

# The anatomy of the king crab *Hapalogaster mertensii* Brandt, 1850 (Anomura: Paguroidea: Hapalogastridae) – new insights into the evolutionary transformation of hermit crabs into king crabs

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Key words: Anomala, carcinization, circulatory system, evolutionary morphology, structural coherence, variability

## Abstract

The emergence of king crabs from a hermit crab-like ancestor is one of the most curious events in decapod evolution. King crabs comprise two taxa, Lithodidae and Hapalogastridae, and while lithodids have formed the focus of various anatomical studies, the internal anatomy of hapalogastrids has never been studied although this group might represent a more ancestral morphological condition within king crabs than lithodids do. To better understand the evolutionary transformation of pagurid-like hermit crabs into king crabs, we studied the hemolymph vascular system and associated organs of representatives of *Hapalogaster* and present here the first micro-computer tomography data pertaining to the internal anatomy of hapalogastrids. Our results for Hapalogastridae are compared with existing and new data on Paguridae and Lithodidae and are discussed in the light of the process of carcinization or evolutionary transformation into a crab-like habitus. *Hapalogaster* resembles both pagurids on the one hand and lithodids on the other, not only with regard to external morphological characters but also in terms of certain internal anatomical features. In this and other respects, *Hapalogaster* represents an evolutionary intermediate form that connects pagurids and lithodids.

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## Introduction

The theory of the transformation of ‘hermit crabs’ into ‘king crabs’ constitutes the most dramatic instance of the evolution into a crab-like habitus, called carcinization. Superficially at least, hermit crabs and king crabs do not seem to have much in common. A closer relationship between ‘hermits’ and ‘kings’, however, has been suggested already in the 19<sup>th</sup> century (Brandt, 1850; Boas, 1880a, b; Bouvier, 1895). It was Boas (1880a, b) who suggested a closer relationship of pagurid hermit crabs (at that time he used the genus name *Eupagurus*) and *Lithodes* and who emphasized the descent of *Lithodes* from an (*Eu*-)*Pagurus*-like ancestor. Bouvier (1895) also favored this close relationship and emphasized the importance of *Hapalogaster* as a ‘forme intermédiaire’ between pagurids and lithodids. More recent morphological studies supporting a closer relationship between pagurids and ‘king crabs’ (Richter and Scholtz, 1994, Reimann *et al.*, 2011; Keiler and Richter, 2011) considered both sub-groups of ‘king crabs’ which are now categorized as Hapalogastridae and Lithodidae. Although the common name ‘king crabs’ is often restricted to certain species of Lithodidae (*e.g.* Stevens, 2014) we use the common name ‘king crabs’ for all representatives of both taxa. We reject to use Lithodoidea for a superfamily taxon including Hapalogastridae and Lithodidae because this classification camouflages the real phylogenetic relationships (Ahyong *et al.*, 2009;

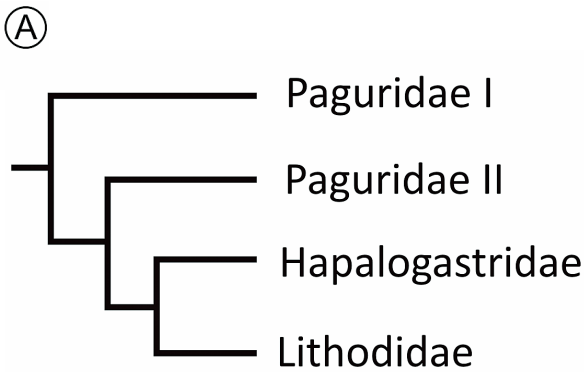


Fig. 1. A. *Hapalogaster mertensii*, living adult specimen on human hand (photograph provided by Ch. Noever). B. Suggested phylogeny supported by molecular (Ahyong *et al.*, 2009; Schnabel *et al.*, 2011; Bracken-Grissom *et al.*, 2013) and morphological data (Reimann *et al.*, 2011) with paraphyletic Paguridae implying that king crabs (Hapalogastridae + Lithodidae) are derived from a hermit crab-like ancestor.

Keiler *et al.*, 2013; Anker and Paulay, 2013). Molecular analyses of king crabs and hermit crabs started with Cunningham *et al.* (1992), but like most of the following molecular analyses they did not include representatives of the Hapalogastridae. These analyses, however, have shown that Lithodidae and Paguridae are closely related (Morrison *et al.*, 2002) or that the former is even nested in the paraphyletic latter (Cunningham *et al.*, 1992; Tsang *et al.*, 2008, 2011; Chu *et al.* 2009). It took more than a decade since the first molecular analysis when hapalogastrids were included in comprehensive molecular analyses on anomurans (Ahyong *et al.*, 2009; Schnabel *et al.*, 2011; Bracken-Grissom *et al.*, 2013), confirming paraphyletic Paguridae and a monophylum Hapalogastridae + Lithodidae nesting in the former (see Fig. 1A). Though some authors dispute this phylogenetic hypothesis (McLaughlin *et al.*, 2004, 2007), the majority of data supports the assumption that king crabs are derived from hermit crabs. The transformations, *i.e.* the evolutionary process of carcinization (Borradaile, 1916; Scholtz, 2014), in the lineage from the pagurid-like ancestor toward king crabs led to the characteristics of a crab-like habitus: a broadened, strongly calcified carapace and a pleon bent under the cephalothorax. Despite the significant differences in their habitus and overall appearance, hermit crabs and king crabs share several morphological characters (Schnabel *et al.*, 2011; Reimann *et al.*, 2011; Keiler and Richter, 2011; Keiler *et al.*, 2013; Jaszkwowski *et al.*, in press), most noticeably the asymmetrical pleon and single-sided left pleopods

in females, a condition which has been interpreted as a morphological heritage from the pagurid-like ancestor (Boas, 1880a, b; Bouvier, 1895; Richter and Scholtz, 1994). In a recent comparative study we showed that the morphology of the hemolymph vascular system differs widely between Paguridae and Lithodidae due to morphological changes in the endophragmal skeleton (cuticular invaginations) in the lineage towards lithodids which affected the internal anatomy (Keiler *et al.*, 2013). While Lithodidae, being more easily available, have formed the focus of that and various other anatomical studies, the internal anatomy of the smaller Hapalogastridae (Fig. 1B) has not been studied at all, though it probably represents in many aspects the plesiomorphic morphological condition within king crabs (Richter and Scholtz, 1994). Most prominent is the soft and rarely calcified sac-like pleon in Hapalogastridae which, apart from the lack of uropods, somewhat resembles that of the soft-tailed hermit crabs, first recognized by Brandt (1850). To better understand the evolutionary transformation of hermit crabs into king crabs, we studied the hemolymph vascular system and associated organs of representatives of Hapalogastridae and present here the first data ever published in relation to the internal anatomy of hapalogastrids. Our results for hapalogastrids are compared with existing and new data on pagurids and lithodids and are discussed in the light of the evolutionary transformation of hermit crabs into king crabs.



## Material and methods

### Studied species

The following species were studied:

Paguroidea Samouelle, 1819

Paguridae Latreille, 1802

*Pagurus hirsutiusculus* (Dana, 1851)  
(San Juan Island, WA, USA, coll. 2010)

*Pagurus pubescens* Krøyer, 1838  
(Svaldbard, Norway, coll. 2012)

*Pagurus bernhardus* (Linnaeus, 1758)  
(Gulmarsfjord, Sweden, coll. 2010)

Hapalogastridae Brandt, 1850

*Hapalogaster mertensii* Brandt, 1850  
(Sitka, Alaska, USA, coll. 2012)

*Hapalogaster grebnitzkii* Schalfew, 1892  
(San Juan Island, WA, USA, coll. 1953)

Lithodidae Samouelle, 1819

*Lithodes santolla* (Molina, 1782)  
(Chile, coll. 2008)

*Lithodes aequispinus* Benedict, 1895  
(Sitka, Alaska, USA, coll. 2012)

A full list of the specimens studied (which are catalogued and stored in the Zoological Collection of the University of Rostock), and a description of each of the methods used are provided in Supporting Information Table S1.

### Resin injection

The acrylic casting resin Mercor 2-CL (Ladd Research, Williston, VT) or the polyurethane-based casting resin PU4ii (vasQtec, Zurich, Switzerland) was injected into the heart of specimens previously killed using CO<sub>2</sub>- or Eugenol-saturated water.

In a first step, the resin was mixed with the appropriate catalyst and placed in a 5 ml syringe (Luer Lock Solo, Braun, Melsungen, Germany) just before use. The resin in the syringe was injected via an injection cannula (diameter 0.3–0.6 mm, Sterican, Braun, Melsungen, Germany) through the carapace into the heart and the specimens were left for several minutes to allow the resin to polymerize and temper.

