Segmentation gene expression in the housefly *Musca domestica*

RALF SOMMER* and DIETHARD TAUTZ*

Institut für Genetik and Mikrobiologie, Universität München, Maria-Wardstrasse 1a, 8000 München 19, FRG

*Present address: Institut für Zoologie, Universität München, Luisenstr. 14, 8000 München 2, FRG

Summary

*Drosophila* and *Musca* both belong to the group of higher dipteran flies and show morphologically a very similar early development. However, these two species are evolutionary separated by at least 100 million years. This presents the opportunity for a comparative analysis of segmentation gene expression across a large evolutionary distance in a very similar embryonic background. We have analysed in detail the early expression of the maternal gene *bicoid*, the gap genes *hunchback*, *Krüppel*, *knirps* and *tailless*, the pair-rule gene *hairy*, the segment-polarity gene *engrailed* and the homoeotic gene *Ultarbithorax*. We show that the primary expression domains of these genes are conserved, while some secondary expression aspects have diverged. Most notable is the finding of *hunchback* expression in 11–13 stripes shortly before gastrulation, as well as a delayed expression of terminal domains of various genes. We conclude that the early developmental gene hierarchy, as it has been defined in *Drosophila*, is evolutionary conserved in *Musca domestica*.

Key words: *Musca domestica*, development, segmentation gene evolution.

Introduction

Extensive genetic and molecular studies have led to a detailed insight into the processes underlying pattern formation in *Drosophila* (reviewed by Ingham, 1988). Segmentation of the *Drosophila* embryo depends on the successive activities of several classes of genes. On top of the hierarchy are the maternal genes, which provide the positional information for the expression of the zygotic gap genes. The gap genes in turn regulate the expression of the pair-rule and segment-polarity genes, which eventually subdivide the embryo into its segmental units. The segmental units are then specified by the homoeotic genes.

The genes involved in the segmentation process in *Drosophila* have been identified on a functional basis in appropriate mutagenesis screens. Cloning and expression analysis of these genes has yielded a very detailed understanding of the molecular interactions involved in the early pattern formation process in *Drosophila*. It is, therefore, now of great interest to ask, whether these molecular interactions have been conserved in evolution. However, it seems unreasonable to perform a similar extensive genetic screen, as in *Drosophila*, for any other insect system. Instead, one should be possible to make these inferences on the basis of the expression analysis of the homologous genes in other species. This requires, first, to find the homologous genes and, second, to assume that they have homologous functions. Such an assumption can be tested, if the first step in the analysis is the comparison of the expression of homologous genes in a species that shows a homologous embryonic development.

We have therefore compared the expression domains of several key genes of the segmentation gene hierarchy of the two higher dipteran fly species *Drosophila* and *Musca*. Though the two species are evolutionary separated by probably at least 100 million years (Hennig, 1981), the morphology and the early embryology of the higher dipterans are very similar (Weismann, 1866). The only difference so far detected is the mitosis behavior of the blastoderm nuclei (Lundquist, 1981; Sommer and Tautz, 1991), which is most likely not related to the segmentation process (van der Meer et al. 1982). One could expect that the molecular mechanisms that lead to the segmentation of the embryo should be conserved. On the other hand, a divergence of the primary segmentation gene expression pattern seems also a theoretical possibility. We know that redundant segmentation pathways exist in *Drosophila* (Hülskamp and Tautz, 1991) and one could, therefore, imagine that these are subject to modification during evolution. One particular function of a gene could for example be lost in favor of the redundant function of another gene and one would then expect a diverged expression pattern of the respective genes. We believe that it is important to test the assumption of homologous segmentation gene expression in a homologous embryonic background.

A recurrent feature of most of the segmentation genes in *Drosophila* is that they are not only involved in...
the segmentation process, but that they are also expressed in various other domains and tissues. These so-called secondary expression aspects can have various functions; some may, however, be functionless. A previous comparison of the expression of the gap gene *hunchback* in *Drosophila melanogaster* and *Drosophila virilis* (Treier et al. 1989) has revealed that these secondary expression domains may become modulated during evolution. The comparison of *Drosophila* and *Musca* should, therefore, give a further insight into the significance of some of these secondary expression domains.

