

Structural investigation of the female genitalia and sperm-storage sites in the terrestrial isopod *Armadillidium vulgare* (Crustacea, Isopoda)

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Abstract

The cuticular genitalia of the terrestrial isopod, *Armadillidium vulgare*, have two distinct states during the reproductive cycle of the females. The structural differences between the reproductive and non-reproductive states, and the structure of the sperm storage sites were investigated employing electron and light microscopy. In both states the genitalia consist of a distal segment that connects to the gonopore, and a cuticular tube-like structure lining the lumen of the oviduct in the middle region of the oviduct. Sheath-like projections, apparently consisting of cuticular material, extend laterally along two sides of the cuticular tube. In the proximal region of the oviduct cuticular structures are lacking. In the non-reproductive state the distal segment consists of endo-, exo- and epicuticle. The exocuticle is three layered with unusual spongy and dense layers at the distal side. On one side the endocuticle doubles in thickness to form a cuticular bulge that fills the lumen of the distal segment leaving just a narrow U-shaped space. The cuticular tube consists of endo- and epicuticle only. In the reproductive state the distal segment is funnel-shaped and forms branched cuticular folds that increase in complexity from distal to proximal. In the cuticular tube these folds tightly fill the lumen of the oviduct. At the confluence of the oviduct with the ovary spermatozoa are stored in a seminal receptacle.

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1. Introduction

The internal reproductive system of female *Armadillidium vulgare* consists of one pair of longitudinal ovaries and one pair of oviducts. The oviducts arise from the middle of the ovaries and descend to the gonopores at the lateral sides of the 5th sternite (Fig. 1). Recent light microscopical studies have shown that during the reproductive cycle of *A. vulgare* the gonopore goes through two main functional states (Suzuki, 2001): either as a copulatory opening to receive the male genitalia or as an oopore allowing for oviposition in addition to copulation. Oopores are present only during a short period of time in the female reproductive cycle. They form just before oviposition, are large in diameter to allow the oocytes to pass through, and lack a

thick cuticular structure behind the pore. Insemination takes place during the intermolt (Mead, 1976) and premolt (Moreau and Rigaud, 2002) stages that precede the parturial molt when the oviducts contain the cuticular genitalia (Suzuki, 2001). The cuticular genitalia comprise a distal segment that is in confluence with the cuticle of the integument surrounding the gonopore and a cuticular tube that lines the lumen of the middle region of the oviduct. Interestingly, recent light-microscopic studies reveal structural changes of the genitalia that depend upon the reproductive condition of the female (Suzuki, 2001, 2002). In females carrying mature oocytes in their ovaries, just after the parturial molt the endopodites at the first five thoracic segments develop into leaf-shaped oostegites. These five pairs of oostegites establish a marsupial space between their dorsal surfaces and the ventral surface of the sternites. Such females have large gonopores, and, after oviposition, form genitalia in the reproductive state, the latter consisting of a funnel-shaped distal segment and a semitransparent cuticular tube. In contrast, females having immature oocytes in their ovaries form genitalia in the non-

