Morphogenesis of the Postabdomen in Ground Beetle Prepupa: Preliminary Results

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In Coleoptera, as in some other Holometabola, the adult structures develop without imaginal disks (Chapman, 2013). This greatly facilitates establishing homologies of many parts, including appendages. In carabids, as in most beetles, the segmentation of the larval abdomen is known to match closely the germ band (Kemner, 1918; Matsuda, 1976; Tikhomirova, 1991; Kobayashi et al., 2013). On the other hand, the pupal abdomen is similar in structure to adult's and carries well-defined genitalia (Kirchner, 1927; Jeannel, 1941; Sturani, 1962; Di Giulio et al., 2007). A crucial step, at which the copulatory parts form and abdomen gets differentiated into pre- and postabdomen, clearly coincides with the last period of the larval life, i. e., the prepupa (term used here as synonymous with 'pharate pupa'; see Costa & Vanin, 1985). The prepupal development of the copulatory system may thus provide conclusive evidence of its parts' homologies and segment associations.

Such changes, that occur hidden by the larval integument, or even a pupal cell, are barely understood in beetles (Kerschner, 1913; Singh Pruthi, 1924a, b; Metcalfe, 1932), and have never been studied in carabids. Moreover, much of the available data is from untypical cases of morphogenesis affected by juvenile hormone analogues or otherwise (Tikhomirova, 1991; Konopova, Jindra, 2008; Lee et al., 2013), thus making the interpretation problematic.

We studied lab-reared larvae and pupae of *Poecilus* (s.str.) *versicolor* (Sturm 1824) and *P.* (s.str.) *reflexicollis* Gebler 1830, obtained in the laboratory between 1.06.2015 and 27.08.2015 at 22–24°C and LD 16:8, served us as study material. Prepupal morphogenetic stages were identified based on shape and position of the ocular pigmented spots that move basad from the ocular bulge to reach the edge of the thorax, at which point the molting occur. Since the duration of the prepupa in the two species is different, it was the position of the pigmented spot that was used to align the developmental stages.

In the pupa, what remains of the larval eye gets replaced with adult compound eye (Sturani, 1962), which can also be used as a morphogenetic marker.

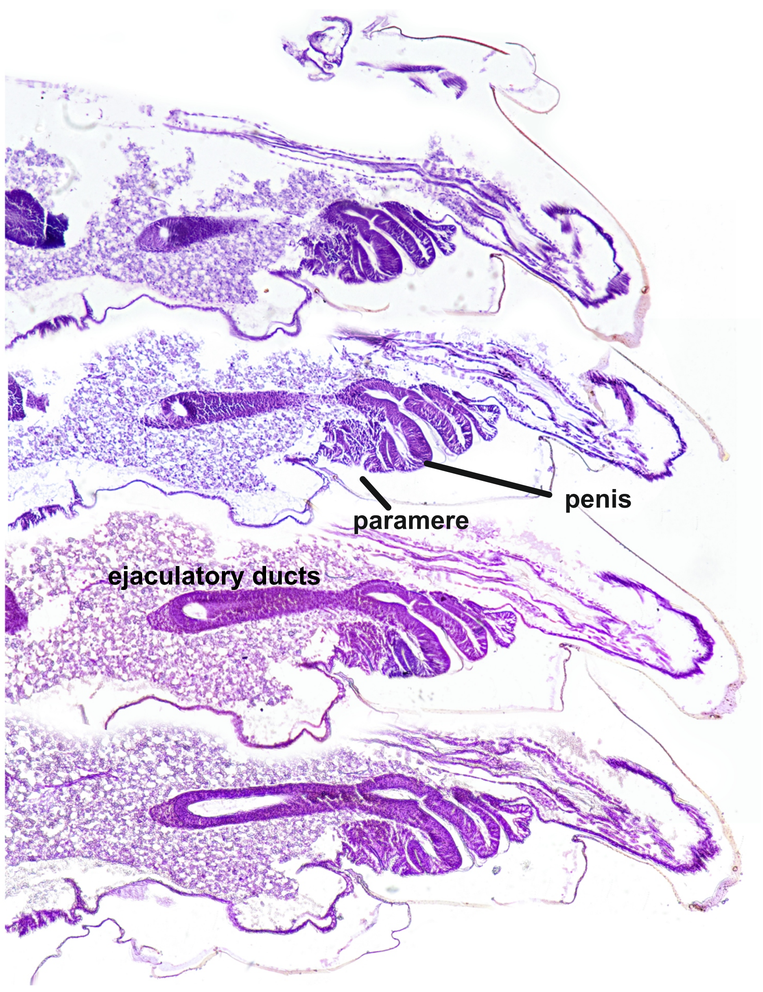
In early prepupa, with the pigmented spot in the postocular furrow area, segments IX and X retain size and structure typical of the larva, but the ventral area of segment IX shows the genital primordiae.

The middle stage, with the pigmented spot between the postocular and occipital furrows, is characterized by the copulatory parts appearing on sternite IX, while the genital ducts differentiate and get much longer. The proportions of the urogomphi and segments IX and X show little change.