### Fixation and dehydration

For MicroCT, specimens (injected and non-injected) were fixed in Bouin's fluid for several days, washed and then critical point (EMITECH K850, UK) or freeze dried (Alpha 1-4, Martin Christ, Osterode a.H., Germany; UniCryo MC2L, UniEquip, Munich, Germany).

### Micro computer tomography (MicroCT)

Dried or macerated specimens were mounted with hot glue on a specimen holder. X-ray imaging was performed with a

- Phoenix Nanotom 180 (Phoenix|x-ray, GE Sensing & Inspection Technologies) high-resolution MicroCT system in high resolution mode using the program datosx acquisition (Target: Molybdenum, Mode: 0-1; Performance: ca. 8-13 W; number of projections: 720-1440; detector timing: 1000-3000 ms; voxelsize ca. 10-30 μm). Using the software datosx reconstruction a volume file was generated, and a stack of virtual sections exported using the software VGStudio Max (Volume Graphics, Heidelberg).
- Xradia MicroXCT-200 X-ray imaging system (Carl Zeiss X-ray Microscopy Inc., Pleasanton, USA) at 20 KV and 4 W (10.0 scintillator-objective lens unit, 5-20 μm pixel size).

### 3D reconstruction

For all 3D reconstructions, the software Imaris 6.4.1 and 7.0.0 (Bitplane) was used (for details of the process see Keiler *et al.*, 2015).

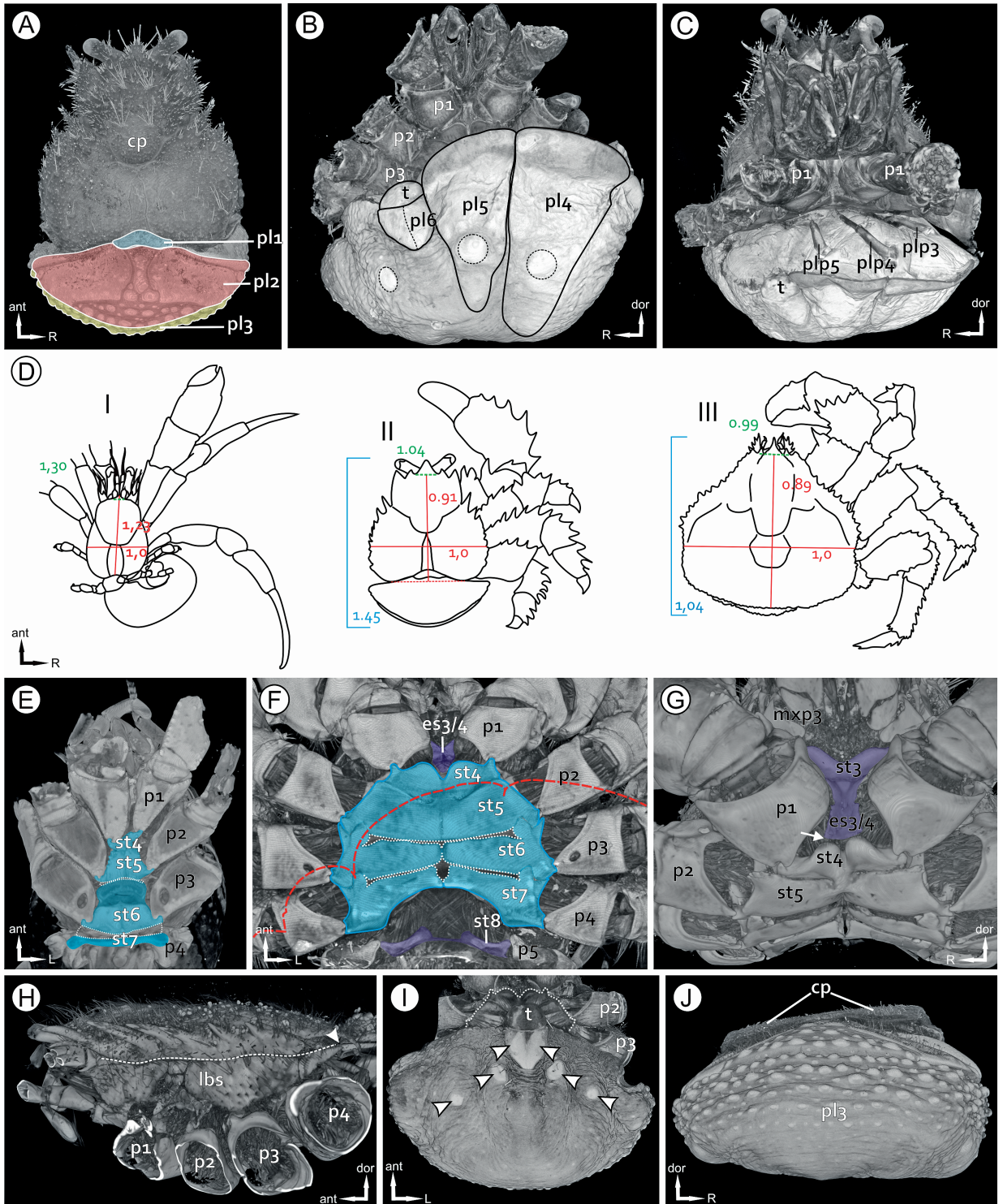
### Image management

All figure plates were arranged using Corel Graphics Suite X3 (Corel, Ottawa). Bitmap images were embedded into Corel Draw X3 files and digitally edited with Corel PhotoPaint X3.

## Results

### External morphology

*Hapalogaster mertensii* (Fig. 1B) and *H. grebnitzkii* have a carapace wider than long (proportions illustrated in Fig. 2DII). The pleon is bent under the cephalothorax (Fig. 2B, C, I), the fourth to six pleonal segments together forming the barely calcified sac-like posterior portion of the pleon (Fig. 2B, I), hidden in dorsal view (Fig. 2A). The overall body shape is fairly oval (Fig. 2A, DII). In females, the pleonal tergites (Fig. 2B) are arranged asymmetrically and pleopods (Fig. 2C) are present on the left side only. In males, the pleonal tergites are arranged fairly symmetrically (Fig. 2I) and pleopods are absent. The fourth to seventh thoracic sternites are fused into a sternal plate, the so-called



plastron (Fig. 2F), which is roughly semioval in ventral view and has a markedly semicircular posterior emargination (Fig. 2F). The plastron is largely covered by the bent pleon (Fig. 2B). The calcification of the plastron is incomplete: the sixth and seventh thoracic sternites are distinctly delimited by a broad median and transverse suture; the third thoracic sternites, which are not part of the plastron, are likewise delimited by a suture (arrow, Fig. 2G), and bent dorsally. The eighth thoracic sternites are distinctly separate from the plastron (Fig. 2F).

### Internal morphology

In the following, the descriptions of soft tissue structures (most inner organs) are restricted to *H. mertensii*, while in *H. grebnitzkii* only integumental structures were studied.

**The digestive system.** The stomach (stc) is situated dorsally in the anterior portion of the cephalothorax, from where the gut extends as a tube into the telson (Fig. 3A-C). A pair of anterior ceca (ce) emanates dorsally from the pylorus (Fig. 3C). A posterior cecum is not present. The hepatopancreas (hp) fills most of the pleon and is formed by two clusters of tubular diverticles which are connected to the pylorus on each side via a main duct (Fig. 3B, C).

**The antennal glands.** The antennal glands (ag) are located anterolaterally in the cephalothorax near the second antennae and are dorsally connected to the antennal bladder (bl; Fig. 3D, E). The sponge-like lobes of the bladder fill most of the cephalothorax and reach into the pleon (Fig. 3A, B, D, E).

**The reproductive system.** The gonads (ovaries and testes) are paired and mainly located in the pleon laterally to the gut (Figs. 3A, 4D, G) and dorsally to the hepatopancreas.

**The endophragmal skeleton.** The endophragmal skeleton consists of paired endosternites (es) and endopleurites – cuticular invaginations located between two

contiguous thoracic segments. Two thin transverse thoracic bridges (tb) connect the paired endosternites 4/5 and 5/6, respectively, and span the ventral portion of the cephalothorax (Fig. 5B). The endosternites 7/8 form the posterior edge of the plastron and are bent anteriorly.

