thorax and its posterior end lies in *L. typicus* in the first pleonal segment (WIRKNER & RICHTER 2007a), while it is reported to lie in the 8th thoracic segment in *N. ingens* (BELMAN & CHILDRESS 1976) and *E. unguiculata* (SIEWING 1956). The heart is equipped with three pairs of ostia (unknown in *N. ingens*; BELMAN & CHILDRESS 1976). The two more posterior pairs lie in close vicinity to each other and are separated by a membrane (see WIRKNER & RICHTER 2007a: fig. 5E). Cardiac arteries occur segmentally throughout the whole thorax. One artery of the eighth pair of cardiac arteries represents the descending artery, which branches above the ventral nerve cord. The heart is elongated into the pleon by a posterior aorta, which is equipped with lateral arteries.

3.8. Mysida (*Boreomysis arctica*, *Neomysis integer*)

The heart starts in the anterior cephalothorax and its anterior end is therefore interpreted as being situated in the 1st thoracic segment. It ends in the 8th thoracic segment. Two pairs of ostia are found in the cephalothorax, and as in Lophogastrida they are positioned close to each other and separated by a membrane (see WIRKNER & RICHTER 2007a: fig. 5E). With respect to the cardiac arteries, Mysida show a distinct and unique pattern: only the anteriormost pair of cardiac arteries is paired, all other four cardiac arteries are unpaired, branching off the heart ventrally. The posteriormost artery represents the descending artery, which branches above the ventral nerve cord. A posterior aorta extends into the pleon, which gives off lateral arteries in each segment.

3.9. Amphipoda (*Hyperia galba*, *Caprella mutica*, *Orchestia cavimana*, *Hyaella azteca*, *Trogloleupia leleupi*)

There is some variation within Amphipoda regarding the extension of the heart. Its anterior border generally lies in the 1st thoracic segment, except in *T. leleupi* where it starts in the 2nd thoracic segment. The latter condition is interpreted as secondary within Amphipoda owing to the troglobiont lifestyle of ingolfiellids and their resulting small body size (WIRKNER & RICHTER 2007b). The posterior border of the heart lies in

the 7th thoracic segment in *O. cavimana*, *H. azteca* and *H. galba*. In *C. mutica* it is found in the 6th and in *T. leleupi* in the 5th thoracic segment. The heart is equipped with three pairs of ostia which are located in the 3rd, 4th and 5th thoracic segments respectively. At least three pairs of cardiac arteries are found in the 4th, 5th and 6th thoracic segment supplying the body cavity in the thorax. Exceptional here is *C. mutica* where no cardiac arteries exist. In *O. cavimana* and *H. azteca* a pair of arteries branches off the anterior part of the heart. A ventral vessel is not existent, as is a descending artery. A posterior aorta extends into the pleon, which has no lateral arteries.

3.10. Spelaeogriphacea (*Spelaeogriphus lepidops*)

Spelaeogriphus lepidops displays a rather reduced HVS. The heart extends from the 2nd to the 8th thoracic segment. Two pairs of ostia are found. Lateral cardiac arteries, a descending artery and a posterior aorta are missing.

3.11. Mictacea (*Mictocaris halope*)

The heart in *M. halope* is short, stretching from the 2nd to the 5th thoracic segment. It is equipped with one pair of ostia which lies in the 2nd thoracic segment. Apart from the anterior aorta, no arteries emanate from the heart.

3.12. Thermosbaenacea (*Tethysbaena argentarii*)

One of the shortest hearts within malacostracans is found in *T. argentarii*, extending from the posterior cephalothorax, i.e. the 1st thoracic segment, to the 2nd thoracic segment. It has one pair of ostia. The only artery branching off the heart is the anterior aorta.

3.13. Tanaidacea (*Tanais dulongii*, *Apseudes bermudeus*, *Neotanais* sp.)

In Tanaidacea the anterior border of the heart is found in the 3rd thoracic segment. Its posterior border lies in the 7th thoracic segment in *T. dulongii*, while in the two other species it is situated in the 8th thoracic segment. With regard to the ostia some variation occurs. *Neotanais* sp. possesses two pairs in the 4th and 5th thoracic segments. *A. bermudeus* possesses one unpaired ostium in the 4th thoracic segment and one pair of ostia in the 5th thoracic segment. However, the unpaired

ostium is regarded as a reduced pair (for argumentation see WIRKNER & RICHTER 2008: 147). In *T. dulongii* only one pair occurs in the 5th thoracic segment. Five pairs of cardiac arteries occur in *T. dulongii*, while *A. bermudeus* and *Neotanais* sp. have four. At least three pairs of cardiac arteries are arranged in three adjacent thoracic segments. A posterior aorta is absent and the pleon is supplied by the last pair of cardiac arteries. A descending artery is missing.

3.14. Cumacea (*Hemilamprops rosea*, *Diastylis rathkei*, *Leucon nasica*)

As in other malacostracans, it is difficult to determine the position of the anterior border of the heart in Cumacea as it lies in the cephalothorax. In Cumacea, the cephalothorax is made up of the cephalon and the first three thoracic segments. As the anterior border of the heart lies in the posterior part of the cephalothorax it is interpreted as lying in the 3rd thoracic segment (see also WIRKNER & RICHTER 2008). The posterior border lies either in the 6th (*L. nasica*) or the 7th thoracic segment (*H. rosea*, *D. rathkei*). One large, very distinctly shaped pair of ostia occurs in all cumacean species studied. Five pairs of cardiac arteries emanate from the heart. The anteriormost pair supplies the anterior thoracopods. The following three pairs supply one pair of thoracopods each. The posteriormost runs into the pleon. A posterior aorta and a descending artery are missing.