Our results show that the primary expression domains of the segmentation genes are indeed very similar in the two species, indicating that the genes are functionally equivalent. This is in part also true for the secondary expression domains. There are, however, some divergent aspects including differences in the intensity and the timing of expression, as well as the appearance of completely new expression domains.

### Materials and methods

#### Cloning and sequencing

The homologs of the maternal gene *bicoid* as well as of the gap genes *hunchback*, *Krüppel*, *knirps* and *tailless* were cloned by PCR (polymerase chain reaction; Saiki et al. 1988) using the following primers (all in 5'-3' direction, redundant nucleotides in brackets):

- **hunchback** - CA(C,T)GGCA(A,G,A)ATGAA(G,A)AA(C,T)TTA(G,A)TTA(G,A)TTA(C,T)AA
- **tailless** - GCATG(T,C)AA(A,G,A)AA(C,T)TGAA(T,G,G)C(T,C)TGAA(T,G,G)C(T,C)TGAA(T,G,G)C(T,C)TTA(T,G)TACAT

The PCR reaction was done using 100 ng genomic DNA in a 20 ml reaction volume. The reaction mixture was subjected to 15 cycles of 1.5 min at 94°C, 2 min at 50°C, 2 min at 72°C and an additional 15 cycles as above, but with 4 min at 72°C to account for the increasing loss of polymerase activity. The primary PCR products were separated on an agarose gel, which was blotted and hybridized under low stringency conditions (washed with 2×SSPE at 65°C, 1×SSPE=180 mM NaCl, 10 mM sodium phosphate pH 7.0, 1 mM EDTA) with the homologous fragment from *Drosophila*. If a signal was seen, the appropriate sized region was isolated from a duplicate gel and subjected to another round of PCR amplification. This second round normally yielded enough DNA for cloning into an M13 vector. For this purpose, the PCR reaction was incubated with 2.5 i.u. Klenow polymerase for 15 min in order to produce blunt ends. The mixture was then run on an agarose gel and the appropriate fragment was isolated. Since the fragments will be flanked by primers that lack a 5'-phosphate group, it is necessary to treat the fragments with polynucleotide kinase before ligating them into the dephosphorylated vector (M13 mp19 cut with Smal). Since the kinase and the ligase work in very similar buffers, this can conveniently be done in a single tube. A ligation reaction is set up without adding the vector and the ligase, but 1 i.u. kinase is added. This mixture is incubated for 15 min at 37°C and the kinase is destroyed by incubation for 10 min at 65°C before adding the vector and the ligase.

The ligation reaction was transformed into XL-1 blue cells (Stratagene) and the resulting plaques were transferred onto nitrocellulose filters in duplicate. One filter was hybridized under low stringency (final wash with 2×SSPE, 65°C) and one under high stringency (final wash with 0.1×SSPE, 65°C) with the homologous *Drosophila* fragment. This double hybridization makes it possible to distinguish between real clones and *Drosophila* contaminants, which are a frequent problem.

Positive clones were sequenced by the dideoxy method from single stranded M13 templates. It is known that sequences obtained from PCR generated cloned fragments are not completely reliable. However, the error rate in our experience is at most 1 to 2 base exchanges per kb, which we consider acceptable for our purpose. Furthermore, the sequences for *hunchback*, *Krüppel* and *knirps* were derived from at least two independent PCR reactions and were found to be identical.

#### Stocks and expression analysis

The flies (*Musca domestica* L., courtesy of Professor Engels, University of Tübingen and of Professor Kirschfeld, MPI für Kybern. Tübingen) were kept according the description of Wügler (1974). Eggs were collected on a mixture of yeast, wheatgerm and curd cheese at 25°C. Embryonic development until hatching takes 24 h for our laboratory strain, similar to that for *Drosophila*. *Musca* eggs are about 1 mm in length (0.4 mm in *Drosophila*), but are not much thicker than *Drosophila* eggs. The eggs were dechorionated in 2.5% NaOCl for 5 min. Fixation, removal of the vitelline membranes and whole-mount hybridization (Tautz and Pfeifle, 1989) was done as described for *Drosophila* but with the following modifications: fixation was for 40 min and Proteinase K treatment was done for 6 min. As probes, we used the isolated fragments of the respective genes labeled by the random priming method with digoxigenin as described (Tautz and Pfeifle, 1989). Antibody stainings were also done according to standard *Drosophila* protocols (McDonald and Struhl, 1986), using antisera that were raised against the *Drosophila* segmentation-gene products. The *hunchback* serum is described in Tautz (1988), the *engrailed* serum in Patel et al. (1989) and the *hairy* serum was a gift from Ken Howard (New York).

