

## Review article

## Genetics, development and composition of the insect head – A beetle's view

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## ARTICLE INFO

## Article history:

Received 19 March 2010

Received in revised form

8 August 2010

Accepted 15 August 2010

## Keywords:

Labrum

Acron

Intercalary

Bend and zipper

Orthodenticle

six3

## ABSTRACT

Many questions regarding evolution and ontogeny of the insect head remain open. Likewise, the genetic basis of insect head development is poorly understood. Recently, the investigation of gene expression data and the analysis of patterning gene function have revived interest in insect head development. Here, we argue that the red flour beetle *Tribolium castaneum* is a well suited model organism to spearhead research with respect to the genetic control of insect head development. We review recent molecular data and discuss its bearing on early development and morphogenesis of the head. We present a novel hypothesis on the ontogenetic origin of insect head sutures and review recent insights into the question on the origin of the labrum. Further, we argue that the study of developmental genes may identify the elusive anterior non-segmental region and present some evidence in favor of its existence. With respect to the question of evolution of patterning we show that the head Anlagen of the fruit fly *Drosophila melanogaster* and *Tribolium* differ considerably and we review profound differences of their genetic regulation. Finally, we discuss which insect model species might help us to answer the open questions concerning the genetic regulation of head development and its evolution.

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## 1. Introduction

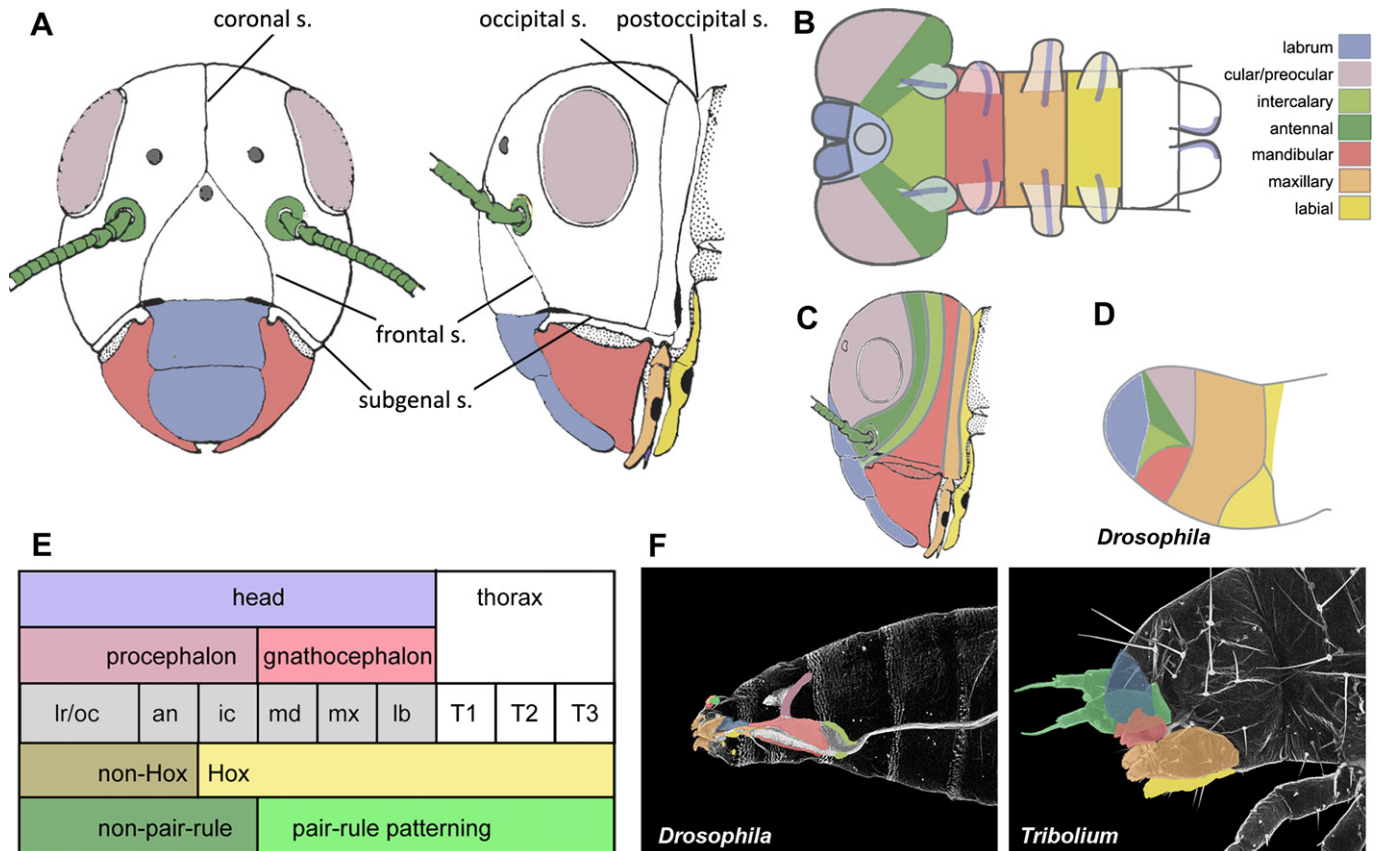
## 1.1. Building blocks of the insect head