3.15. Isopoda (*Paramphisopus palustris*, *Porcellio scaber*, *Asellus aquaticus*)

The position of the heart in Isopoda has been a matter of some discussion (SILEN 1954; NYLUND et al. 1987; WÄGELE 1992) and is reported to lie in the posterior part of the trunk. However, a detailed analysis showed that at least in Phreatoicidea the anterior border lies in the 3rd thoracic segment and shifted posteriorly within the Isopoda (see WIRKNER & RICHTER 2003). In *P. scaber* and *A. aquaticus* the anterior border lies in the 6th thoracic segment. The posterior border of the heart lies in the posterior pleonal segments, which corresponds to the position of the pleonal gills occurring in isopods. Pairs of ostia are arranged asymmetrically in that the two ostia of a pair are offset along the heart and do not lie opposite each other (for details see WIRKNER & RICHTER 2003). The studied species have five or six pairs of cardiac arteries. However, a pattern is discernable with one pair of arteries supplying the anterior thoracopods, followed by three pairs supplying one pair of thoracopods each and a posterior pair supplying the pleon (for details see WIRKNER & RICHTER 2008).

A posterior aorta and a descending artery are missing.

4. Evaluation of character evolution

To evaluate character evolution on the basis of alternative phylogenetic branching patterns the following hypotheses were chosen: firstly, the cladogram proposed by WIRKNER & RICHTER (in press), as it includes 22 circulatory system characters (6 of which will be discussed below). POORE (2005) was chosen as the most recent proponent of a close relationship between Amphipoda and Isopoda (Edriophthalma concept; see also e.g. SCHRAM 1986; WAGNER 1994). WIRKNER & RICHTER (in press) and POORE (2005) both put forward hypotheses on the monophyly of Peracarida (see Introduction). The hypotheses of WATLING et al. (2000) and MELAND & WILLASSEN (2007) were picked as representatives proposing polyphyly of the Peracarida (see also JARMAN et al. 2000; SPEARS et al. 2005). The latter constitutes one of the most recent molecular analyses for Malacostraca (but see also JENNER et al. 2009).

4.1. Position of the anterior border of the heart

Figs. 1–4

The transition between the heart and the anterior and posterior aortae is quite distinct in that both sites display a valve which allows the hemolymph to leave the heart but not re-enter it. Furthermore, the musculature of the heart, i.e. the myocardium, ends at these transitions. I argue that the position of the anterior and posterior borders changed independently over time, not the length of the heart itself, and therefore code both the anterior and the posterior borders of the heart separately. With regard to the anterior border, its position in the first thoracic segment seems to be the plesiomorphic condition (Figs. 1, 2, 4). Only in the WATLING et al. (2000) hypothesis is this state ambiguous (Fig. 3). In the hypotheses on monophyletic Peracarida, this state is still observable within the Lophogastrida and Mysida (Figs. 1, 2). Depending on their phylogenetic position, the Thermosbaenacea might have either retained this state (Fig. 2) or have regained it secondarily (Fig. 1). Within Peracarida, the anterior border of the heart shifted backwards (Fig. 1; arrows). This stepwise shift could be interpreted as predisposition for the further backward shift within the Isopoda (WIRKNER & RICHTER 2003). The trend of a backward shift of the anterior border of the heart within Malacostraca only

changes slightly when evaluated through the other hypotheses (Figs. 2–4).

4.2. Ostia

Figs. 5–12

Though ostia are present in all euarthropod species with a heart, the variation they display in terms of number and distribution along the heart makes it difficult to analyze the way in which they evolved. This becomes obvious when visualized on the different phylogenetic hypotheses (Figs. 5–12).

Functionally, another aspect is interesting. A number of taxa possess a tubular heart which stretches over a number of segments, but still only very few ostia (the only sites where hemolymph can enter the heart) are present. One such example are the Lophogastrida, where the heart extends through the whole thorax but only three pairs of ostia exist in the anterior part (WIRKNER & RICHTER 2007a).

The evolutionary analysis shows that in all hypotheses, the common pattern in Amphipoda and Tanaidacea evolved once (Figs. 5–8). With regard to the number of pairs of ostia, both a decrease and an increase occurred several times (Figs. 9–12). In the WATLING et al. (2000) scenario, two pairs of ostia would have already occurred in the ground pattern of Eumalacostraca, while this number would have been the ground pattern of Peracarida in the WIRKNER & RICHTER (in press) hypothesis (Fig. 9).

4.3. Patterns of cardiac arteries

Figs. 13–16

The arteries emanating from the heart are the principally unpaired anterior and posterior aorta and descending artery, and the usually paired cardiac arteries (partly also unpaired only in Mysida; WIRKNER & RICHTER 2007a).

At its origin, each artery is equipped with a valve made up of two flaps to prevent hemolymph backflow into the heart. The lateral cardiac arteries irrigate either the organs in the trunk or the appendages. Due to the fact that their segmental affiliation is often complicated, e.g. by their position on the border of two adjacent segments, patterns of arteries were coded.