At the final stage of prepupal development, with the pigment spot basad of the occipital furrow, the urogomphi and segment X shorten considerably, and the genitalia get differentiated enough to make sexes easily recognizable.

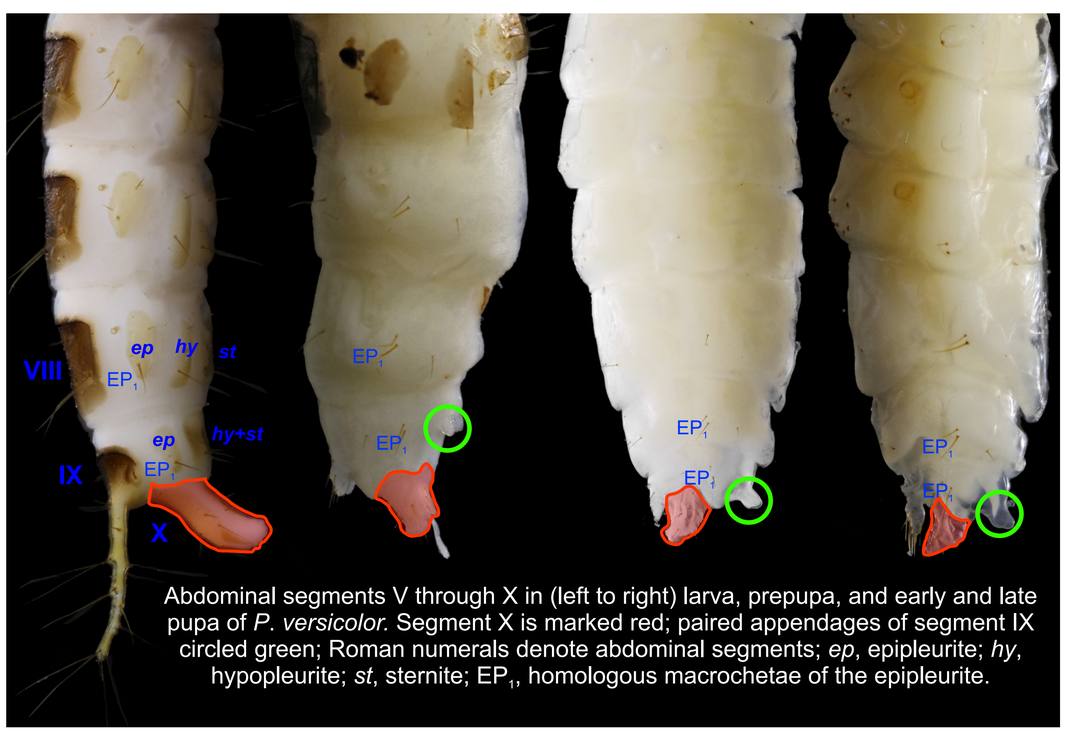
In the pupa, the urogomphi further shorten and segment X shrinks and invaginates into segment IX, while segments VII and VIII expand to assume structure typical of the adult.

Changes in eye shape and position during the larval (left) and pupal (right) stages in *P. versicolor.* Pigmented spots encircled.



Primordiae of penis and parameres in late prepupa of *P. versicolor* on 10μm sections.

Serial sections clearly show that primordial genitals form at the posterior margin of ventrite IX. In both sexes they emerge similarly, with the paired parts and the axial part forming simultaneously. Musculature and chaetotaxy suggest that in all larval carabids ventrite IX is a product of fusion between the sternite and the hypopleura. Those paired primordiae may thus be interpreted as primordial limbs. Their fate is different, though: in females, they grow to occupy the sides of segment IX, eventually forming the gonocoxite and gonostyli; in males, they gradually shrink and undergo no differentiation, while the parameres emerge as longitudinal folds and swellings of the genital pocket wall.



Abdominal segments V through X in (left to right) larva, prepupa, and early and late pupa of *P. versicolor.* Segment X is marked red; paired appendages of segment IX circled green; Roman numerals denote abdominal segments; *ep*, epipleurite; *hy*, hypopleurite; *st*, sternite; EP_1, homologous macrochetae of the epipleurite.

The above observations generally agree with what is known about prepupae of Polyphaga (Singh-Pruthi, 1924a; Metcalfe, 1932). Interpreting the postabdominal structures from adult morphology may be, however, misleading. Further studies of the prepupal development are unlikely to overhaul the existing ideas on the origin of coleopteran genitalia, but will help reassessing the interpretations. Our data suggest that:

- Segment X, subject as it is to reduction in the course of metamorphosis, is not involved in the formation of genitalia (contrary to Jeannel, 1941; Snodgrass, 1957; and others);
- The original location of the genital opening is on segment IX (not VII, as argued by Deuve, 1993);
- Copulatory organs are formed from ventrite IX; the involvement of pleura or terga (see Verhoeff, 1918; Bils, 1976; Deuve, 1993) cannot be confirmed;
- There is no evidence of male copulatory organs having evolved from limbs (Singh-Pruthi, 1924a; Dupuis, 1950; Matsuda, 1976); and
- The male aedeagus is a new structure (Sharp & Muir, 1912; Matsuda, 1976).

These preliminary results should be verified on other models, especially those representing basal carabid lineages.

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