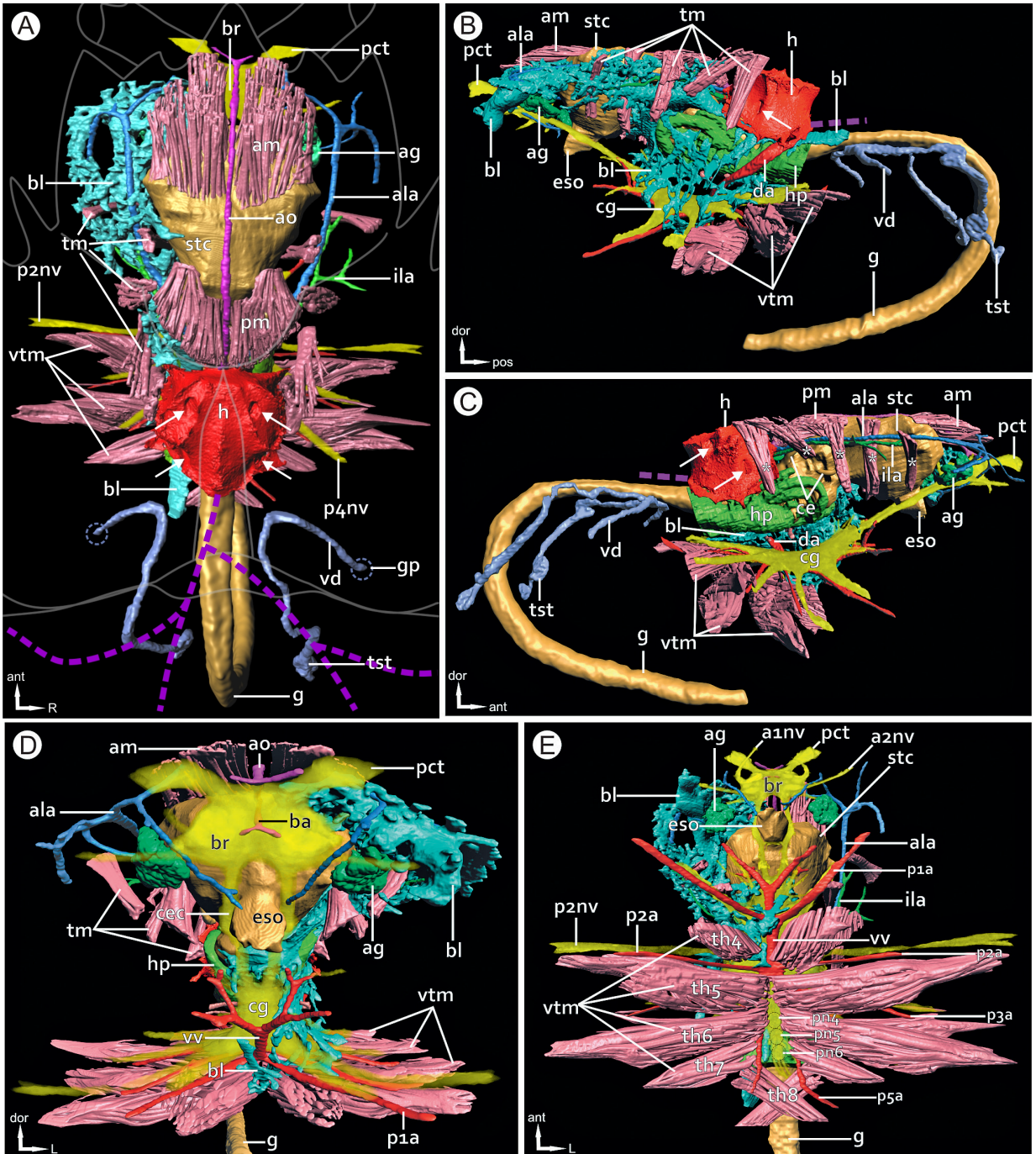
**Ventral thoracic muscles.** The ventral thoracic muscles (vtm) are extrinsic muscles of the pereopods and are located directly above the plastron. The muscles of the fourth to seventh thoracic segments, which correspond to the chelipeds, p1, and the walking legs, p2-p4, are separated from each other medially (Figs. 3E, 6A). The muscles of the eighth thoracic segment which correspond to the grooming limbs, p5, are crossed, forming an X (Figs. 3E, 6A).

**Pleonal muscles.** The pleonal muscles are largely reduced. The dorsal (dpm1) and lateral (lpm1) muscles of the first pleonal segment are pronounced and fairly symmetrical (Fig. 4D) while the muscles of the subsequent segments appear to be thinner and more scattered. The fibers of the ventral pleonal muscles (vpm) form a vague, rudimentary layer (Fig. 4F, G).

**Ventral nerve cord.** The neuromeres of the mandibular, of the first and second maxillar segments and of the thoracic segments are fused with the first pleonal neuromere to form the cephalothoracic ganglion (cg; Figs. 4A, 6A), which is located in the anterior portion of the cephalothorax (thoracic segments th3 – th6, Fig. 7II). Anteriorly, the cephalothoracic ganglion is connected with the brain (br) via the circumesophageal connectives (cc; Fig. 4A, B). The paired neuropils of the anterior neuromeres (mp; which correspond to the segments of the mouthparts) lie close together, while the neuropils of the posterior neuromeres (tn4 – tn8; correspond to the pereopods) are further apart (Fig. 6B, C, E). Posteriorly, the pleonal ganglia (pn2 – pn6) are connected to the cephalothoracic ganglion via connectives and lie close together within the sixth to seventh thoracic segment (Fig. 7II).

◀ **Fig. 2.** External integumental structures (volume renderings). A-C. *Hapalogaster mertensii*: A. Dorsal view; only first and second and part of the third pleonal segment are visible *in vivo*; B. Ventral view of a female specimen; note the asymmetry of the pleon in females; calcified areas are outlined; tergites are shown by dashed outlines; C. Anteroventral view revealing asymmetrical arrangement of pleopods on the left side only. D. Schematic drawings of a pagurid (I), a hapalogastrid (II), a lithodid (III); pleon in *in vivo* condition; values beneath red lines show the relative ratios of carapace length to width (width set to 1.0); green values show the relative lengths when the rostrum is included. E. *Pagurus hirsutiusculus* (Paguridae): ventral view showing separated sternites. F. *H. mertensii*: ventral view with pleon removed (virtually) to show sternal plastron (blue outline); red dashed line indicates pleon margin; uncalcified areas between sternites outlined with dotted lines. G. *Hapalogaster grebnitzkii*: anteroventral view; note vertically oriented third thoracic sternites (st3); arrow points to suture. H. *H. grebnitzkii*: lateral view; dashed line indicates linea anomurica (fracture line during ecdysis). I. *H. mertensii*: male; ventral view showing bent sac-like pleon; note roughly symmetrical shape of pleon (visible portion corresponds to pleonal segments 4-6) and symmetrical arrangement of calcified areas (tergites, arrowheads). J. *H. mertensii*: male; posterior view. Abbreviations: cp, carapace; pl, pleon; p1-p5, pereopods; pl1-pl6, pleonal segments; plas, sterna plastron; plp3-plp5, pleopods; st3-st8, thoracic sternites; t, telson.





**Fig. 3.** Spatial relationships between the hemolymph vascular system and other internal organs (surface and volume renderings). The pdf in A contains interactive 3D content. Please click on the figure to activate the content and then use the mouse to rotate the objects. A-E. *Hapalogaster mertensii*: male; for clarity, only right portion of bladder is shown; arrows in A-C point at ostia; dashed violet line indicates posterior aorta system. A. Dorsal view; B. Left-sided lateral view; C. Right-sided lateral view; D. Frontal view; E. Ventral view. Abbreviations: a2, antennal artery; ag, antennal gland; ala, anterior lateral artery; am, anterior gastric muscle; ao, anterior aorta; bl, bladder; br, brain; ce, cecum; cg, cephalothoracic ganglion; da, descending artery; eso, esophagus; f, fringe artery; g, gut; h, heart; hp, hepatopancreas; ila, inferior lateral arteries; p1a-p5a, pereopodal arteries; pm, posterior gastric muscle; ra, rostral artery; stc, stomach; tm, (vertical) thoracic muscles; tst, testes; vd, vas deferens; vtm, ventral thoracic muscles; vv, ventral vessel.



**Circulatory system.** Hemolymph vascular system: All the organs mentioned above are supplied by the hemolymph vascular system (hvs). The terminology used herein is an extended version of that used in the descriptions of the hvs of galatheid squat lobsters and porcelain crabs published by Keiler *et al.* (2015).

**Heart (Fig. 3):** The heart is located dorsally in the cephalothorax, under the carapace and above the anterior portion of the gut, suspended in place by several ligaments (Fig. 3A). The heart is enclosed in a hemolymph-filled space, the pericardial sinus, which is framed laterally by the endopleurites of the endophragmal skeleton, ventrally by the pericardial septum and dorsally by the epidermis of the carapace (not shown). The heart is almost pentagonal in horizontal profile. The ventral side is slightly concave and the dorsal markedly convex. The heart is equipped with three pairs of ostia, slit-like openings which are arranged transversely to the anteroposterior body axis. Two pairs are located dorsally (anterodorsal and posterodorsal ostia) (arrows, Fig. 3A) and one pair is located ventrolaterally (arrows, Fig. 3C). Several muscle strands cross the lumen of the heart (not shown).