It seems obvious that a segmental arrangement of cardiac arteries is the plesiomorphic state in Malacostraca as it is present in the basal off-branching taxa Stomatopoda and Leptostraca (Figs. 13, 15, 16). With the exception of the WATLING et al. (2000) hypothesis (Fig. 15), this pattern would have been regained within

Lophogastrida. Two patterns have to be discussed together: on the one hand that found in Amphipoda and Tanaidacea (WIRKNER & RICHTER 2008), where three pairs of arteries occur in adjacent thoracic segments, and on the other the pattern of one pair of arteries supplying the anterior thoracopods followed by three pairs supplying one pair of thoracopods each and the last pair of cardiac arteries running into the pleon, as found in Cumacea and Isopoda (WIRKNER & RICHTER 2008). The latter would have evolved once in the stem lineage leading to the Cumacea and Isopoda (Figs. 13, 16) while in the two other hypotheses either the amphipod / tanaidacean or the cumacean / isopod pattern would have evolved twice (Figs. 14, 15).

4.4. Descending artery

Figs. 17–20

In Decapoda, Anaspidacea, Euphausiacea, Mysida and Lophogastrida, the dorsal vessel and the ventral vessel are connected by a descending artery. Intraspecific variation occurs in that the descending artery can pass the gut on either the right or the left side or can even be paired (see VOGT et al. 2009). Two states are observed: either the descending artery runs down through the ventral nerve cord and connects to the ventral vessel, or it splits above the ventral nerve cord.

In the hypothesis proposed by MELAND & WILLASSEN (2007), the descending artery would have either evolved independently in the lineage leading to Eumalacostraca and in Lophogastrida (with an intermediate loss), or would have evolved once in Eumalacostraca and been lost four times (Fig. 20). With regard to the other hypotheses, a descending artery would have evolved and lost once, respectively (Figs. 17–19). Moreover, in the WATLING et al. (2000) hypothesis it could be seen as an apomorphy of the lineage including Anaspidacea, Lophogastrida, Mysida and Eucarida (Fig. 19).

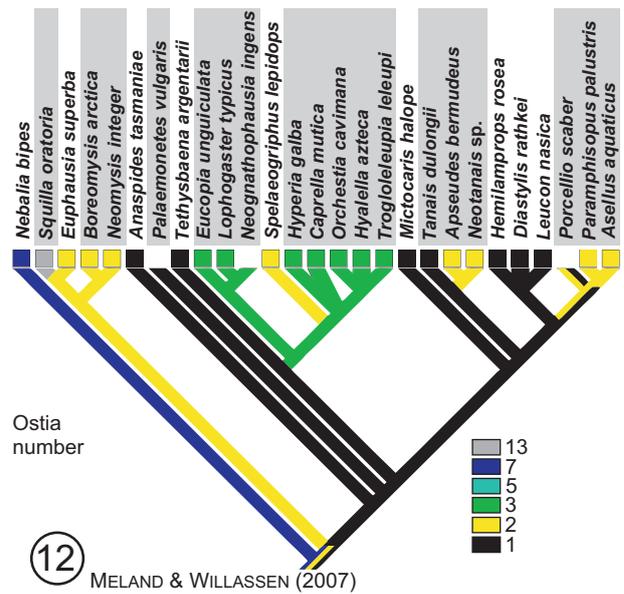
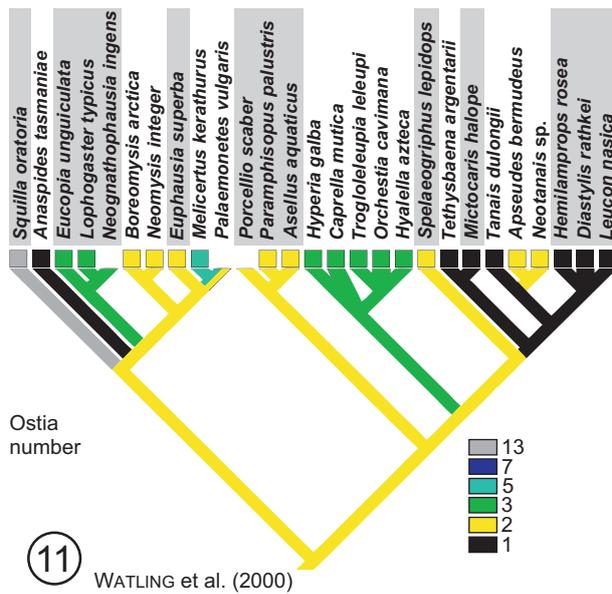
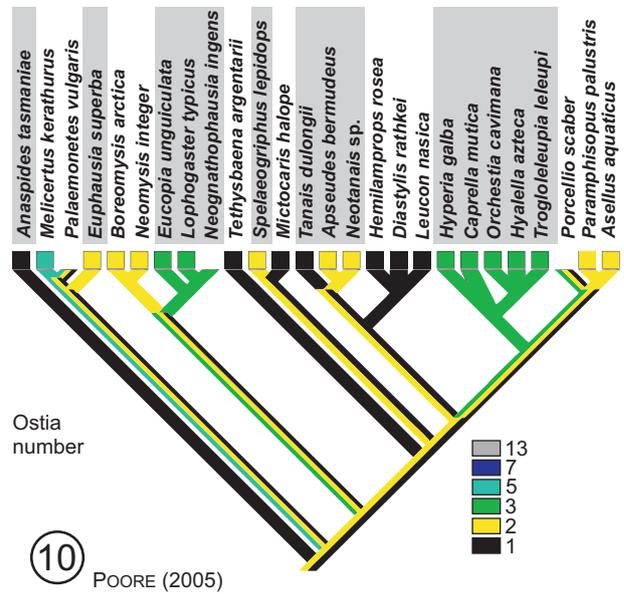
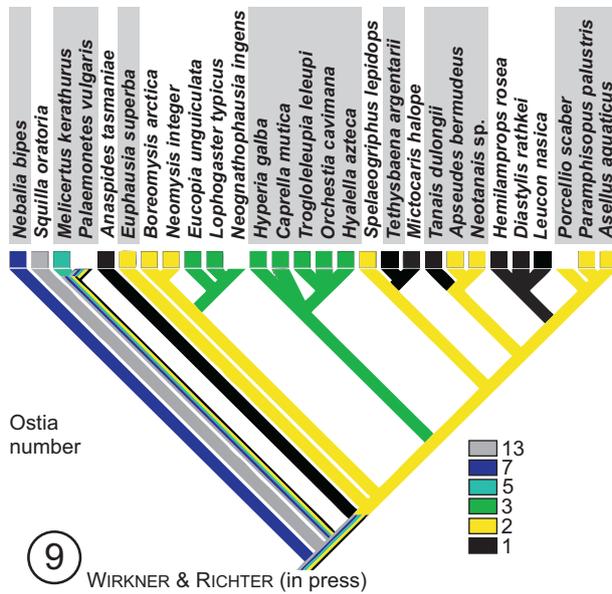
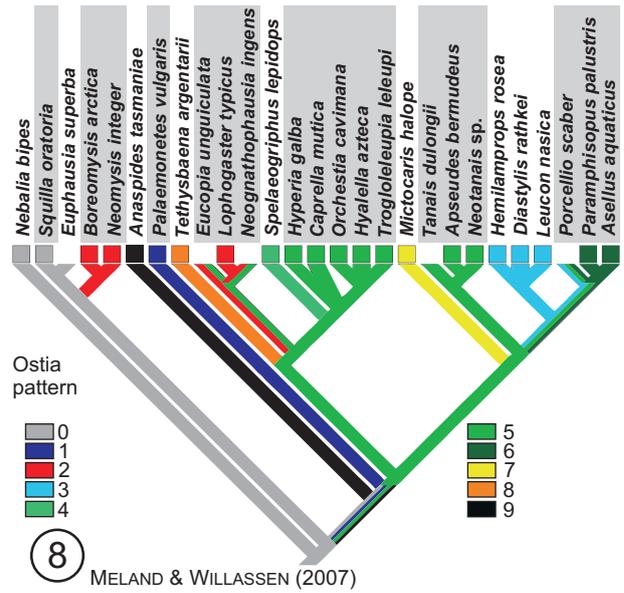
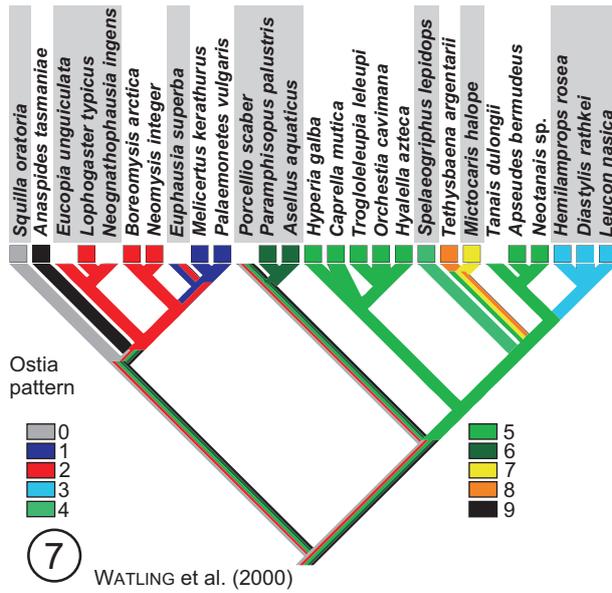
4.5. Posterior aorta

