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Cell lineage analysis of the mandibular segment of the amphipod *Orchestia cavimana* reveals that the crustacean paragnaths are sternal outgrowths and not limbs

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Abstract

The question of arthropod head segmentation has become one of the central issues in Evolutionary Developmental Biology. The number of theories pertaining to head segments progressively enlarges, old concepts have been revitalized, and nearly every conceivable composition of the arthropod head has at some point received discussion. One contentious issue involves a characteristic mouthpart in crustaceans – the lower lips or the so-called paragnaths. The paragnaths build the posterior border of the mouth region antagonistic to the upper lip – the labrum. We show here the development of the appendage-like structures in the mandibular region of the amphipod crustacean *Orchestia cavimana* at a high level of cellular resolution. The embryos are examined during development of the mouthparts using *in vivo* labeling. An invariant cell division pattern of the mandibular segment was detected by 4D-microscopy and a preliminary model for pattern of the first cleavages in the mandibular region created. With this indispensable precondition single ectodermal cells of the grid-like pattern were labeled with Dil – a lipophilic fluorescent dye – to trace cell lineages and determine the clonal composition of the developing mouthparts, especially the mandibular segment. From our data it is evident that the paragnaths are sternal outgrowths of the mandible segment. The assumption of the limb nature of paragnaths and the presence of an additional head segment between the mandibular and the second antennal segments are clearly refuted by our data. Our results show the power of cell lineage and clonal analyses for inferences on the nature, origin and thus homology of morphological structures. With this kind of investigation morphological and gene expression data can be complemented.

We discuss notable similarities of paragnath anlagen to those of the hypopharynx complex in myriapods and hexapods. The fact that both structures grow out as two lateral buds in the same region of the mandibular sternite during development, and their important role in the formation of the feeding apparatus as a highly specialized chewing chamber in adults of crustaceans, myriapods, and hexapods argue for the paragnaths/hypopharynx anlagen being an additional potential apomorphy of Mandibulata.