**Artery Systems:** Five artery systems branch off the heart: the unpaired **anterior aorta system**, the paired **anterior lateral artery system**, the paired **inferior lateral artery system**, the unpaired **posterior aorta system** and the **ventral vessel system**. The latter consists of the vertical descending artery and the horizontal ventral vessel and its side branches. The proximal portion of all these artery systems lies within the pericardial sinus. Between the heart and each artery system there is a valve.

**Anterior aorta system (Figs. 3A, D, 4A-C):** The anterior aorta (ao) emanates anteriorly from the heart, passes the posterior gastric muscles (pm) and runs in anterior direction above the stomach (stc) just below the carapace into the cephalic region, passing the anterior gastric muscles on the way (Fig. 3A). Above the brain, the unpaired brain artery (ba) branches off and descends ventrally into the brain (Figs. 3D, 4B, C), where it turns anteroventrally and bifurcates. Both branches then turn in a posterior direction towards the olfactory lobes of the brain (Fig. 4B). A myoarterial formation (maf) is observable as a slight widening of the anterior aorta directly posterior to the brain artery (Fig. 4C). The anterior aorta continues anteriorly and bifurcates horizontally at a 45° angle into the optic arteries (oa) which run into the eye stalks (Figs. 3A, 5A).

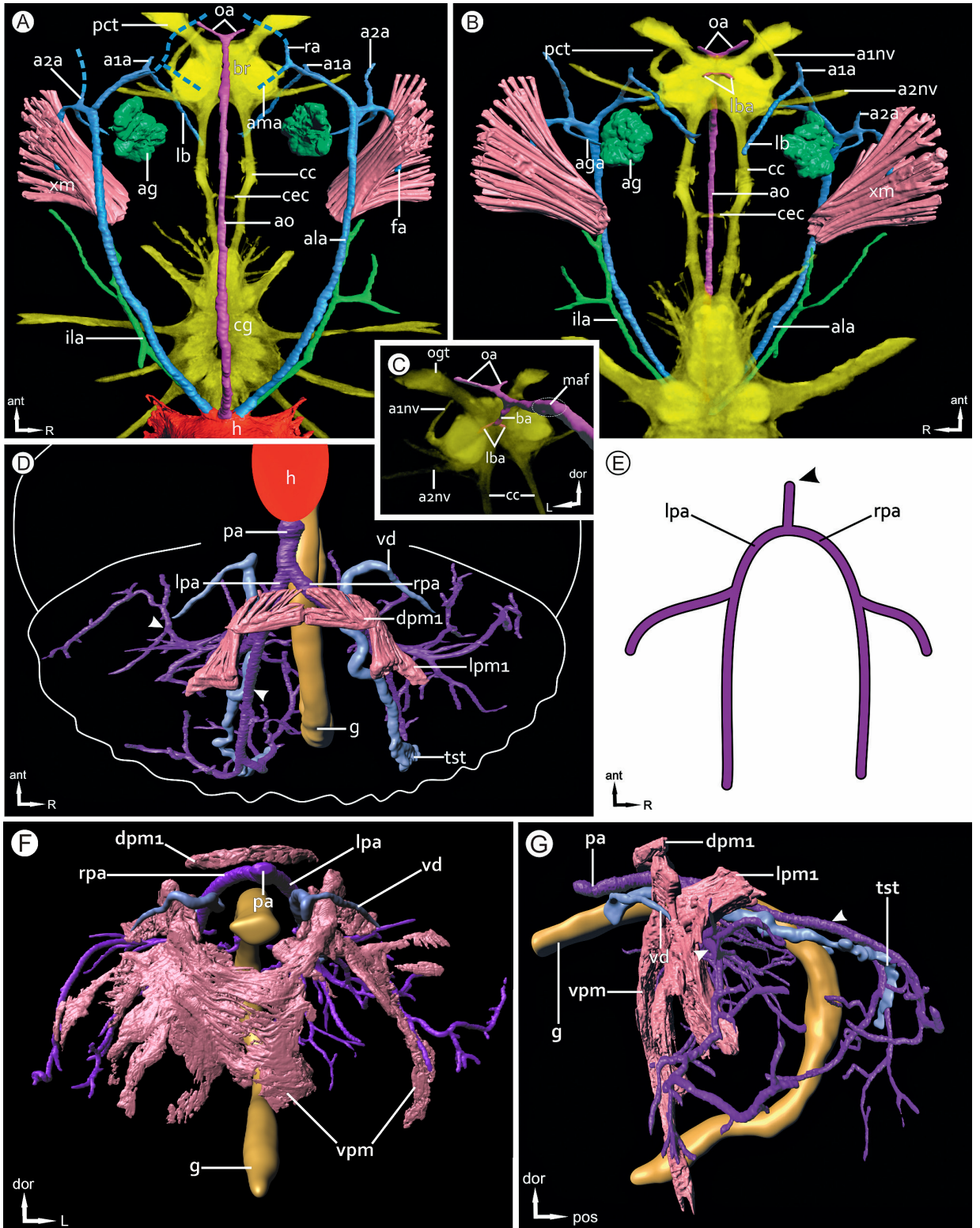
**Anterior lateral artery systems (Figs. 3, 4A, B):** The paired anterior lateral arteries (ala) emanate from

the heart directly laterally to the anterior aorta. They run (above the antennal bladder) in an anterior direction at a lateral angle of approximately 45° and then follow an almost parallel course to the anterior aorta (Figs. 3A, 4A, B). Medially, the anterior lateral arteries give rise to the gastric arteries (not shown) which supply the lateral muscles of the stomach. In the cephalic region, a distinct set of arterial branches (defined by their target organ or region) is present, and can be broken down as follows: Anterolaterally, a branch turns laterally backwards and gives off several smaller arteries which supply the external mandible adductor muscles (xm, Fig. 4A, B). It then continues in a posterior direction (fa, fringe artery) along the branchiostegites. Anteriorly, a side branch runs into the second antennae (a2a, antennal artery). Ventromedially, a branch (aga, antennal gland artery) runs into the antennal gland (Fig. 4A, B). Dorsomedially, a branch emanates and bifurcates into the arteries which supply the rostrum (ra, rostral artery) and the anterior gastric muscles (ama, anterior gastric muscle artery) (Fig. 4B). Distomedially, a branch runs into the first antennae (a1a, antennular artery) (Fig. 4B, C).

**Inferior lateral artery systems (Figs. 3A, C, E, 4A, B):** The paired inferior lateral arteries (ila) branch off directly beneath the anterior lateral arteries and continue their course parallel to and just underneath them (Fig. 6B, C), giving rise to several branches which run between the lobes of the antennal bladder. These arteries correspond to the hepatic arteries described in other decapods, but as they do not supply the hepatopancreas in king crabs and pagurid hermit crabs, this new term is suggested.

**Posterior aorta system (Fig. 4D-G):** The posterior aorta (pa) emanates from the posteroventral portion of the heart and runs above the gut (g) in a posterior direction. In the eighth thoracic segment, it bifurcates into two equally sized but asymmetrical main arteries, the left (lpa) and right pleonal artery (rpa) (Fig. 4D). Between the first and second pleonal segment, the left pleonal artery bifurcates again into two arteries which are equal in size (arrows, Fig. 4D, E). The left one runs ventro-laterally into the left portion of the pleon, the right one takes a basically median course along the dorsal portion of the pleon. On the way, several small lateral vessels emanate from them which mainly supply the hepatopancreas, the gonads and the gut.

**Ventral vessel system (Figs. 3D, E, 6, 7):** The ventral vessel system is made up of the descending artery (da), the ventral vessel (vv) and its side branches, and mainly supplies the ventral nerve cord (vnc), the



legs (pereopods p1-p5) and the mouthparts.

The descending artery, which has the greatest diameter of all arteries branching off the heart, emanates from the left side of the posteroventral part of the heart, directly beside the root of the posterior aorta, and runs ventrally (Figs. 3B, 6A, B). In all specimens studied the descending artery crosses the gut on the left (Fig. 3B). The descending artery takes a curved antero-ventral course, pierces the ventral nerve cord between the sixth and seventh thoracic neuromeres (tn6+tn7) and merges into the ventral vessel below. On the level with the second leg arteries, the descending artery merges with the ventral vessel (p2a) (Fig. 6B). Taking the ventral thoracic muscles (vtm) as a point of reference, the merging point is located roughly between the fourth and fifth thoracic segments (Fig. 7II), under the two transverse thoracic bridges (Fig. 5B). The ventral vessel gives rise to the paired leg arteries (leg arteries, p1a–p5a) and to the arteries supplying the mouthparts (Fig. 6E). Before the leg arteries run into their respective leg, they proceed between the cuticular walls formed by the endosternites and endopleurites. The pattern of the leg arteries is variable and asymmetrical in some specimens (Fig. 6DI-III). However, in all specimens, the fifth leg arteries (p5a) emanate from the preceding fourth leg arteries (p4a; Fig. 6DI-III). Anteriorly, the ventral vessel bifurcates into the arteries of the mouthparts (Fig. 6F).