### Results

#### Cloning of the genes

PCR is a useful method to clone homologous genes from other species, since only short regions of
homology are required for the annealing of the primers (Saiki et al. 1988). We could show that even these short regions need not be completely conserved (Sommer and Tautz, 1989). The only requirement appears to be a complete conservation of three nucleotides at the 3'-end of the primer and a 50–60% match over the remainder of the primer. The choice of a suitable homologous region for the primers depends on the gene of interest. bicoïd contains a homeobox (Frigerio et al. 1986; Berleth et al. 1988), while hunchback and Krüppel contain DNA-binding finger regions of the Cys–Cys/His–His type (Tautz et al. 1987; Rosenberg et al. 1986) and knirps and tailless contain DNA-binding finger regions of the Cys-only type (Nauber et al. 1988; Pignoni et al. 1990). Since these regions are mandatory for the function of the proteins, they are expected to be most conserved. This expectation is supported by a comparison of the homologous bicoïd gene from Drosophila pseudoobscura (Seeger and Kaufman, 1990) as well as by the comparisons of the hunchback and knirps genes from Drosophila virilis (Treier et al. 1989; Neumann and Jäckle, personal communication). For bicoïd, we have chosen primers that lie within the homeobox and, for hunchback and Krüppel, we have chosen primers that lie at the beginning and at the end of the first finger domain. For knirps and tailless, only the proximal primers were chosen in the finger domain, while the distal primer for knirps was chosen in a region that is conserved in the Drosophila virilis homolog of knirps (Neumann and Jäckle, personal communication) and, for tailless, in a region that shows homology to the ligand binding domain of steroid hormone receptors (Pignoni et al. 1990). The relative locations and the sequences of the primers, as well as the sequences of the amplified fragments are shown in Fig. 1.

The protein sequences in the finger regions of Krüppel and hunchback are highly conserved between the two species (Fig. 1). Most conserved is the Krüppel sequence with only one amino acid change out of 74 analysed (1.4% divergence), hunchback shows 11 changes out of 106 (10.4% divergence). The bicoïd homeobox box shows 6 changes out of 44 analysed (13.6% divergence), which is an unusually high divergence for a homeobox homolog (Akam, 1989). The knirps sequence is conserved only in the finger region as well as in the so-called ‘knirps box’ (Rothe et al. 1989). The remainder of the sequence is highly diverged with a number of insertions/deletions, which make the calculation of a divergence score difficult. In spite of this, we believe that the knirps sequence represents the true knirps homolog from Musca, since the 3'-primer was chosen in a region that occurs neither in knirps-related (Oro et al. 1988) nor in embryonic gonad (Rothe et al. 1989), which are the two other genes known to carry the ‘knirps-box’ (Rothe et al. 1989). The tailless primer was chosen at the very end of the finger domain and we can, therefore, make no statement about its conservation. The general conservation of the amplified fragment is however clearly higher than that of the equivalent knirps region, though it shows also some deletions/insertions.

bicoïd bicoïd has been classified as a maternal coordinate gene, which organizes the segmentation pattern of the anterior region of the embryo (Frohnhofer and Nüsslein-Volhard, 1986). Its RNA is localized maternally in the anterior tip of the oocyte (Berleth et al. 1988). This RNA is translated during early development and the protein product diffuses towards the posterior forming a morphogenetic gradient across the anterior two thirds of the embryo (Driever and Nüsslein-Volhard, 1988).

