Genital System Development of *Williamia radiata* (Pulmonata, Siphonariidae)

Sabine Schopf, Gerhard Haszprunar & Bernhard Ruthensteiner
Zoologische Staatssammlung Muenchen, Munich, Germany
Email: haszi@zsm.mwn.de

Introduction

Because of its high complexity the hermaphroditic genital system of pulmonates and other euthyneuran gastropods has been used for dealing with deep as well as shallow phylogenetic questions. However, the significance of this data-set is limited because of convergences mainly due to functional constraints. Knowledge of ontogeny might be useful to clarify some homology problems. To date, within euthyneurans detailed ontogenetic data are available for nudibranch opisthobranchs and stylommatophoran pulmonates only. The latter taxon exhibits highly derived developmental features within pulmonates, which consist of a number of fairly heterogeneous taxa. The investigation of a member of the primitive family Siphonariidae is a pilot study to assemble general knowledge of pulmonate genital system development.

Material and Methods

Juveniles of all sizes ranges and adults of Williamia radiata (Pease, 1861) were serially sectioned after embedding in araldite or paraplast (only fully grown adults). Based on digital photographs of every or every fourth section, they were reconstructed and visualised with the help of the software package Amira (versions 2.3 and 3.0, TGS Europe, S.A., France inc.). Rendering of organ and specimen surfaces was performed by applying the " SurfaceGen" (="GMC") module onto manually prepared ("segmentation") "label fields".

Figure 1. *Williama radiata*. Genital system of an adult (nidamental glandular system not fully grown), body surface bright transparent. A. Dorsal view. B. Lateral from the left side. ag - albumen gland, ah - ampulla of the spermoviduct, bc - bursa copulatrix, co - copulatory organ, eg - epiphallic gland, fp - fertilization pouch, mg - mucus gland, ng - nidamental gland portion, ot - ovotestis, so - spermoviduct.

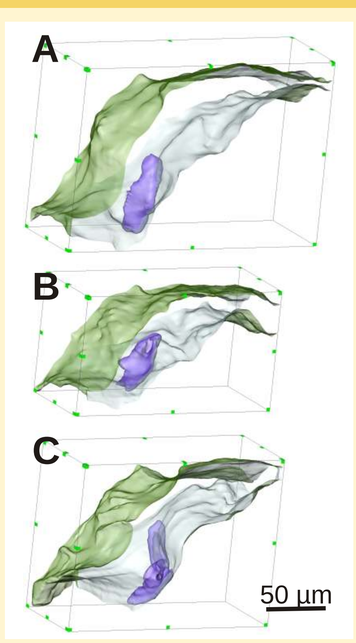

Figure 3. *Williama radiata*. Details of juvenile specimens showing successive stages in early development of the pallial anlage, pallial cavity surface (greenish/greyish) and increasingly invaginating pallial anlage (bluish) obliquely from right-anterior, angle and size of crops shown by boxes. A. Same specimen as figure 4A. B. and C. Intermediate stages between specimens of figures 4A and 4B.

