



Evolution of Developmental Control Mechanisms

Formation of the insect head involves lateral contribution of the intercalary segment, which depends on *Tc-labial* function

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ABSTRACT

The insect head is composed of several segments. During embryonic development, the segments fuse to form a rigid head capsule where obvious segmental boundaries are lacking. Hence, the assignment of regions of the insect head to specific segments is hampered, especially with respect to dorsal (vertex) and lateral (gena) parts. We show that upon *Tribolium labial* (*Tc-lab*) knock down, the intercalary segment is deleted but not transformed. Furthermore, we find that the intercalary segment contributes to lateral parts of the head cuticle in *Tribolium*. Based on several additional mutant and RNAi phenotypes that interfere with gnathal segment development, we show that these segments do not contribute to the dorsal head capsule apart from the dorsal ridge. Opposing the classical view but in line with findings in the vinegar fly *Drosophila melanogaster* and the milkweed bug *Oncopeltus fasciatus*, we propose a “bend and zipper” model for insect head capsule formation.

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Introduction

The insect head is built by two major parts, each of which is formed by tissues derived from at least three embryonic segments. The posterior gnathal region (gnathocephalon) comprises three segments that bear the mouthparts, namely, the labial (lb), maxillary (mx), and mandibular (md) (Fig. 1A). The anterior pregnathal region (procephalon) is composed of the intercalary segment (ic), the antennal (ant), the ocular segments (oc), and other preantennal tissues (Rogers and Kaufman, 1996, 1997; Snodgrass, 1935). However, the overall number of segments in the pregnathal region is controversial, since the presence of a labral segment remains disputed (Budd, 2002; Haas et al., 2001a,b; Rempel, 1975; Rogers and Kaufman, 1996; Schmidt-Ott et al., 1994; Scholtz and Edgecombe, 2006). As alternatives, it has been proposed that the labrum represents a non-segmental appendage (Posnien et al., 2009a) or that it is the appendage of the intercalary segment (Haas et al., 2001a,b; Scholtz and Edgecombe, 2006). The latter view has been criticized based on the finding that crustaceans have a fully developed appendage on the homologous segment (second antennal segment) as well as a labrum (Scholtz and Edgecombe, 2006).

While the parasegmental boundaries of arthropods (except for the disputed labral segment) are clearly defined in the embryo by adjacent expression of *engrailed* and *wingless*, it remains unclear where these borders are located in the fully developed head. Classical morphological studies suggest that the postoccipital suture (a cuticular inflection close to the posterior margin of the head) represents the maxillary–labial segment boundary. Hence, the labial and maxillary segments are proposed to contribute to the dorsal head. Analogous to the situation in trunk segments, it has been suggested that the more anterior head segments contribute similarly to the dorsal head, although no clear evidence has been put forward to support this view (Fig. 1B) (Bucher and Wimmer, 2005; Snodgrass, 1935; Weber, 1966). Another open question is the development of the position of the gnathal appendages: during early embryonic development of insects, the gnathal segments and their appendages are formed in a linear series similar to the more posterior trunk segments (Fig. 1A). Later, however, they end up surrounding the mouth opening (Fig. 1B), which suggests extensive morphogenetic movements involving the migration of the mouthparts to the anterior. Both these morphogenetic movements and the formation of the dorsal head capsule of the first larval instar have remained enigmatic.

Embryonic pattern formation is best understood in *Drosophila melanogaster*. The patterning of the maxillary and labial segments occurs through the same segmentation cascade as in the trunk involving maternal morphogens, gap-, pair-rule and segment polarity genes (Nakano et al., 1989; Pankratz and Jackle, 1990; St Johnston and Nusslein-Volhard, 1992). Segment identity is specified by the action of

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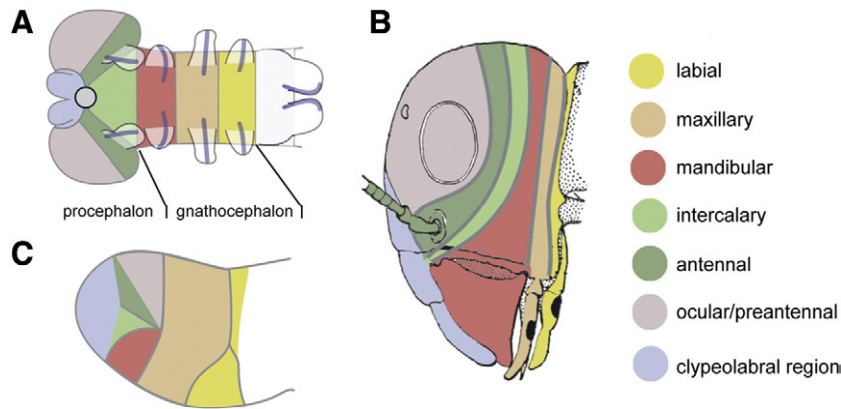


Fig. 1. Contribution of head segments to lateral and dorsal portions of the insect head—opposing views based on morphological data and *Drosophila* work. (A) In the embryo, the segments of the gnathocephalon (labial, maxillary, mandibular segments) are established similar to the more posterior trunk segments. The procephalon is composed of the intercalary and antennal segments and the preantennal region including the ocular segment and the labrum. In insects, the intercalary segment lacks appendages. (B) Morphological and molecular data confirm that the labial and maxillary segments contribute to the dorsal portion of the posterior head (dorsal ridge). The segment boundary between these segments is morphologically visible in adult heads (postoccipital suture). All other head sutures most likely do not reflect segment boundaries. Therefore, the depicted contribution of the more anterior segments to the dorsum of the head is speculative. Taken from Snodgrass (1935) and Weber (1966) with minor modifications: the antennal segment has been included as *bona fide* segment (in contrast to Snodgrass) and the disputed nonsegmental acron and/or labral segment are not depicted (in contrast to Weber). (C) An alternative model that does not invoke dorsal closure movements of the anterior head segments. This view is based on *engrailed* stainings in *Drosophila* and *Oncopeltus* and the phenotype of *Drosophila* head segments that have been partially transformed into abdominal identity by ectopic *Ubx* expression (Rogers and Kaufman, 1996). Schematically depicted is the cuticle shown in Rogers and Kaufman (1996) with the grey boundaries representing the *engrailed* staining. The separation of the antennal and ocular regions is arbitrary. All remaining anterior tissues have been assigned to the clypeolabral anlagen. The contribution of labial tissue posterior to the dorsal ridge *engrailed* stripe is based on *Tc-scr* expression posterior to this stripe (Shippy et al., 2006).

