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Postembryonic development of pycnogonids: A deeper look inside

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ABSTRACT

Sea spiders form a small, enigmatic group of recent chelicerates, with an unusual bodyplan, oligosegmented larvae and a postembryonic development that is punctuated by many moults. To date, only a few papers examined the anatomical and ultrastructural modifications of the larvae and various instars. Here we traced both internal and external events of the whole postembryonic development in *Nymphon brevirostre* HODGE 1863 using histology, SEM, TEM and confocal microscopy. During postembryonic development, larvae of this species undergo massive reorganization: spinning apparatus and chelar glands disappear; larval legs redifferentiate; three new segments and the abdomen are formed with their corresponding internal organs and appendages; circulatory and reproductive systems develop anew and the digestive and the nervous systems change dramatically. The body cavity remains schizocoelic throughout development, and no traces of even transitory coeloms were found in any instar. In *Nymphon brevirostre*, just like in *Artemia salina* LINNAEUS 1758 the heart arises through differentiation of the already existing schizocoel, and thus the circulatory systems of arthropods and annelids are not homologous. We found that classical chelicerate tagmata, prosoma and opisthosoma, are inapplicable to adult pycnogonids, with the most striking difference being the fate and structure of the seventh appendage-bearing segment.

1. Introduction

Pycnogonids form a small group of primarily marine arthropods (Arnaud and Bamber, 1987). For a long time their position in the phylogenetic tree was hotly debated (see, e.g., review by Dunlop and Arango, 2005). Consensus is not yet reached, although recently many authors place the sea spiders among chelicerates. Pycnogonids are typically seen as sister group to the rest of the chelicerate lineage, which is often called Euchelicerata, or Chelicerata *sensu stricto* (Wheeler and Hayashi, 1998; Arango, 2002; Mallatt et al., 2004; Giribet and Edgecombe, 2013). This is hardly surprising, given the unusual bauplan of the adult sea spiders. Their bodies include (*i*) an anterior unsegmented part bearing the proboscis with a terminal mouth, cheliphores, palps, ovigers and the first pair of walking legs; (*ii*) three to five free segments, each with a pair of walking legs; and (*iii*) an abdomen – an unsegmented posterior lobe with terminal anus.

Originally, the bodies of these animals were interpreted as having a prosoma (with all the appendages) and a severely reduced opisthosoma (Wirén, 1918). Currently this analogy with the tagmosis of typical chelicerates appears, at best, far-fetched. Still, all the attempts at equating the tagmata in the adult pycnogonids with other chelicerates so far have failed to deliver unequivocal results, free of reservations (Wirén, 1918; Arnaud and Bamber, 1987; Dunlop and Arango, 2005). Some questions present especially difficult challenges, e.g. the nature of the proboscis, homology and fate of the pycnogonid larval legs and their derivates (Wirén, 1918; Vilpoux and Waloszek, 2003; Dunlop and Arango, 2005), and the origin of the sea spiders with five and even six pairs of walking legs (Calman, 1920; Calman and Gordon, 1933; Arabi et al., 2010).

Studies of the larvae and development, especially postembryonic development, are of great help in finding parallels between the sea spiders and other chelicerates. As we follow the formation of an adult body, we gain deeper understanding of patterns and origins of the body parts. For instance, Vilpoux and Waloszek (2003) made much progress in the analysis of tagmosis in *Pycnogonum litorale* STRØM 1762. They provided the current interpretation of the pycnogonid body which distinguishes cephalosoma (bearing the proboscis, cheliphores, palps, ovigers and walking legs 1), free body segments, and abdomen (Vilpoux and Waloszek, 2003). Unfortunately, this excellent study does not contain information on the inner structure of the animals, only on