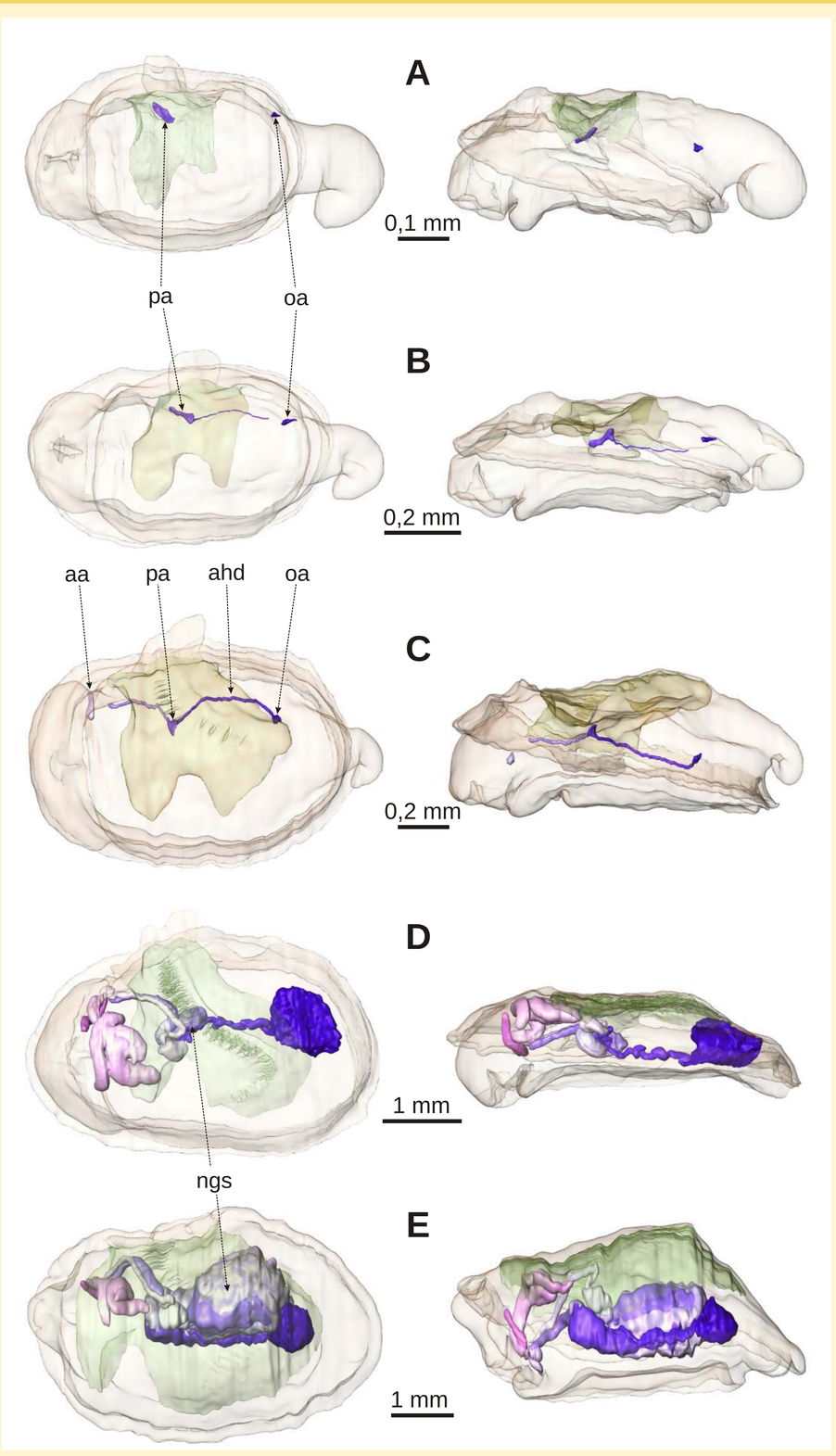

Figure 4. *Williama radiata*. Successive juvenile and adult stages from dorsal (left column) and lateral from the left side (right column) with transparent body surface and pallial cavity (green-brownish). aa - anterior anlage, ahd - anlage of hermaphrodite duct, ngs - nidamental glands, oa - ovotestis anlage, pa - pallial anlage.

Results

Adult genital system (figs. 1, 2):
As typical for siphonariids, the genital system of Williamia radiata is relatively simple compared with other euthyneuran gastropods. From a posterior located ovotestis (= hermaphrodite gland, "gonad") the hermaphrodite duct, with a widening, the ampulla, leads into a narrow winded duct comprising the spermatheca (= carrefour) and the fertilization pouch. The voluminous nidamental glandular system (= female genital glands) consists of three nidamental glands, which together enclose a continuous lumen and also forms the connection from the spermatheca to the off leading spermoviduct. The spermoviduct runs anteriorly to the right towards the genital atrium, which opens to the body surface. Thus, W. radiata, with a single releasing duct and a single genital opening, has a monaulic und monotremous genital system. The large bursa copulartrix (= gametolytic gland) lies dorsal to the posterior end of the spermoviduct. The stalk of this organ also opens into the genital atrium. Anteriorly lies the prominent epiphallic complex, with the voluminous epiphallic gland and the copulatory organ, which as well opens into the genital atrium.

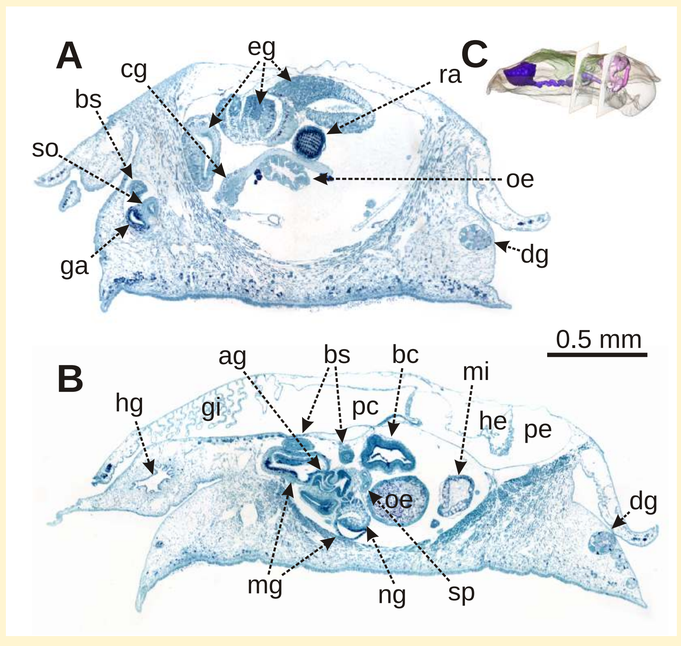

Figure 2. *Williama radiata*. Same specimen as figure 1. A. Transverse section in the area of the epiphallic gland. B. Transverse section in the area of the nidamental glandular system. C. Total specimen with genital system and transparent body surface, obliquely shown from right-anterior. "Ortho slices" give section positions of A and B. ag - albumen gland, ahd - anlage of hermaphrodite duct, bc - bursa copulatrix, bs - stalk of bursa copulatrix, cg - cerebral ganglion, dg - defensive gland, eg - epiphallic gland, ga - genital atrium, gi - gill, he - heart, hg - hindgut, mg - mucus gland, mi - midgut gland, ng - nidamental gland portion, oe - oesophagus, pc - pallial cavity,