homeotic selector genes of the HOX cluster (Lawrence and Morata, 1994; Lewis, 1978; McGinnis and Krumlauf, 1992). Also in *Tribolium*, the formation of gnathal segments and the specification of their identity appear to rely on the same mechanisms as in the trunk (Beeman et al., 1993; Brown et al., 2002; Choe and Brown, 2007; Choe et al., 2006; Maderspacher et al., 1998; Tomoyasu et al., 2005). In contrast, the pregnathal region is patterned differently, e.g., without pair-rule function. In *Drosophila*, a set of head gap genes is required for proper pregnathal segment polarity gene expression (Cohen and Jurgens, 1990; Crozatier et al., 1999; Grossniklaus et al., 1994; Wimmer et al., 1993, 1997). The identity of these segments is specified largely independently from HOX genes, since the intercalary is the anterior-most segment expressing a HOX cluster gene, the *Hox1* ortholog *labial* (Merrill et al., 1989; Nielsen, 2001).

Molecular studies designed how the dorsal head is formed in *Drosophila* have been hampered by the extensive morphogenetic movements and reductions associated with head involution, whereby the larval head becomes internalized into the thorax (Akam, 1989; Jurgens et al., 1986; VanHook and Letsou, 2008; Younossi-Hartenstein et al., 1997). Experiments based on ectopic *Dm-Ultrabithorax* (*Ubx*) expression in *Drosophila* indicate that segments anterior to the maxillary segment do not undergo dorsal closure. Actually, the border between the head and the thorax, the Dorsal Ridge (Dr I), which is composed of parts of the labial and maxillary segments, is thought to be the anterior-most tissue capable of adapting a dorsal identity by means of dorsal closure movements (Gonzalez-Reyes and Morata, 1991; Rogers and Kaufman, 1996, 1997). How then is the dorsal head cuticle formed? Rogers and Kaufman (1996) suggest that the dorsal cells of maxillary, mandibular, intercalary, and antennal segments (Dorsal Ridge II; Dr II) fold to join the Dr I and thus close the cephalic region. This leads to an arrangement in which ocular and antennal tissues end up dorsal to intercalary and mandibular tissues (Fig. 1C) (Rogers and Kaufman, 1996). This view is different from the classical model (Fig. 1B), but it is largely based on a rather artificial situation, where the embryonic head segments have been homeotically transformed to abdominal identity by misexpression of the Hox gene *Ubx*. These transformed segments behave—at least in part—like abdominal segments, and hence, they do not undergo head involution but form denticle belts like abdominal segments. These have been used to infer the location of segmental boundaries (Fig. 1C).

It remains unclear which tissues form the dorsal or lateral portions of the head capsule in a typical insect head. This is especially true with respect to the contribution of the intercalary segment to the larval cuticle, since it has no landmarks, e.g., appendages that can be followed throughout development. Also the function of *labial* is difficult to analyze because in *Drosophila labial* mutants, head involution is defective leading to several secondary defects, which obscure any direct effects (Merrill et al., 1989). It has been suggested, though, that the intercalary segment contributes to lateral and ventral regions of the larval pharynx (Rogers and Kaufman, 1997). Also the embryonic hypopharyngeal lobes have been assigned to the intercalary segment; however, a mandibular origin has also been suggested (Economou and Telford, 2009; Mohler et al., 1995). RNAi experiments in the milkweed bug *Oncopeltus fasciatus* with its non-involved head have not revealed any phenotype (Angelini et al., 2005).

In order to discover the contribution of the intercalary and gnathal segments to the insect head, we have analyzed the red flour beetle *Tribolium castaneum*. *Tribolium* larvae have a fully developed head and well-formed external mouthparts (Bucher and Wimmer, 2005). Furthermore, a detailed map of bristles of the first larval instar head provides landmarks for mapping patterning defects in dorsal and lateral portions of the head (Schinko et al., 2008). Extensive work has been done on *Tribolium* Hox gene function both using mutants and RNAi knock down analysis (Brown et al., 2000, 2002; Curtis et al., 2001; DeCamillis and French-Constant, 2003; DeCamillis et al., 2001; Denell et al., 1996; Shippy et al., 2006, 2008a; Tomoyasu et al., 2005) including the analysis of a deletion mutant removing most of the Hox cluster but leaving *Tc-labial* intact (Beeman et al., 1989; Stuart et al., 1991). Unfortunately, a mutant defective at the *Tc-labial* locus has not been available. Hence, to our knowledge, no *Tc-labial* phenotype has been described for any arthropod except for *Drosophila*.

In this study, we find that RNAi against the *Hox1* ortholog *Tc-labial* leads to the deletion of the intercalary segment in the embryo and of lateral portions of the head cuticle. Mutant and RNAi phenotypes of pair-rule and gap genes that interfere with gnathal segment development suggest that the gnathal segments do not significantly contribute to the dorsal head capsule. Finally, we propose a “bend and zipper” model of how the insect head capsule is formed.

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