Arterial supply to the mouthparts (Fig. 6E, F):

In the cephalic region, the ventral vessel ascends at an angle of 30–45° (Fig. 6E) and bifurcates anteriorly on a level with endosternites 3/4, giving off successive side branches to the maxillipeds (mp1a–mp3a), the first and second maxillae (mx1a–mx2a) and the mandibular arteries (mda) (Fig. 6F).

## Discussion

The hemolymph vascular system in Paguridae and Lithodidae has recently been discussed in the context of

carcinization, or evolutionary transformation into a crab-like habitus (Keiler *et al.*, 2013). Our present investigations now reveal that the morphology of the hemolymph vascular system in *Hapalogaster* differs distinctly in several respects from that in Lithodidae, in some respects more closely resembling that in Paguridae. This is not unexpected, since hapalogastrids are hypothesized to be morphologically more ‘primitive’ within king crabs on account of their less pronounced carcinized shape and smaller size (Richter and Scholtz, 1994).

### *Evidences of a close relationship between hermit crabs and king crabs*

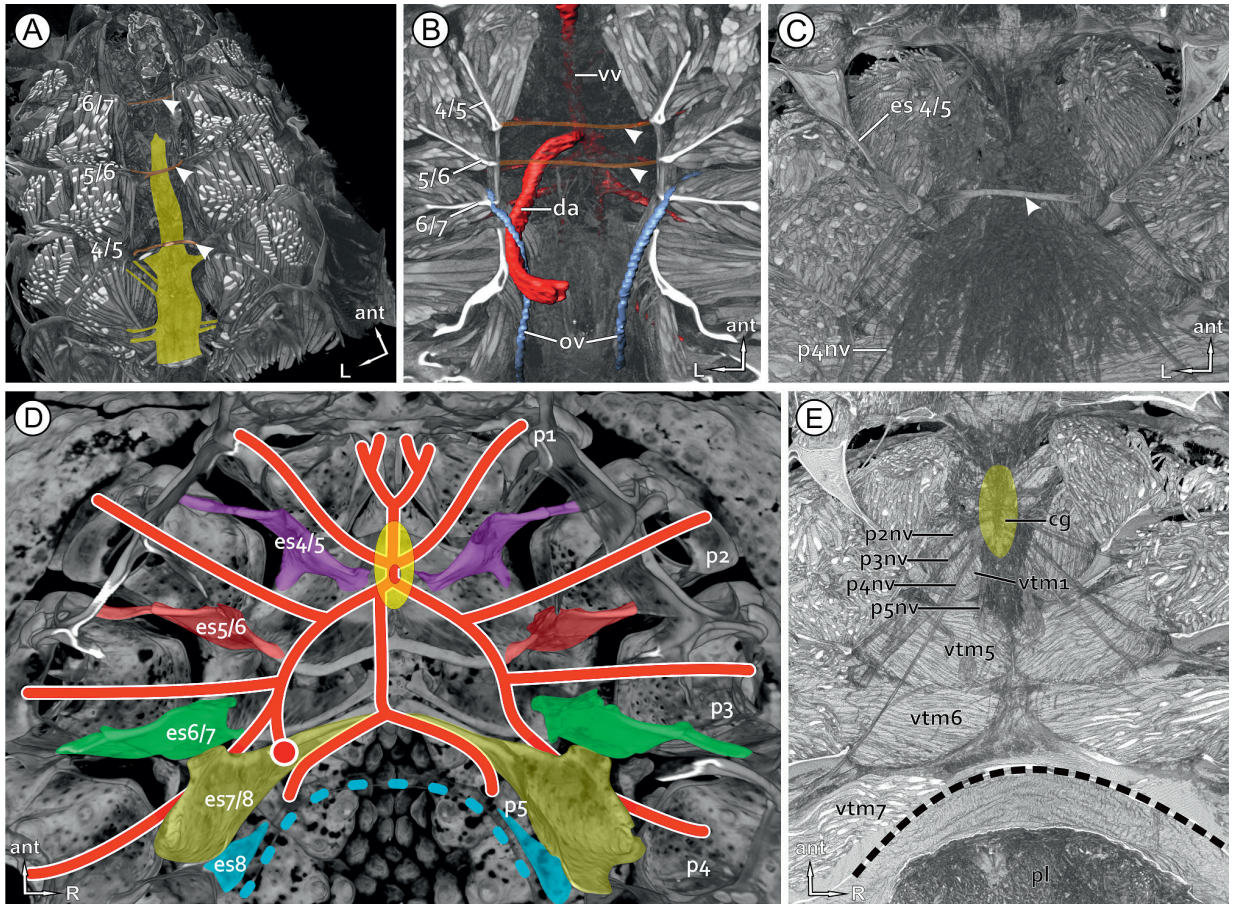
The artery systems in the dorsal cephalothorax (anterior aorta, anterior lateral arteries and inferior lateral arteries) in Hapalogastridae exhibit the same pattern as in Lithodidae, which in turn closely resembles that found in Paguridae. The asymmetrical course of the pleonal arteries corresponds in pagurids and king crabs, likewise supporting the theory of a close relationship between both groups (for detailed descriptions of the hemolymph vascular system in Lithodidae (see McGaw and Duff, 2008 and Keiler *et al.*, 2013; for Paguridae see Jackson, 1913 and Keiler *et al.*, 2013). Remarkably enough, the sponge-like antennal bladder in *Hapalogaster* corresponds to the bladder in *Pagurus* (see Jackson, 1913; pl. 4, fig. 29) in both shape and extension (the condition is unknown in lithodids), leading us to assume that this state is homologous. Moreover, it is not present in any other anomuran so far studied (Keiler *et al.*, 2015; unpubl. data) and therefore represents another potential synapomorphy of king crabs and pagurids.

### *New insights into the evolutionary process of carcinization*

Previously, we were able to reconstruct the transformations of the internal anatomy as consequence of carcinization in one step only, from the last common ancestor

◀ *Fig. 4. Hapalogaster mertensii* (surface and volume renderings): dorsal anterior artery systems (A–C) and posterior aorta system (D–G). The pdf in F contains interactive 3D content. Please click on the figure to activate the content and then use the mouse to rotate the objects. A. Dorsal view of anterior cephalothoracic portion. B. Ventral view of anterior cephalothoracic portion. C. Posterolateral view of the anterior aorta system and the brain. D. Dorsal view of the pleonal region; arrowheads indicate main branches of the left pleonal artery. E. Schematic drawing of the posterior aorta system. Only main branches are shown. Arrowhead points to the proximal portion of the posterior aorta. F. Frontal view of the pleonal region. G. Lateral view of pleonal region; arrowheads indicate main branches of the left pleonal artery. Abbreviations: a1a, antennular arteries; a2a, antennal arteries; a1nv/a2nv, antennal nerves; ag, antennal gland; aga, antennal gland artery; ama, anterior gastric muscle artery; ba, brain artery; cc, circumesophageal connective; cec, circumesophageal commissure; dpm, dorsal pleonal muscles; fa, fringe artery; g, gut; h, heart; ila, inferior lateral arteries; lba, lateral brain artery; lpa, left pleonal artery; lpm, lateral pleonal muscles; maf, myoarterial formation; oa, optic arteries; pct, protocerebral tract; ra, rostral artery; rpa, right pleonal artery; t, telson; tst, testes; vd, vas deferens. vpm, ventral pleonal muscles.