hunchback hunchback has been originally classified as a gap gene, but it has since become clear that it has also a maternal function (reviewed in Hülskamp and Tautz, 1991). Maternal hunchback RNA is at first homogeneously distributed in the freshly laid egg, but is then progressively degraded from the posterior end. The reason for this degradation appears to be the translational inhibition of this RNA in response to maternal posterior factors. The result of this inhibition is an early anterior–posterior gradient of hunchback protein distribution. This gradient is required for the correct spatial expression of the gap genes Krüppel and knirps (Hülskamp et al. 1990). The morphogenetic function of this gradient can, however, be functionally substituted in Drosophila by the zygotic expression of hunchback. It is possible to remove genetically the maternal hunchback expression and still get fully viable larvae (Lehmann and Nüsslein-Volhard, 1987; Hülskamp et al. 1989; Irish et al. 1989; Struhl, 1989). It was, therefore, particularly interesting to see whether this seemingly dispensable maternal expression of hunchback occurs in Musca as well. Fig. 3 shows that this is indeed the case. The RNA is synthesized in the nurse cells in a similar way in both species (Fig. 3A,B). The freshly laid Musca egg shows a homogeneous distribution of this RNA, which later on is degraded from the posterior (Fig. 3C). Antibody staining reveals that the protein is distributed in a similar gradient as in Drosophila (Fig. 3D). This shows that the maternal hunchback expression is fully conserved, inspite of being functionally redundant in Drosophila.

The comparison of the zygotic expression of the hunchback RNA is shown in Fig. 4. hunchback is expressed at early blastoderm stage in the anterior half of the embryo (Fig. 4A,F). In Drosophila, this expression is directly dependent on the maternal bicoïd gradient (Driever and Nüsslein-Volhard, 1989) and is correlated with the gap gene function of hunchback (Hülskamp and Tautz, 1991). There is a secondary
expression of hunchback at blastoderm stage, which occurs in several stripes in Drosophila (Tautz and Pfeifle, 1989). Two of these stripes, the posterior one and the 'parasegment 4 (PS4)-stripe' (Hülskamp and Tautz, 1991) are similarly seen in Musca (Fig. 4B,G). These two stripes of expression can be correlated with specific segmentation defects in Drosophila, while the more anterior stripes have no known function. Interestingly, the most anterior stripe appears in Musca as well, but its expression is clearly delayed and occurs only towards the end of blastoderm stage (Fig. 4C). With the beginning of gastrulation, Musca shows a novel expression pattern of hunchback in 11-13 (depending on whether the PS4 stripe and the posterior stripe are included or not) of somewhat irregular stripes (Fig. 4D,E). Such an expression pattern is not known for any other segmentation gene, including the segment-polarity genes, which would be expressed in at least 14 stripes and more regularly (compare the engrailed expression below). It is thus completely unclear what function this expression of hunchback might have, if it has any.
Segmentation genes in Musca

Krüppel
The Krüppel expression starts with a broad domain in the middle of the embryo, similar to that in Drosophila (Fig. 5A, E). This domain splits up in several stripes at late blastoderm stage, which is evident in both, Drosophila and Musca (Fig. 5D, H). As with hunchback, Krüppel shows also secondary expression domains at late blastoderm stage, namely in an anterior stripe and in a posterior cap (Knipple et al. 1985). The anterior stripe is also readily seen in Musca (Fig. 5B), though it is much narrower than in Drosophila. In contrast, the expression in the posterior cap is delayed in Musca and becomes very weakly visible only towards the end of blastoderm formation (Fig. 5D). Krüppel expression in this region is required for the development of the Malpighian tubules in Drosophila (Hartbecke and Janning, 1989; Gaul and Weigel, 1991).

kniirps
The posterior kniirps expression domain, which is associated with the kniirps phenotype in Drosophila, appears at nuclear cleavage stage 13 in Musca, where its posterior border coincides with the border region of a domain of delayed mitosis in this species (Fig. 6A; Sommer and Tautz, 1991). It is, however, not clear whether this is of functional significance. The expression in this domain ceases at late blastoderm stage, similar to that in Drosophila (Fig. 6C, F). The secondary kniirps expression in Drosophila includes first an anterior cap with a dorsoventral asymmetry and later a narrow stripe in the region of the developing head fold (Rothe et al. 1989). The function of these expression domains is unknown, since they are not associated with a phenotype in kniirps mutant embryos. Nonetheless, both expression patterns can similarly be observed in Musca, though the exact shape of the stripe and of the cap are somewhat different (Fig. 6C, F).

tailless
Tailless is a gap gene that is regulated by the terminal maternal system. In Drosophila it first appears in two more or less symmetrical caps covering the termini of the embryo (Pignoni et al. 1990). Later at blastoderm stage, the anterior domain forms a stripe with a dorsoventral asymmetry, while the posterior domain persists as a cap of expression (Fig. 7B). The Musca expression pattern differs in several aspects. First, the

Fig. 2. bicoid expression in Musca during oogenesis (A) and in the early embryo (B). Note the essentially homogeneous distribution of bicoid RNA in the nurse cells, which is in contrast to the situation in Drosophila (St Johnston et al. 1989).