Figs. 21–24

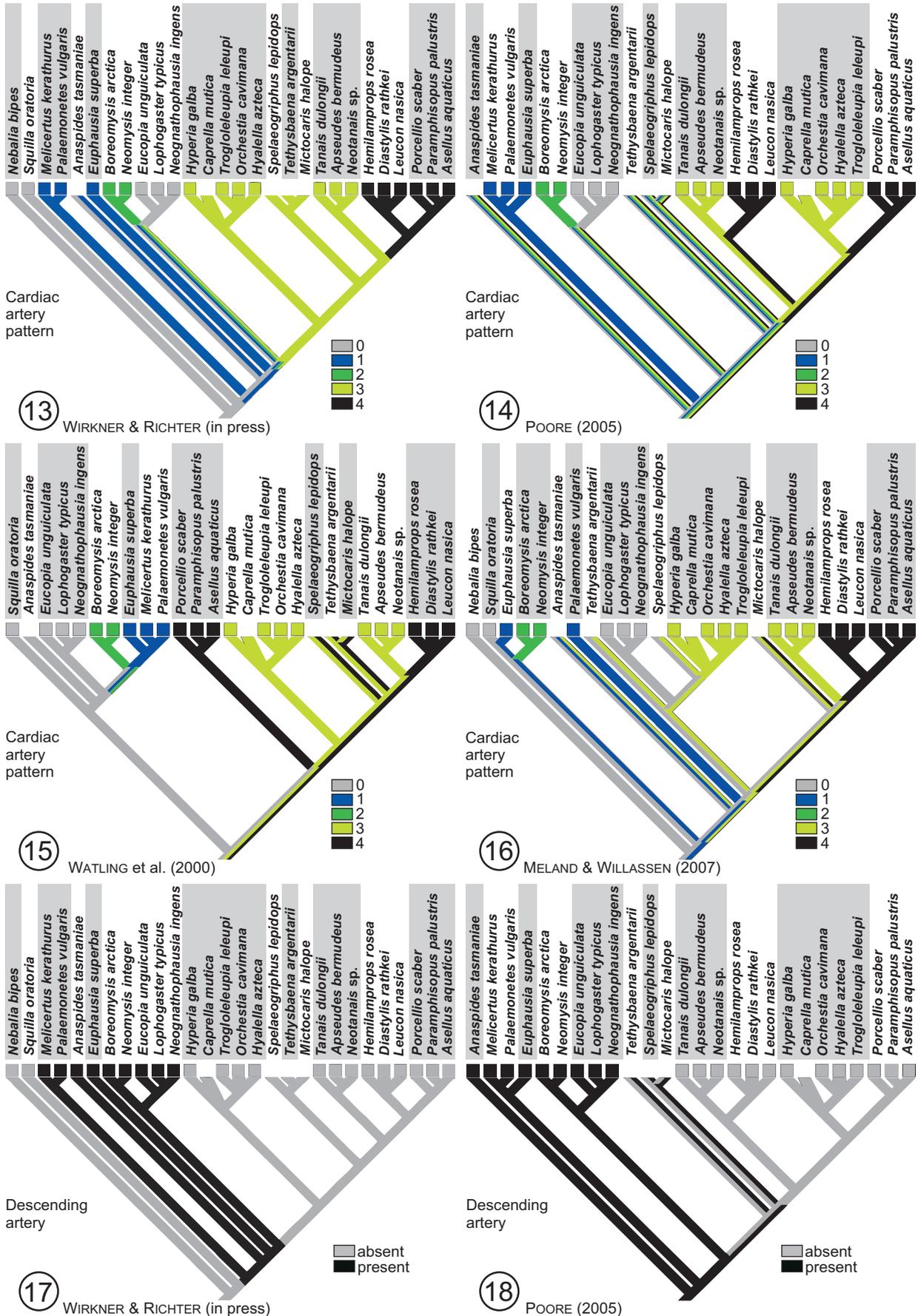
A posterior aorta is described as an artery extending the heart in a posterior direction. It is present in Leptostraca, Stomatopoda, Decapoda, Anaspidacea, Mysida, Lophogastrida and Amphipoda. In Euphausiacea, Cumacea and Isopoda a pair of arteries runs in a posterior direction to supply the musculature in the pleon. This pair has also been termed posterior aorta (e.g. OELZE 1931; SIEWING 1952). To be able to establish coherent homology hypotheses, the definition of a posterior aorta was restricted to an unpaired artery emanating



