A "protonephridial" stage in kidney development of *Antalis entalis* (Mollusca, Scaphopoda)

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Introduction:

The renopericardial system of adult Scaphopoda is exceptional among the Mollusca in lacking a clearly defined heart. Functionally it is also of interest. Previous studies on Scaphopods show inconsistencies on details like the presence of a connection between the pericardium and kidney. This structure, usually present in molluscs, channels the primary urine from the pericard to the kidney (= metanephridium). There is only one old vague description of such a duct (Distaso, 1906) on the left side of the animal and another observation (Reynolds, 1990) of a duct on the right side. In the course of extensive studies on the larval excretory system of molluscs (e.g. Haszprunar and Ruthensteiner, 2000) we investigated the transition from the larval proto- to the metanephridial organization in early juvenile development of *Antalis entalis*. The mode of the formation of the renopericardial system in other molluscs (Polyplacophoren: Salvini-Plawen and Bartolomaeus, 1995), has been used to establish the homology relations of such organs among different phyla. Additional data on other molluscs like scaphopods would be helpful for testing such hypotheses. A prerequisite for the understanding of the juvenile condition was the reinvestigation of the adult organization.

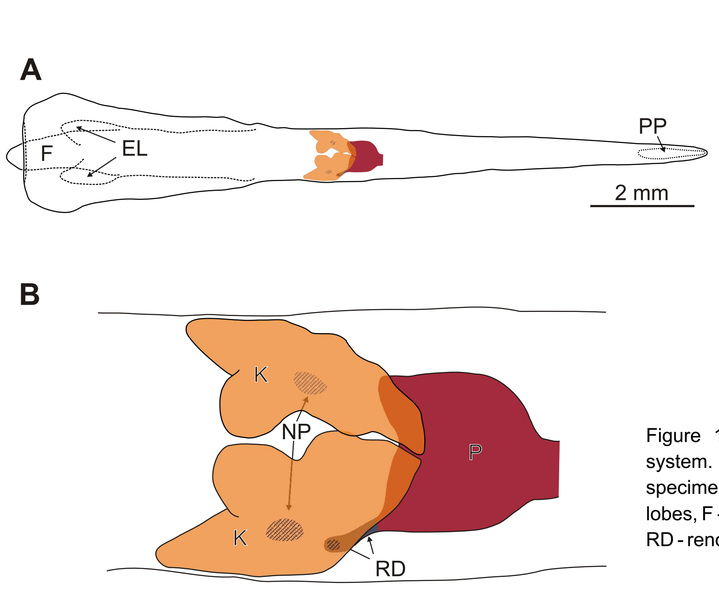

Figure 1. *Antalis entalis*. Organization of the renopericial system. Reconstruction from serial sections of a subadult specimen. A. General organization. B. Details. EL - epipodial lobes, F - foot, K - kidney, NP - nephropore, PP - pavillon proper, RD - renopericardial duct.

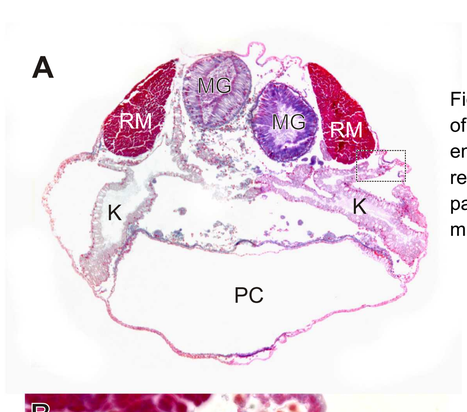

Figure 2. *Antalis* sp. Cross section in the area of the opening of the renepericardioduct into the left kidney. Paraffine embedding, Azan staining. A. Overview. Area in stippled rectangle is enlarged in B. K - kidney, MG - midgut, PC - pallial cavity, RD - renepericardial duct, RM - retractor muscle.

Results:

Reconstructions of serial sections of adult *Antalis* spp. revealed paired kidneys. The right kidney shows some differentiation for channeling eggs or sperm from the gonad to the outside. The left one is connected via a long tube to the pericardium which represents the renopericardial duct. The pericardium is located posteriorly to the kidneys. It shows a dorsal infolding, probably representing a homologue to the heart of other Molluscs.

In 13 days postmetamorphic juveniles the organization is strikingly different to the adult. There are paired compact renopericardial complexes. The kidneys resemble the adult ones in consisting of the same two cell types, a lumen and a nephropore. However, there is no trace of a pericardium or a heart yet. Instead there is a small duct connected to each kidney, consisting of several cells. The distal end of this duct is formed by a cell that gives rise to a ciliary flame extending into the lumen of the duct. The surface of this cell shows areas with diaphragms and slits, strikingly resembling the ultrafiltration sites of protonephridial terminal cells. Obviously, this whole kidney complex forms a functional unit with the ducts plus "protonephridial" terminal cells producing the primary urine for the kidneys. In the same juvenile stages remains of the protonephridia, the degenerated duct releasing cells can be found somewhat anterior to the kidney complex.