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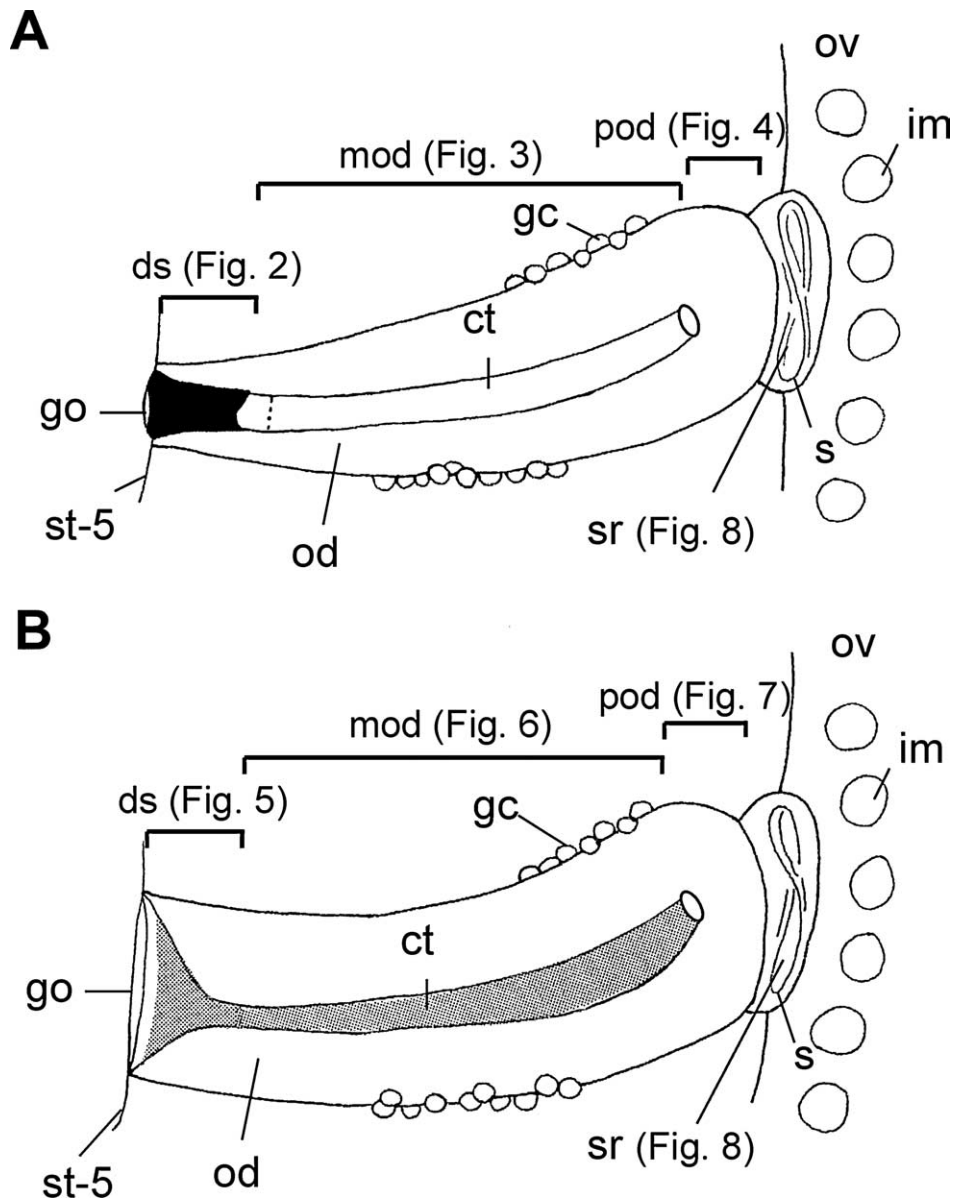


Fig. 1. Schematic overview of the oviducts of *A. vulgare* with genitalia in the non-reproductive A and the reproductive state B as formed after oviposition. The oviduct (od) connects the ovary (ov) with the gonopore (go) in the 5th sternite (st-5); ct, cuticular tube; ds, distal segment; gc, gland cells; im, immature oocyte; mod, middle region of the oviduct; pod, proximal region of the oviduct; s, sperm; sr, seminal receptacle.

reproductive state during non-parturial molts and they lack a marsupium. Their gonopores are rather small. The new genitalia consist of a thick slightly cone-shaped distal segment with an almost transparent tube at the more proximal part of the genitalia. Since the genitalia are cuticular structures, the reconstruction of both types of genitalia and their conversion from the non-reproductive state to the reproductive state and vice versa must occur during and after each molt. It is important to note that reproductive females with mature ovaries still have genitalia in the nonreproductive state when the preceding molt was non-parturial. Because insemination occurs internally, it is likely that the structural changes in the genitalia are functionally related to copulation and, possibly, to later

sealing of the oviduct. Although cuticular structures of isopod oviducts are well described through light-microscopical observations (Calman, 1909; Vandel, 1925; Veuille, 1978; Lincoln, 1985; Wilson, 1986, 1991; Wägele, 1990, 1992), the methods employed enable only insufficient deduction of the function of the genitalia.

There is also increasing evidence that female isopods can store functional spermatozoa within their reproductive system for long periods (Lueken, 1963; Johnson, 1982; De Luca et al., 1987; Wilson, 1991; Wägele, 1992; Warburg, 1993; Longo et al., 1998; Zimmer, 2001; Moreau et al., 2002). Adult females of *A. vulgare*, for example, can produce 4–5 marsupial broods more than a year after the last copulation (Lueken, 1963), but the presence of a sperm-

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