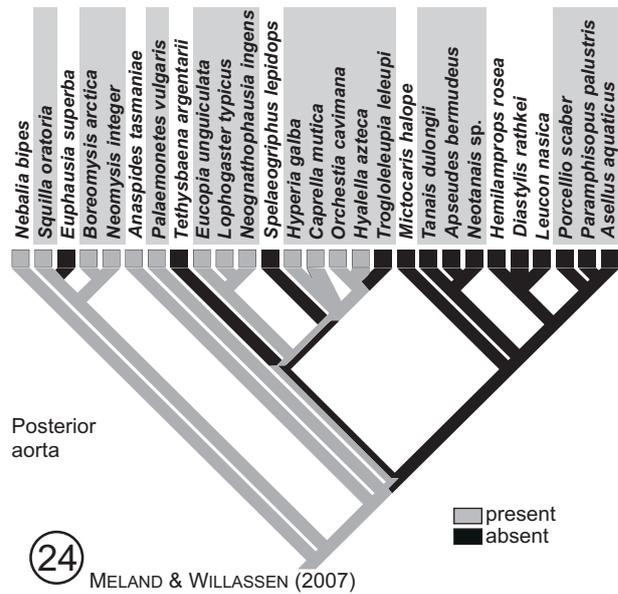
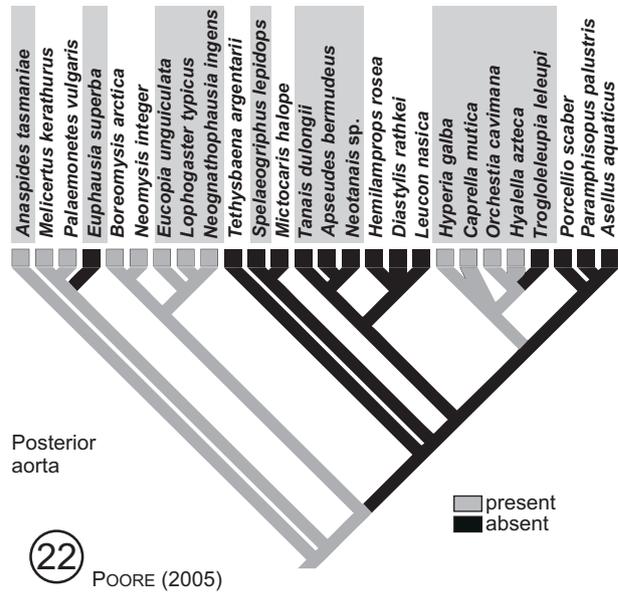
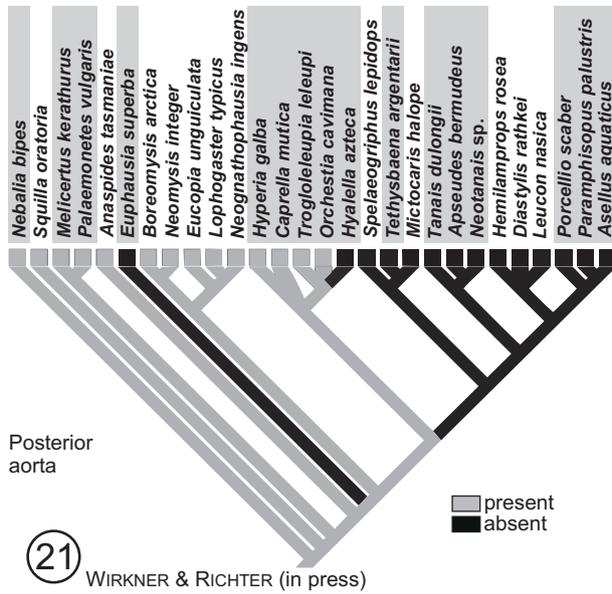
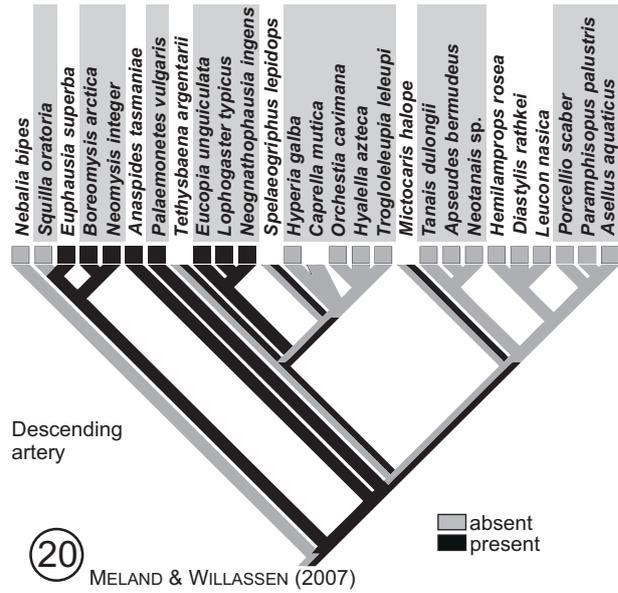
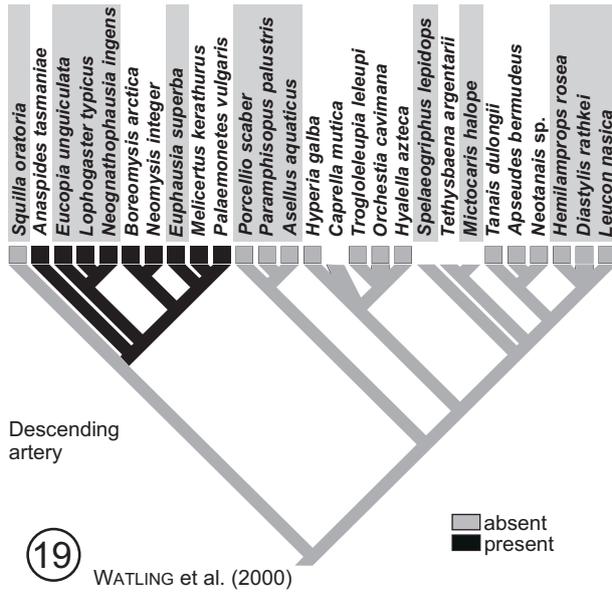
Figs. 1–12. Tracing character history on the basis of four alternative phylogenetic hypotheses (see chapter 2). 1–4: Character “Anterior border of heart”. Th1, Th2, Th3, Th6 – anterior border lying in first, second, third, or sixth thoracic segment. 5–8: Character “Ostia pattern”. 0 – segmental; 1 – two pairs dorsally, two pairs laterally and one pair latero-ventrally; 2 – two pairs in close vicinity,



separated by membrane (see WIRKNER & RICHTER 2007a: fig. 5E); 3 – one distinct, large pair; 4 – one pair at transition Th5 to Th6, one pair at transition Th6 to Th7; 5 – one pair in Th4, one pair in Th5; 6 – two pairs, arranged asymmetrically; 7 – one pair in Th2; 8 – one pair in Th1; 9 – one pair in Th3. 9–12: Character “Ostia number”. State numbers refer to numbers of pairs of ostia.



Figs. 13–24. Tracing character history on the basis of four alternative phylogenetic hypotheses (see chapter 2). 13–16: Character “Cardiac artery pattern”. 0 – segmental; 1 – two pairs off anterior part of heart, descending artery; 2 – one pair, three unpaired, descending artery; 3 – three pairs in adjacent thoracic segments; 4 – one pair supplying anterior thoracopods, three pairs supply-



ing one pair of thoracopods each, one pair supplying pleon; 5 – no lateral cardiac arteries. 16–20: Character “Descending artery”. 21–24: Character “Posterior aorta”.

Tab. 2. Homoplasy indices (= HI) of 22 circulatory system characters for alternative hypotheses on malacostracan relationships.

Phylogenetic hypothesis	HI
WIRKNER & RICHTER (in press)	0.41
POORE (2005)	0.43
WATLING et al. (2000)	0.43
MELAND & WILLASSEN (2007)	0.49

from the posterior end of the heart and running into the pleon (see WIRKNER & RICHTER in press). In this character conceptualization the paired arteries described in Euphausiacea, Cumacea and Isopoda are not posterior aortae but resemble the posteriormost pair of cardiac arteries. However, this lack of irrigation in the pleon via a posterior aorta was compensated independently in the lineage leading to Cumacea and Isopoda and in the Euphausiacea.