The insect head functions as anterior sensory and feeding center of the animal, harboring essential structures like the brain, complex eyes and ocelli, antennae and the mouth opening. It is composed of several specialized and fused segments and is movable relative to the trunk. We will use the term segment in the sense of a unit serially homologous to trunk segments. Based on this at least 5 segments contribute to the head. The three posterior segments (labial, maxillary and mandibular) form the gnathocephalon carrying the gnathal appendages which are located around the mouth opening and are essential for food uptake (Fig. 1A). The respective three segmental ganglia fuse to form the subesophageal ganglion of the brain. Also the intercalary and antennal segments are clearly serially homologous to trunk segments and they contribute to the procephalon (Brusca and Brusca, 2003; Snodgrass, 1935; Weber, 1966). The boundary between antennal and ocular regions has many similarities with trunk parasegment boundaries and has hence been called the ocular parasegment boundary, which

in turn has been interpreted as indication for the presence of an ocular segment, (e.g., by Rogers and Kaufman, 1996, 1997; Schmidt-Ott et al., 1994). Scholtz more cautiously proposes using the term “ocular/protocerebral region” rather than “ocular segment” (Scholtz and Edgecombe, 2006) – a view we would like to adopt but for the sake of simplicity we will call it “ocular region”. Besides segmental contribution, also an anterior non-segmental region called acron is thought to contribute to the head. Another enigmatic structure is the labrum that constitutes the anterior border of the preoral cavity. One reason for the ongoing debate on the segmental composition of the insect head is the lack of unequivocal morphological correlates to segment boundaries. Some head sutures (cuticular inflexions) are found in many (but not all) insects but only the postoccipital suture is thought to correspond to a segment boundary (i.e. the maxillary/labial boundary) (Fig. 1A) (Snodgrass, 1935; Weber, 1966). The coronal suture separates left and right parts of the dorsal head (vertex) and anteriorly splits into the two frontal sutures which enclose an inverted V shaped tissue enclosing the frons. Together, these three sutures form an inverted “Y” and are called the “epicranial suture”. Interestingly, the epicranial suture appears to be used for eclosion during ecdysis in many insects (Weber, 1966). Finally, the subgenal suture separates the lateral part of the head (gena) from the ventrally located gnathal appendages. The evolutionary or ontogenetic origin of the sutures remains enigmatic.