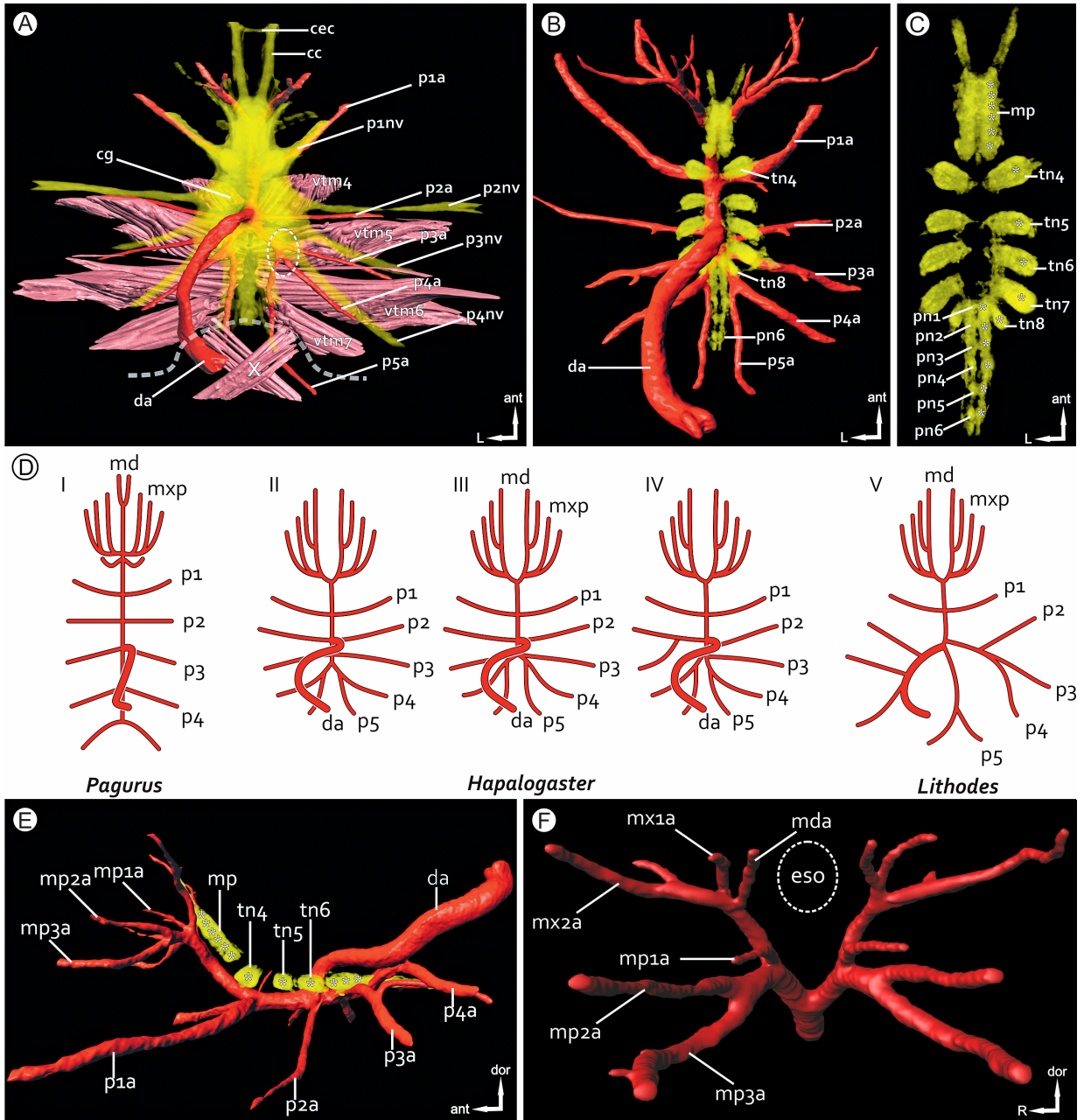


**Fig. 5.** Volume renderings of virtually cut cephalothorax. **A.** *Pagurus bernhardus* (Paguridae): three thoracic bridges (arrows); antero-dorsal view; yellow area indicates ventral nerve cord. **B.** *Hapalogaster mertensii*: two thoracic bridges (arrowheads); reconstructed ventral vessel system and oviducts (surface renderings); dorsal view. **C.** *Lithodes aequispinus* (Lithodidae): one thoracic bridge (arrowhead); dorsal view. **D.** *Lithodes santolla* (Lithodidae): virtually cut specimen; endosternites are colored; ventral vessel system (red) and cephalothoracic ganglion (yellow ellipse) lie between endosternites. **E.** *L. aequispinus*: spatial relationships between cephalothoracic ganglion (yellow overlay) and ventral thoracic muscles (vtm); black dashed lines indicate posterior margin of plastron. Abbreviations: cg, cephalothoracic ganglion; da, descending artery; es, endosternites; od, oviducts; p1-4, pereiopods; p2nv-p5nv, leg nerves; pl, pleon; vtm5-7, ventral thoracic muscles; vv, ventral vessel.

(LCA) of Paguridae and king crabs whose external and internal anatomy was most probably pagurid-like (Keiler et al., 2013) to the last common ancestor of Lithodidae (represented by the lithodid genera *Lithodes* and *Paralomis*). The present study now allows including an intermediate step – the LCA of Hapalogastridae and Lithodidae (Fig. 8). Since hapalogastrids and lithodids have undergone the same period of evolution beginning with their calculated divergence 18 million years ago (see Bracken-Grissom et al., 2013), the exact morphology of this ancestor neither corresponds to one group or to the other. We consider all characters of Hapalogastridae which are

either shared with Paguridae (plesiomorphies) or with Lithodidae (synapomorphies) as belonging to the ground pattern of the LCA of Hapalogastridae and Lithodidae. Characters which are neither shared with pagurids nor lithodids are autapomorphies of hapalogastrids. The process of carcinization proper was completed already in the lineage from the LCA of Paguridae and king crabs towards the LCA of Hapalogastridae and Lithodidae (Fig. 8). Internal changes which are coherent with (*i.e.* structurally dependent on) external changes into a crab-like habitus (see Keiler et al., 2013, 2015 for further details) logically appeared in the same lineage.





**Fig. 6.** Spatial relationships between the organ systems of the ventral body side (surface and volume renderings). The pdf in F contains interactive 3D content. A-C. *Hapalogaster mertensii*: A. dorsal view of ventral thoracic muscles (pink), ventral vessel system (red) and nervous system (yellow); dashed semi-transparent white line indicates posterior margin of plastron; B. Dorsal view of ventral vessel system (red) and neuropil clusters (yellow) of the ventral nerve cord; descending artery (da) merges with the ventral vessel on a level with the second leg arteries (p2a); C. Neuropil clusters (asterisks) of ventral nerve cord. D. Schematic drawing of the ventral vessel system in *Pagurus* (I), *Hapalogaster* (II-IV), *Lithodes* (V); branching pattern of leg arteries p2a-p5a in *Hapalogaster* is variable. E-F. *H. mertensii*: E. Lateral view of ventral vessel system and neuropil clusters (asterisks) of the ventral nerve cord; F. Frontal view of ventral vessel system showing the arteries supplying the mouthparts. Color code: pink, ventral thoracic muscles; light blue, sternal plastron; dark blue, endosternites; red, ventral vessel system; yellow, neuropil clusters of the ventral nerve cord. Abbreviations: cec, circum esophageal commissure; cg, cephalothoracic ganglion; da, descending artery; eso, esophagus; mp, neuromers of the mouthparts; p1-p5, legs (pereiopods); p1a-p5a, leg arteries; p1nv-p5nv, leg nerves; pn1-pn6, pleonal neuromers; pvv, posterior ventral vessel; tn4-tn8, thoracic neuromers; vtm, ventral thoracic muscles; vv, ventral vessel; X, crossed ventral muscles of the 8<sup>th</sup> thoracic segment.

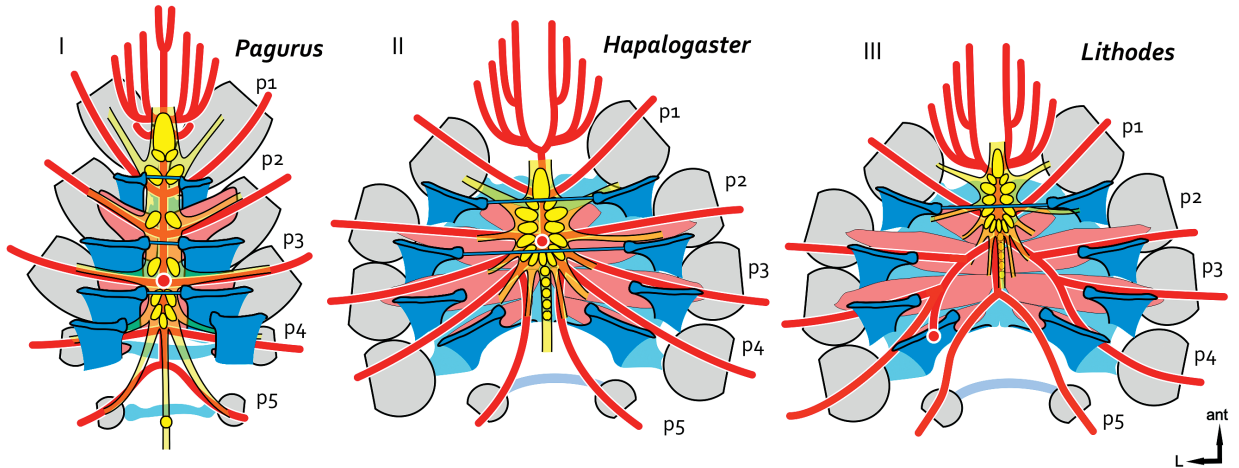


Fig. 7. Schematic drawing of the ventral organs in species of *Pagurus* (I), *Hapalogaster* (II), *Lithodes* (III) in dorsal view. The condition in *Pagurus* represents the state in the last common ancestor of hermit crabs and king crabs (LCA PK), that in *Hapalogaster* represents the state in the last common ancestor of hapalogastrids and lithodids (LCA HL). Color code: pink, ventral thoracic muscles; light blue, sternal plastron; dark blue, endosternites; red, ventral vessel system; yellow, neuropil clusters of the ventral nerve cord.