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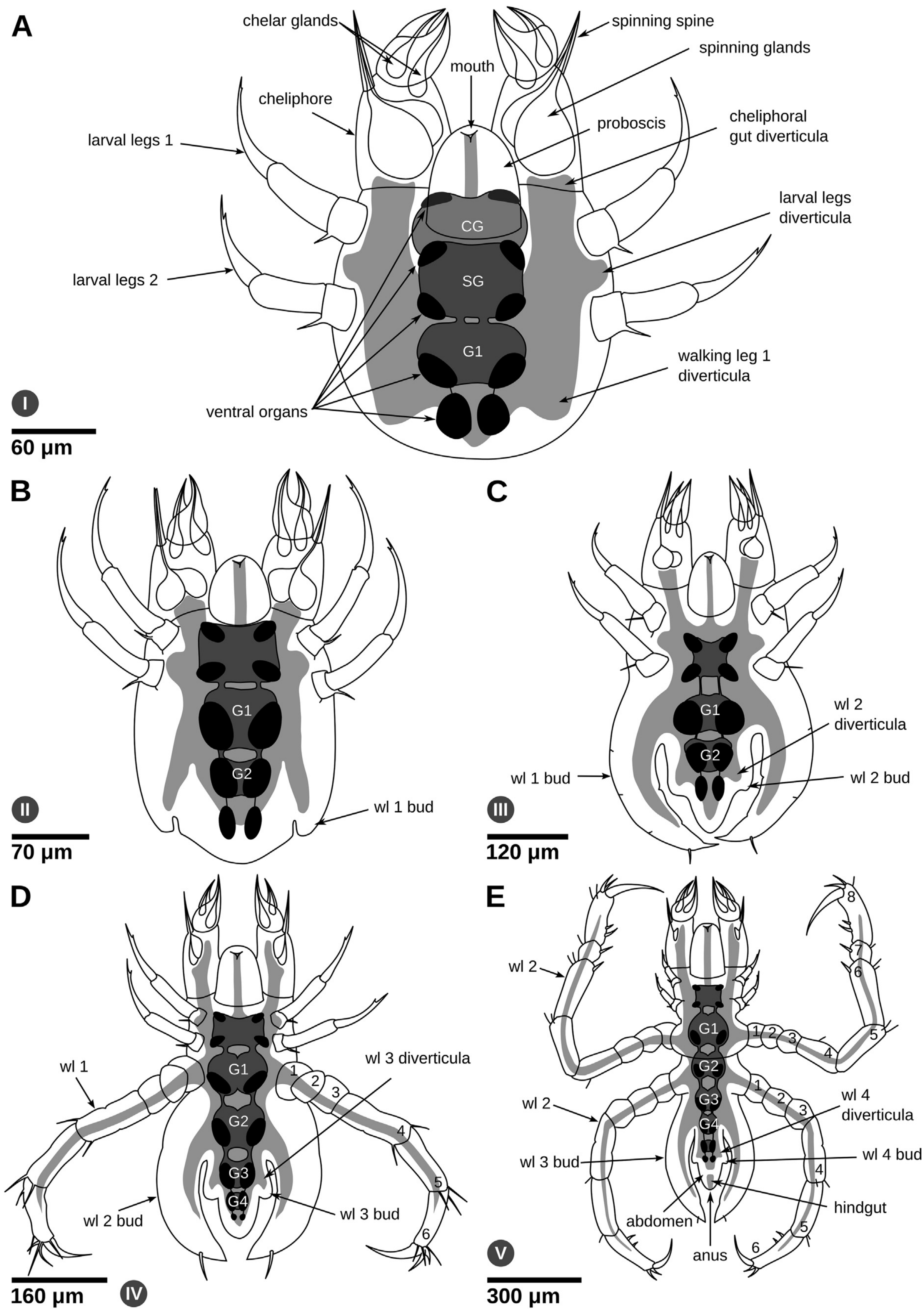

Fig. 1. Stages of the postembryonic development of *Nymphon brevirostre* (schematic drawings). A: protonypmphon larva, instar I. B: instar II. C: instar III. D: instar IV. E: instar V. F: Iinstar VI. G: instar VII. H: instar VIII. I: instar IX. Abbreviatons: CG – cerebral ganglion, G1 – first ganglion of the VNC, SG – subesophageal ganglion, wl1-4 – walking legs.