A posterior aorta was most probably already present in the stem lineage leading to the Eumalacostraca (Figs. 21–24). Within Malacostraca a posterior aorta was reduced at least three times independently (Figs. 21–24). In POORE's (2005) hypothesis, the posterior aorta in Amphipoda would have evolved convergently (Fig. 22).

5. Evaluation of the alternative phylogenetic hypotheses

After having evaluated the different transformation series on the basis of the alternative phylogenetic hypotheses it is also of interest to evaluate the general compatibility of these hypotheses with circulatory system characters. In other words, which of the alternative hypotheses can explain character evolution with the lowest degree of homoplasy? As a value for homoplasy the homoplasy index (HI) is chosen, which corresponds to $1 - CI$ ($CI =$ consistency index). To evaluate the different hypotheses the total HIs of all 22 circulatory system characters (see WIRKNER & RICHTER in press) were calculated (shown in Tab. 2). It is apparent and logical that the WIRKNER & RICHTER (in press) hypothesis fits the characters best as they were actually included in the analysis. Nonetheless, the two other exclusively morphologically-based hypotheses perform almost as well, while the only molecular-based phylogeny yields poorer results. This should not be read as an argument for morphology and against molecular phylogenetics, but rather for the fact that morphological

data can at least challenge molecular hypotheses to some extent.

6. Conclusion

Though a number of contradictory hypotheses on malacostracan phylogeny prevail, it is still possible to trace a few evolutionary trends with regard to circulatory system structures.

Firstly, a general backwards shift of the anterior border of the heart within Malacostraca is obvious. This means that a tubular heart extending through the greater part of at least the thorax is the plesiomorphic state in Malacostraca. With the diversification of Malacostraca a localization of the heart took place. This trend was most probably a predisposition for the further change of heart position in Isopoda (see also WIRKNER & RICHTER 2003). One open point in terms of heart structure and extension are the globular hearts in Euphausiacea and Decapoda. Further investigations are required here to show whether the structure of the myocardium, the position and structure of the ostia and the arrangement and destinations of lateral cardiac arteries evolved once or independently. Such studies will also shed light on the relationship between Decapoda and Euphausiacea, which has long been a matter of controversy. Ostia make a tricky subject for evolutionary analysis as they show a high degree of change. However, both the decrease and the increase in the number of pairs of ostia occurred various times in all the phylogenetic hypothesis chosen. An analysis on a lower taxonomic level might be of interest here. As with the ostia, cardiac artery patterns changed extensively in Malacostraca but it can be summarized that a change from segmental arrangements to more specialized patterns occurred. Functional analyses would be of great interest here in an attempt to explain these changes. A descending artery most probably evolved once within Malacostraca. In the case of the monophyly of Peracarida, the presence of this artery within Lophogastrida and Mysida (Figs. 17, 18) would be a plesiomorphy. A posterior aorta was present in the stem lineage to the Eumalacostraca and was reduced at least three times within Eumalacostraca.