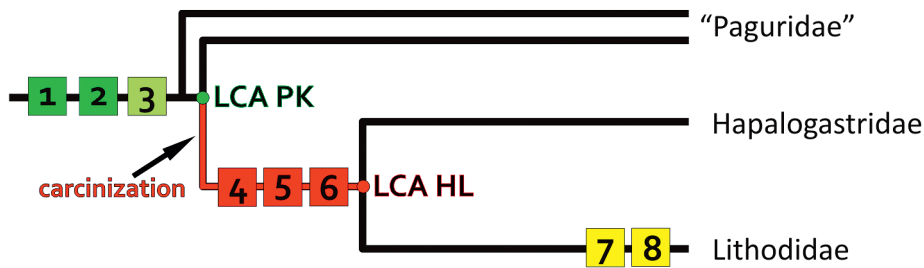


Fig. 8. Simplified phylogenetic tree (note that Paguridae are most probably paraphyletic with respect to king crabs) displaying anatomical characteristics and evolutionary morphological changes in the different lineages. Abbreviations: LCA PK, last common ancestor of Paguridae and king crabs; LCA HL, last common ancestor of Hapalogastridae and Lithodidae.

### Transformations of the pleon

Due to the weak calcification in pleonal segments pl4-pl6, the pleon in *Hapalogaster* is rather sac-like and differs from the more compact and more calcified pleon in lithodids. In this, hapalogastrids still resemble hermit crabs, which possess a sac-like although markedly coiled pleon. In our view, the well calcified tergite plates (and nodules) in Lithodidae represents a secondary condition (contrary to McLaughlin *et al.*, 2004). That the condition in pagurids is the plesiomorphic one is the necessary result of the nested position of king crabs within hermit crabs. McLaughlin *et al.* (2004) might be correct that the developmental sequence of the formation of tergite plates in king crabs might not be entirely congruent with the hypotheses of Bouvier (1895) and Boas (1924). What is shared by pagurids and

king crabs, however, is the separation of tergite plates which in pagurids (summarized in McLaughlin *et al.*, 2004) and apparently in hapalogastrids (Crain and McLaughlin, 2000) is the result of decalcification.

As in species of *Pagurus*, the dorsal pleonal musculature in *H. mertensii* is substantially reduced and pronounced muscular bundles are restricted to the first pleonal segment. The ventral pleonal musculature in *H. mertensii*, however, is thin and arranged in a thin layer of fibers which appears patchy and disorganized (Fig. 4F, G) in comparison to the much thicker and more compact ventral pleonal muscle in species of *Pagurus* (see fig. 6A in Keiler *et al.*, 2013), which is responsible for the rapid withdrawal into the gastropod shell (Stephens, 1986). Apart from this, the transformation of the internal pleonal morphology which took place in the lineage from the LCA of Paguridae and king crabs

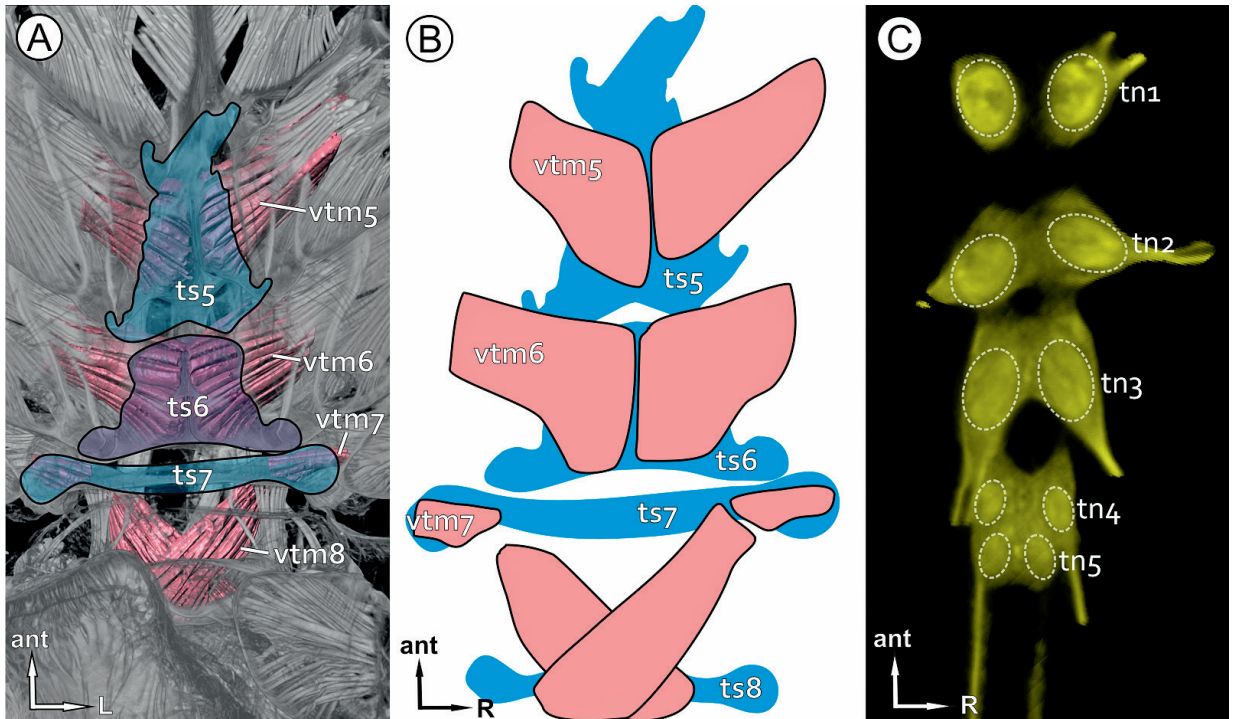


Fig. 9. A-B. *Pagurus bernhardus* (Paguridae): A. Ventral view of cephalothorax revealing spatial relationships between ventral thoracic muscles and sternites (transparent overlay). Volume and surface renderings. B. Schematic drawings of ventral thoracic muscles (pink) and sternites (blue) as seen in A in dorsal view. C. *Pagurus pubescens* (Paguridae): dorsal view of spatially divided neuropils (dashed semi-transparent white circles) of cephalothoracic ganglion (horizontally sectioned); neuropil of first pleonal neuromer hidden between neuropils tn5. Abbreviations: tn1-5, thoracic neuromers; ts5-8, thoracic sternites; vtm5-8, ventral thoracic muscles.

towards king crabs (or the LCA of Hapalogastridae and Lithodidae, respectively) was relatively minor. Based on the findings in *Pagurus* (Keiler *et al.*, 2013) and *Hapalogaster*, the posterior aorta in the LCA of Hapalogastridae and Lithodidae bifurcated into two asymmetrical branches of equal diameter, the left and right pleonal artery, representing the situation in the LCA of Paguridae and king crabs. In the lineage from the LCA of Paguridae and king crabs towards the LCA of Hapalogastridae and Lithodidae, the left pleonal artery developed another bifurcation into two arteries of equal size (the ventro-lateral and the dorso-medial artery; arrowheads in Fig. 4D, G). This may be functionally interpreted as an adaptation which was needed to provide sufficient hemolymph to the broadened pleon. Our findings for *Hapalogaster* support the previously hypothesized homology of the branches of the posterior aorta system in pagurids and lithodids (Keiler *et al.*, 2013). In terms of position and course, the distal portion of the ‘left pleonal artery’ in lithodids corresponds with the ventro-lateral branch in *H. mertensii*, while the slightly thinner ‘medial pleonal artery’ in

lithodids corresponds to the dorso-medial artery in *H. mertensii*.