Development (figs. 3 - 5):
The genital system develops from three separate anlagen which first appear in the early juvenile development phase. The posterior one is first detectable at a body length of 0.7 mm (fig. 4A). It gives rise to the ovotestis and part of the hermaphrodite duct. The nidamental glandular complex, the spermatheca with fertilisation pouch, the anterior part of the hermaphrodite duct, the posterior part of the spermoviduct and the bursa copulatrix with stalk develop later from the pallial anlage. This ectodermal anlage is formed by an invagination of the ventral mantle cavity epithelium (fig. 3). The last appearing anlage (body length: 1.38 mm) is the anterior one. Initially it is a sac-like epithelial - thus ectodermal - infolding at the right body side posterior of the head (figs. 4C, 5D). This anlage gives rise to the genital atrium, the epiphallic complex and the anterior spermoviduct. Final differentiation of female components with enormous growth of the nidamtal glands, after achievement of male sexual maturity, suggests protandic hermaphroditism in this species.

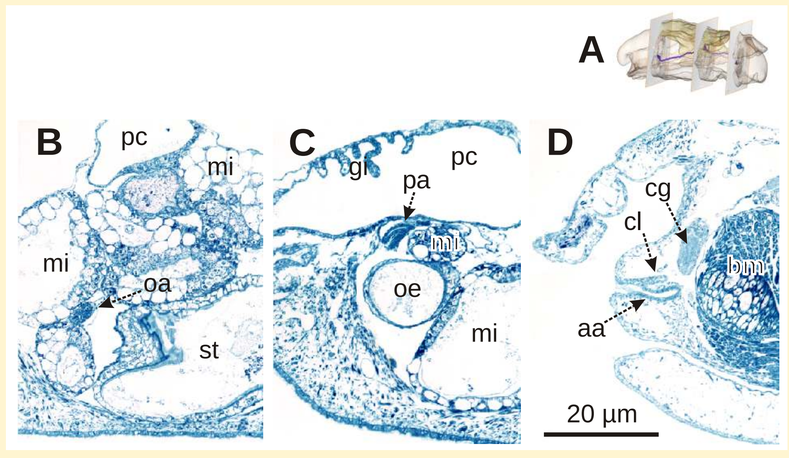

Figure 5. *Williama radiata*. Same specimen as figure 4C. A. Total specimen with genital system and transparent body surface, obliquely from right-anterior. "Ortho slices" give section positions of B, C and D. B. Transverse section in the area of the ovotestis anlage. C. Transverse section in the area of the pallial anlage. D. Transverse section in the area of the anterior anlage. aa - anterior anlage, bm - buccal mass, cg - cerebral ganglion, cl - cerebral gland, gi - gill, mi - midgut gland, oa - ovotestis anlage, oe - oesophagus, pa - pallial anlage, pc - pallial cavity, st - stomach.

Discussion and Conclusions

This formation of the genital system from three, locally separated anlagen, differs strikingly from that of most other euthyneuran gastropods. In both the opisthobranch nudibranchs (e.g. Schönenberger, 1969) and the pulmonate stylommatophorans (e.g. Hochpöchler, 1979) development proceeds from a single site. A similar pattern like that of Williamia radiata is described from the basommatophoran Lymnaea stagnalis (Fraser, 1946) only. Based on these observations together with additional, unpublished data on bullomorph opisthobranchs (Schaefer, pers. comm.) and ellobiid pulmonates (Ruthensteiner, unpubl.) we assume that this represents the plesiomorphic condition in Euthyneura.
Despite of the lack of detailed data on most other pulmonate taxa comparison of development allows to establish first homology relations. Organs usually called bursa copulatrix are homologous throughout the pulmonates. The proximal vas deferens of freshwater basommatophorans appears to be derived from one fold of the bipartite W. radiata spermoviduct. Thus, these two structures must be regarded as homologous.

References

Fraser, L.A. 1946 The embryology of the reproductive system of *Lymnaea stagnalis* appressa SAY. Trans. Am. Microsc. Soc. **65**: 279-298.
Hochpöchler, F. 1979 Vergleichende Untersuchungen über die Entwicklung des Geschlechtsapparates der Stylommatophora (Gastropoda). Zool. Anz. **202**: 289-306.
Schönenberger, N. 1969 Beiträge zur Entwicklung und Morphologie von *Trinchesia granosa* Schmekel (Gastropoda, Opisthobranchia). Pubbl. Stat. Zool. Napoli. **37**: 236-292.