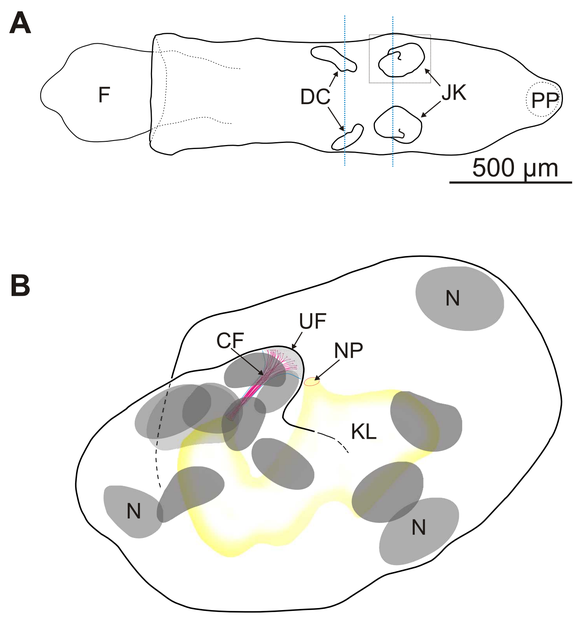

Figure 3. *Antalis entalis*. Organization of the juvenile kidney system. Reconstruction from serial sections of a juvenile specimen (13 days postmetamorphosis). A. General organization. Blue dotted lines indicate plane of sections of figure 4. B. Enlarged right juvenile kidney complex. CF - ciliary flame, DC - duct-releasing cell, F - foot, JK - kidney complex, KL - kidney lumen, N - nucleus, NP - nephropore, PP - pavillon proper, duct-releasing cell of the protonephridium, UF -

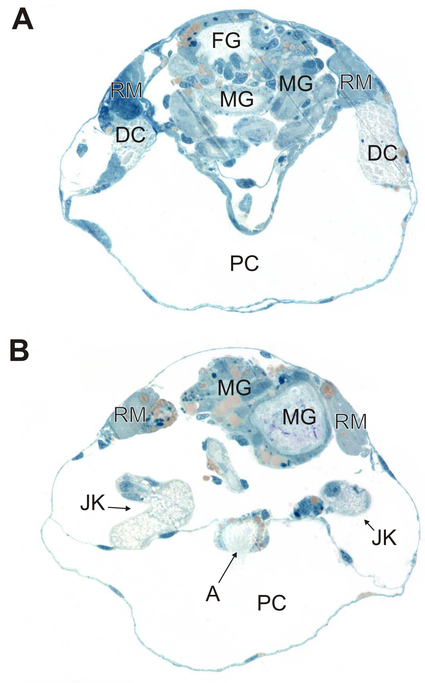

Figure 4. *Antalis entalis*. Cross section of a juvenile specimen (13 days postmetamorphosis, same specimen as figure 3.). Spurr embdding, Richardson staining. A. Area of the duct-releasing cell of the protonephridium. B. Area of the juvenile kidney complex. A - anus, DC - duct-releasing cell, FG - foregut, JK - juvenile kidney complex, MG - midgut, PC - pallial cavity, RM - retractor muscle.

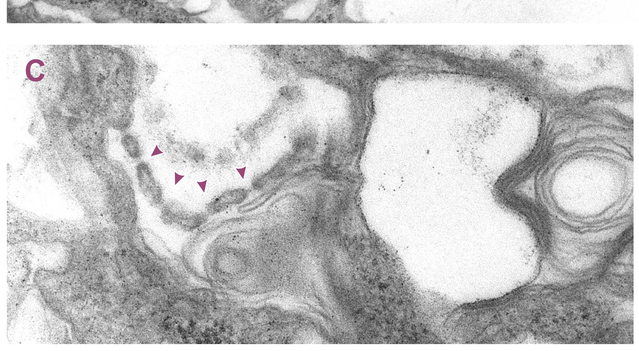

Figure 5. *Antalis entalis*. TEM cross sections of a juvenile specimen (13 days postmetamorphosis, from same development sample as specimen in figures 3. and 4.). A. Overview in the area of the anus. Area in left (big) rectangle is enlarged in figure B. Area in right (small) rectangle is enlarged in figure C. B. Base of the ciliary flame of the terminal cell with ultrafiltration site (arrow heads). B. ultrafiltration slits in the terminal cell (arrow heads).

Conclusions:

The confirmation of the presence of a renopericardial duct partly clarifies the long debated question of urine formation in Scaphopods. The way of primary urine production remains unclear for the right kidney, which shows no connection to the pericardium.

The kidney complex of the juveniles is a functional "protonephridium" in having a terminal cell and a differentiated excretory duct. However, the presence of a portion of the real protonephridium makes clear that this is a different organ. Although this kidney complex differs extremely from the adult renopericardial system, there is no question on the homology of at least the kidney portion. Intermediate development stages are needed to clarify the homology relationship of the terminal cell and duct of the juveniles with the renopericardial duct and pericardium of the adults. However, the organization found in the juvenile does not indicate a formation mode of heart and kidney as observed in Polyplacophorans, where the kidney is formed as an outgrowth from the pericard (Salvini-Plawen and Bartolomaeus 1995), at all. As there is no doubt that the kidneys of the two molluscan classes are homologous, the way of formation of the organ is no decisive criterion for a homology of such organs. This should be considered when hypothesizing about the homology of such organs among different phyla like Mollusca and Annelida.

References:

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