#### *Transformations of the ventral cephalothorax – coherences in the course of carcinization*

The transformations of the ventral cephalothorax which took place in the lineage from the LCA of Paguridae and king crabs towards the LCA of Hapalogastridae and Lithodidae basically affected five components which, in varying respects, are structurally dependent on each other (*i.e.* coherent). These are a) the sternites, b) the endosternites, c) the ventral thoracic muscles, d) the ventral nerve cord and e) the ventral vessel system.

a) In the lineage from the LCA of Paguridae and king crabs (Fig. 9B) towards the LCA of Hapalogastridae and Lithodidae, thoracic sternites 4-7 fused to form a broad sternal plastron. The antero-ventral bend in the pleon gave the plastron its distinct concave posterior emargination.

b) The endophragmal skeleton, which appears to have been particularly affected by the transformational



processes of carcinization (Keiler *et al.*, 2013, 2015), is relatively similar in hapalogastrids and lithodids but differs distinctly between pagurids and king crabs. The emergence of the broad sternal plastron resulted in an increase in the medial distance between the endosternites (Keiler *et al.*, 2013; see Fig. 5D), and a successive reduction in the number of transverse thoracic bridges seems likely to have occurred in the lineage towards Lithodidae (Figs. 5A-C, 7).

c) The size and spacing of the sets of ventral thoracic muscles also changed due to modifications in the sternites. On the one hand, the muscles moved closer together along the body axis due to the posterior emargination of the plastron. On the other hand, the medial distance between the muscles increased as a result of the broadening of the ventral cephalothorax (Fig. 5E). The most substantial modification, however, affected the ventral thoracic muscles of the fourth pereopods (= vt7). The fourth pereopods evolved from short limbs providing grip in a gastropod shell in the LCA of Paguridae and king crabs to walking legs in king crabs (Richter and Scholtz, 1994; Keiler and Richter, 2011). The ventral thoracic muscles, changed from small bundles in the LCA of Paguridae and king crabs (Fig. 9A) to relatively large bundles in king crabs.

d) The ventral nerve cord underwent a marked change in arrangement and position in the lineage from the LCA of Paguridae and king crabs (Fig. 9C) toward the LCA of Hapalogastridae and Lithodidae (compare schematic drawings I and II in Fig. 7). The cephalothoracic ganglion became more planar due to the planar inner surface of the plastron, the cephalothoracic ganglion became distinctly compact and the pleonal ganglia were shifted anteriorly. The transformation of the pleonal ganglia was apparently coherent with functional-morphological changes in the pleon and the pleonal muscles. In hermit crabs, the pronounced ventral pleonal muscles are responsible for rapid withdrawal into the gastropod shell (Stephens, 1986). This function and biological role were lost in the evolution of king crabs, whose pleons are bent and remain in an idle state most of the time. Although it was already compact and had shifted anteriorly, the transformation of the ventral nerve cord continued in the lineage from the LCA of Hapalogastridae and Lithodidae to Lithodidae. The cephalothoracic ganglion in lithodids is situated further anterior (the posterior margin is located in the fourth thoracic segment) and proportionally smaller (Figs. 5E, 7III).

In the context of the changes in the fourth pereopods it should be pointed out that, in contrast to the preced-

ing neuropils, the neuropils of the seventh and eighth thoracic and first pleonal neuromer were tightly packed and rather small in the LCA of Paguridae and king crabs (as in *Pagurus*; Fig. 9C, see also Bouvier, 1889 plate 7; Stephens, 1986). This condition changed in the lineage towards the LCA of Hapalogastridae and Lithodidae, resulting in the distinctly larger and more separated neuropils corresponding to the fourth pereopods. This, in turn, corresponds secondarily with the neuropil arrangement in other anomurans (Keiler *et al.*, 2015, unpubl. data), whose fourth leg is developed as a 'normal' walking leg.

e) The distinct left-handed curve in the course of the descending artery in *H. mertensii* (Figs. 5B, 6A, B) represents the condition in the LCA of Hapalogastridae and Lithodidae and corresponds with the course of this artery in Lithodidae (Marukawa, 1933; McGaw and Duff, 2008; Keiler *et al.*, 2013). This distinct curve is most likely the result of the comparatively large proximal main ducts of the hepatopancreas and the gut, which the descending artery skirts (Fig. 3B). Variability notwithstanding, the fourth and fifth leg arteries in *H. mertensii* always possess a common root which emanates relatively close to the third leg arteries. The same pattern we assume for the LCA of Hapalogastridae and Lithodidae, meaning that a shift in artery roots appeared in the lineage from the LCA of Paguridae and king crabs toward the LCA of Hapalogastridae and Lithodidae. Remarkably, the branching pattern of the leg arteries differs significantly between *H. mertensii* and Lithodidae, suggesting a second transformational step in the lineage from the LCA of Hapalogastridae and Lithodidae towards lithodids which resulted in a fusion of arteries p2a-p4a. The pronounced curve of the descending artery in the LCA of Hapalogastridae and Lithodidae and the anterior shift in the cephalothoracic ganglion presumably both represented prerequisites for the subsequent condition in Lithodidae, in which the descending artery skirts around the cephalothoracic ganglion (Keiler *et al.*, 2013). This in turn led to the gently sloping arterial course in lithodids, which presumably facilitated the fusion of the leg arteries and the descending artery. On the other hand, it could be said that the loss of the bottleneck in the form of the pierced ganglion made the new condition a prerequisite for the high level of variability in the branching pattern of the leg arteries seen in some lithodids (Keiler *et al.*, 2013). The distance between the endosternites (*i.e.* the lack of 'guard rails'), however, seems to constitute a more important prerequisite for the presence of variability (Keiler *et al.*, 2013, 2015).



Table 1. Conditions of selected anatomical features in Paguridae, Hapalogastridae and Lithodidae. Correspondences are color-coded.

Paguridae	Hapalogastridae	Lithodidae
unpaired mandibular artery	mouthpart arteries with proximal bifurcation	mouthpart arteries with proximal bifurcation
leg arteries separated	leg arteries fused (p4a and p5a)	leg arteries fused (p2a, p3a and p4)
descending artery with angled course	descending artery with curved course	descending artery with curved course
descending artery pierces cephalothoracic ganglion	descending artery pierces cephalothoracic ganglion	descending artery skirts around cephalothoracic ganglion
pleonal ganglia segmentally arranged	pleonal ganglia condensed	pleonal ganglia condensed
cephalothoracic ganglion elongated	cephalothoracic ganglion condensed	cephalothoracic ganglion condensed
posterior aorta bifurcates into asymmetrical pleonal arteries	posterior aorta bifurcates into asymmetrical pleonal arteries	posterior aorta bifurcates into asymmetrical pleonal arteries
left pleonal artery unfurcated	left pleonal artery bifurcates into a symmetrical arteries	left pleonal artery bifurcates into asymmetrical arteries
hepatopancreas located largely in the pleon	hepatopancreas located largely in the pleon	hepatopancreas located largely in the pleon
gonads located largely in the pleon	gonads located largely in the pleon	gonads located largely in the pleon
sponge-like antennal bladder	sponge-like antennal bladder	condition unknown
pleonal segments 1-3 poorly calcified	pleonal segments 1-3 calcified	pleonal segments 1-3 calcified
pleonal segments 4-6 poorly calcified	pleonal segments 4-6 poorly calcified	pleonal segments 4-6 calcified

### Hapalogaster – the connecting link between hermit crabs and lithodid king crabs?

*Hapalogaster* resembles both pagurids and lithodids, not only in external morphology but, as we have shown here for *H. mertensii*, also in certain internal anatomical features (see Tab. 1). Compared to lithodids, hapalogastrids possess more anatomical characters that are plesiomorphic, meaning that these characters have not changed since the LCA of Paguridae and king crabs (e.g. the weakly calcified last pleonal segments or the piercing of the cephalothoracic ganglion by the descending artery). Furthermore, *Hapalogaster* exhibits anatomical conditions which can be interpreted as less derived than those in lithodids, e.g. the cephalothoracic ganglion, which is more anterior and more compact than in pagurids, but not as small or as far anterior as in lithodids. In this and other respects, *Hapalogaster* can be interpreted as representing an evolutionarily intermediate form, i.e. a connecting link between hermit crabs and lithodid king crabs.

### Acknowledgements

The authors would like to thank Christoph Noever (University of Bergen) for providing the *H. mertensii* and some of the *Pagurus* specimens. Craig Staude (Friday Harbor Labs) is thanked for his contribution of *H. grebnitzkii* specimens. The authors would also like to thank the staff of the Electron Microscopy Centre (University of Rostock) for assistance with critical point drying. Peter Michalik and his colleagues (Zoological Institute, University of Greifswald) are thanked for providing their microCT for some scans. Lucy Cathrow helped to improve the English of the text. Finally, thanks go to the authors' colleagues at the Zoological Institute of the University of Rostock and three anonymous reviewers for comments and suggestions which improved the manuscript; and the German Science Foundation (DFG) for funding this study (grant numbers WI 3334/1-2 and 3334/3-1).

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Received: 7 October 2014

Revised and accepted: 3 February 2015

Published online: 30 July 2015

Editor: R. Vonk

## Online supplementary information

*S1.* Studied specimens. ZSRO#, collection number of the Zoological Collection of the University of Rostock; m, male; f, female; inj, injection: m2, Mercox2 resin; pu4, PU4 resin; fix, fixation: PFA, paraformaldehyde; ga, n.a., not determined; glutaraldehyde; kar, Karnofsky's fixative; CT, micro computer tomography; n.a., not determined.

*S2. Lithodes maja* (Lithodidae): A. Ventral view; pleon virtually cut to show sternal plastron (outlined in blue); red dashed line indicates pleon margin; uncalcified areas between sternites shown with dotted outlines. B. Anteroventral view; note the vertically oriented third thoracic sternites (st3); arrow indicates suture. Abbreviations: cp, Carapace; mxp3, maxilliped 3; p1-5, pereopods; pl, pleon; pl3, third pleonal segment; pla, sternal plastron; st3-7; sternites; t, telson.