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8. References

- BALSS, H., W. VON BUDDENBROCK, H.-E. GRUNER & E. KORSCHULT 1961. Blutgefäßsystem. Pp. 470–517 in: A. SCHELLENBERG & H.-E. GRUNER (eds.), Klassen und Ordnungen des Tierreichs, Fünfter Band, I. Abteilung, 7. Buch Decapoda. – Geest & Portig K.G., Leipzig.
- BELMAN, B.W. & J.J. CHILDRESS 1976. Circulatory adaptations to the oxygen minimum layer in the bathypelagic mysid *Gnathophausia ingens*. – Biological Bulletin **1050**: 15–37.
- BOLLBACK, J.P. 2006. SIMMAP: Stochastic character mapping of discrete traits on phylogenies. – BMC Bioinformatics **7**: 88.
- BRODY, M.S. & E.B. PERKINS 1930. The arterial system of *Palaemonetes*. – Journal of Morphology and Physiology **50**: 127–142.
- FARRIS, J.S. 1983. The logical basis of phylogenetic analysis. Pp. 1–36 in: N.I. PLATNICK & V.A. FUNK (eds.), Proceedings of the Second Meeting of the Willi Hennig Society. Advances in Cladistics, Vol. 2. – Columbia University Press, New York.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. – American Naturalist **125**: 1–15.
- HARVEY, P.H. & M.D. PAGEL 1991. The Comparative Method in Evolutionary Biology. – Oxford University Press. 239 pp.
- HENNIG, W. 1966. Phylogenetic Systematics. – University of Illinois Press, Chicago, IL. 263 pp.
- JARMAN, S.N., S. NICOL, N.G. ELLIOTT & A. McMINN 2000. 28S rDNA evolution in the Eumalacostraca and the phylogenetic position of krill. – Molecular Phylogenetics and Evolution **17**: 26–36.
- JENNER, R.A., C. NI DHUBGHAILL, M.P. FERLA & M.A. WILLS 2009. Eumalacostracan phylogeny and total evidence: limitations of the usual suspects. – BMC Evolutionary Biology **9**: 21.
- KLUGE, A.G. 1999. The science of phylogenetic systematics: explanation, prediction, and test. – Cladistics **15**: 429–436.
- KOMAI, T. & Y.M. TUNG 1931. On some points of the internal structure of *Squilla oratoria*. – Memoirs of the College of Science / Kyoto University, Series B **6**: 1–16.
- MADDISON, W.P. & D.R. MADDISON 2008. Mesquite: a modular system for evolutionary analysis. Version 2.5 <http://mesquiteproject.org>
- MAYRAT, A. 1958. Le système artériel des Pénéides – comparaison avec les autres Décapodes et les Mysidacés (Recherches sur l'appareil circulatoire des Crustacés, II). – Archives de Zoologie Expérimentale et Générale **95**: 69–78.
- MELAND, K. & E. WILLASSEN 2007. The disunity of “Mysidacea” (Crustacea). – Molecular Phylogenetics and Evolution **44**: 1083–1104.
- MINDELL, D.P. & A. MEYER 2001. Homology evolving. – Trends in Ecology and Evolution **16**: 434–440.
- NYLUND, A., S. ØKLAND & A. TJØNNELAND 1987. The crustacean heart ultrastructure and its bearing upon the position of the isopods in the eumalacostracan phylogeny. – Zoologica Scripta **16**: 235–241.
- OELZE, A. 1931. Beiträge zur Anatomie von *Diastylis rathkei* Kr. – Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere **54**: 235–294.
- POORE, G.C.B. 2005. Peracarida: monophyly, relationships and evolutionary success. – Nauplius **13**: 1–27.
- RICHTER, S. & G. SCHOLTZ 2001. Phylogenetic analysis of the Malacostraca (Crustacea). – Journal of Zoological Systematics and Evolutionary Research **39**: 113–136.
- SCHRAM, F.R. 1986. Crustacea. – Oxford University Press, New York, Oxford. 606 pp.
- SIEWING, R. 1952. Morphologische Untersuchungen an Cumaceen (*Cumopsis goodsiri* v. Beneden). – Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere **72**: 522–559.
- SIEWING, R. 1954. Über die Verwandtschaftsbeziehungen der Anaspidaceen. – Verhandlungen der Deutschen Zoologischen Gesellschaft **16**: 240–252.
- SIEWING, R. 1956. Untersuchungen zur Morphologie der Malacostraca (Crustacea). – Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere **75**: 39–176.
- SIEWING, R. 1963. Zur Morphologie der aberranten Amphipodengruppe Ingolfiellidae und zur Bedeutung extremer Kleinformen für die Phylogenie. – Zoologischer Anzeiger **171**: 75–91.
- SILEN, L. 1954. On the circulatory system of the Isopoda Oniscoidea. – Acta Zoologica (Stockholm) **35**: 11–70.
- SPEARS, T., R.W. DEBRY, L.G. ABELE & K. CHODYLA 2005. Peracarid monophyly and interordinal phylogeny inferred from nuclear small-subunit ribosomal DNA sequences (Crustacea: Malacostraca: Peracarida). – Proceedings of the Biological Society of Washington **118**: 117–157.
- SZUCSICH, N.U. & C.S. WIRKNER 2007. Homology: a synthetic concept of evolutionary robustness of patterns. – Zoologica Scripta **36**: 281–289.
- TJØNNELAND, A., S. ØKLAND & A. NYLUND 1987. Evolutionary aspects of the arthropod heart. – Zoologica Scripta **16**: 157–175.
- VOGT, G., C.S. WIRKNER & S. RICHTER 2009. Symmetry variation in the heart-descending artery system of the parthenogenetic Marbled Crayfish. – Journal of Morphology **207**: 221–226.
- WÄGELE, J.W. 1992. Isopoda. Pp. 529–617 in: F.W. HARRISON & A.G. HUMES (eds.), Microscopic Anatomy of Invertebrates, Crustacea, 9. – Wiley-Liss, New York.
- WAGNER, H.P. 1994. A monographic review of the Thermosbaenacea (Crustacea: Peracarida) – A study on their morphology, taxonomy, phylogeny and biogeography. – Zoologische Verhandlungen **291**: 3–338.
- WATLING, L., C.H.J. HOF & F.R. SCHRAM 2000. The place of the Hoplocarida in the malacostracan pantheon. – Journal of Crustacean Biology **20**: 1–11.
- WIRKNER, C.S. & S. RICHTER 2003. The circulatory system in Phreatoicoidea: implication for the isopod ground pattern and peracarid phylogeny. – Arthropod Structure & Development **32**: 337–347.

- WIRKNER, C.S. & S. RICHTER 2007a. The circulatory system in Mysidacea – implications for the phylogenetic position of Lophogastrida and Mysida (Malacostraca, Crustacea). – *Journal of Morphology* **268**: 311–328.
- WIRKNER, C.S. & S. RICHTER 2007b. Comparative analysis of the circulatory system in Amphipoda (Malacostraca, Crustacea). – *Acta Zoologica* **88**: 159–171.
- WIRKNER, C.S. & S. RICHTER 2007c. The circulatory system and its spatial relations to other major organ systems in Spelaeogriphacea and Mictacea (Malacostraca, Crustacea) – a three-dimensional analysis. – *Zoological Journal of the Linnean Society* **149**: 629–642.
- WIRKNER, C.S. & S. RICHTER 2008. Morphology of the hemolymph vascular system in Tanaidacea and Cumacea – implications for the relationships of “core group” Peracarida (Malacostraca; Crustacea). – *Arthropod Structure & Development* **37**: 141–154.
- WIRKNER, C.S. & S. RICHTER 2009. The hemolymph vascular system in *Tethysbaena argentarii* (Thermosbaenacea, Monodellidae) as revealed by 3D reconstruction of semi-thin sections. – *Journal of Crustacean Biology* **29**: 13–17.
- WIRKNER, C.S. & S. RICHTER in press. Evolutionary morphology of the circulatory system in Peracarida (Malacostraca; Crustacea). – *Cladistics*.
- ZIMMER, C. 1913. Untersuchungen über den inneren Bau von *Euphausia superba* Dana. – *Zoologica* **67**: 65–127.