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**Fig. 1.** Composition and fate maps of the insect head. In all panels, the color code for specific segments is the same. (A) The insect head is composed of several segments. The gnathocephalon is built by the labial, maxillary and mandibular segments, the appendages of which surround the mouth opening. From the front, the preoral cavity is covered by the labrum. The procephalon is built by intercalary, antennal segments and the ocular region – a non-segmental contribution is disputed. Note that the antennae are located dorsal to the gnathal segments and the eyes are posterior to the antenna while in the flattened embryo (B) these segments are anterior to the gnathal segment. Several sutures (i.e. cuticular inflexions) are usually found on insect heads. Only the postoccipital suture is thought to correspond to a segment boundary. The coronal and frontal sutures together form a “Y”. (B) In the flattened embryo, the segmental composition is clearly distinguishable. Note the “V” shaped tissue harboring the labrum and the mouth opening (blue tissues). (C) The classical head fate map proposes that the insect dorsal and lateral head – like the trunk – is built by the dorsal parts of the gnathal segments. (D) A different composition is seen in *Drosophila* L1 larvae with their head segments transformed to abdominal identity. They do not undergo head involution and in this artificially everted head, the maxillary and labial segments fuse dorsally and form the dorsal ridge which is the anterior-most part undergoing trunk like dorsal closure. The more anterior segments do not perform trunk like dorsal closure. (E) Schematic of the subdivision of the insect head. The gnathocephalon is largely patterned like the trunk by pair rule input. The anterior-most segment, the identity of which is determined by genes of the Hox cluster is the intercalary segment. The patterning mechanism of the procephalon is not well understood. (F) Because of its involutioned head, the *Drosophila* L1 larval head is scarce in markers. The insect-typical head of *Tribolium* has all mouth parts in the ancestral biting condition and the setae and bristles on dorsal and lateral head capsule provide ample markers for phenotypic cuticle analysis. an: antenna, ic: intercalary, lb: labium, lr/oc: preocular region comprising the labrum Anlagen, md: mandible, mx: maxilla.

## 1.2. Diversity and evolution of the insect head

Insects are a monophyletic group. Therefore, all head morphologies observed in extant insects are derived from one ancestral form. Indeed, a tremendous diversity of head forms has evolved that show many crucial adaptations to different life styles. The ancestral orthognath (hypognath in some English literature (Snodgrass, 1935; Weber, 1966)) situation with biting mouth parts facing towards the ground (shown in Fig. 1A, Orthoptera, model system: *Gryllus bimaculatus*) has been modified to morphologies with the mouth being directed anteriorly (prognath; many Coleoptera, model system: *Tribolium castaneum*) or posteriorly (hypognath; many Hemiptera, model system: *Oncopeltus fasciatus*). Moreover, the feeding apparatus has been adapted to various derived life styles e.g. for sucking (e.g. *O. fasciatus*) or licking (e.g. *Drosophila melanogaster*). Other changes of the head capsule involve the anterior elongation (e.g. snout beetles) or lateral extension of the anterior parts of the capsule (e.g. stalked eyed flies) and many others. The genetic basis for these differences is only poorly studied.

The arthropod head evolved in a process called cephalization. Starting from an ancestor with homonomous segmentation, more

and more trunk segments became fused to the putative anterior non-segmental region called acron (Snodgrass, 1935; Weber, 1966) harboring the ancestral brain (archicerebrum). In some arthropod taxa, more segments have fused to form the anterior-most tagma than in others. Therefore, the insect head as a whole is not homologous to anterior tagmata of other arthropods, while the segments involved can be clearly homologized e.g. by the expression of Hox genes (Abzhanov and Kaufman, 1999; Damen et al., 1998; Eriksson et al., 2010; Hughes and Kaufman, 2000; Jäger et al., 2006; Janssen and Damen, 2006; Rogers et al., 2002; Telford and Thomas, 1998).

## 1.3. Developing answers for an endless dispute

Despite extensive efforts of many skillful morphologists, several questions with respect to the insect head morphology have remained open (extensively reviewed in Rempel, 1975; Scholtz and Edgecombe 2006 and Rogers and Kaufman, 1997). In the light of recent molecular data, this discussion has boiled down to a few key questions: Does a labral segment exist? Does an acron (i.e. non-segmental anterior region) exist and if so, what parts does it

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