Fig. 3. Maternal expression of hunchback. hunchback RNA can be detected in the nurse cells during oogenesis in a similar pattern both in Musca (A) and in Drosophila (B). hunchback RNA (C) and protein (D) distribution during the first cleavage stages of Musca embryos. The RNA is almost homogeneously distributed, while the protein forms a clear anterior-posterior gradient in the posterior half of the embryo, similar to that observed in Drosophila (Tautz, 1988).
expression appears to be generally much weaker, as we can judge from the comparison of signal intensities of equivalent probes from other genes in parallel experiments. This is in line with the observation that the signal intensities of terminal expression aspects of the other segmentation genes are also weaker. But also the pattern itself shows remarkable differences. We observe an additional stripe of expression in the anterior region, while the posterior expression domain forms a stripe with a dorsoventral asymmetry, rather than a cap. These differences point to a more complex regulation of tailless in Musca (see discussion).

hairy and engrailed
The pair-rule gene hairy belongs to the class of primary pair-rule genes in Drosophila, that are directly con-
Musca

![Segmentation genes in Musca](image)

---

Drosophila

![Segmentation genes in Drosophila](image)

---

Fig. 5. Comparison of the RNA expression pattern of Krüppel between Musca and Drosophila. Progressively older embryos are shown from the top to the bottom. (A,E) early blastoderm, (B,F) mid blastoderm, (C,D,G,H) late blastoderm. Note that the posterior Krüppel expression domain is only very weak and appears rather late in Musca.

trolled by the gap gene products (reviewed by Carroll, 1990). It is expressed in seven stripes and in a region in the head (the ‘head patch’; Ingham et al. 1985). The seven stripes can be correlated with the segment defects seen in hairy mutant embryos, while the head patch can be correlated with specific head defects (Hooper et al. 1989). We have used antibodies raised against the Drosophila hairy protein to stain Musca embryos. Seven stripes can be seen at late blastoderm stage, but the relative timing of the appearance of some of the stripes appears to be different for the two species. Stripe 6 is expressed earlier in Musca and is also much broader (Fig. 8A,C). However, it becomes narrower later on and the final stripe pattern is very similar in the two species (Fig. 8B,D). A clear difference exists with respect to the head patch. It is not detectable in Musca during the early stages (Fig. 8A) and occurs only very weakly at the end of blastoderm stage (Fig. 8B).

The segment-polarity gene engrailed represents a gene from the last step of the segmentation gene cascade (Ingham, 1988). engrailed expression in Musca can be detected using the universal monoclonal
Fig. 6. Comparison of the RNA expression pattern of *knirps* between *Musca* and *Drosophila*. Progressively older embryos are shown from the top to the bottom. (A,D) early blastoderm, (B,E) mid blastoderm, (C,F) late blastoderm. Note the region of delayed mitosis, which is evident in the *Musca* embryo in (A) (marked with an arrowhead).

**Discussion**

Molecular techniques make it easy to clone homologs of the *Drosophila* segmentation genes from a variety of different species and to analyse their expression patterns in these species. However, since a functional analysis will not be possible in most cases, one has to rely on the comparative analysis of the expression domains of the various genes. This analysis will then allow conclusions to be drawn on the interactions among the genes in the system under investigation, if one assumes that homologous genes have homologous functions. This is, however, not a trivial assumption. The analysis of *engrailed* expression in different species has, for example, shown that although *engrailed* may be involved in the segmentation process in other Arthropods, it may have different functions in the other phyla (Patel et al. 1989). It is thus necessary to show step by step that homologous functions can be assumed for the various genes.

The comparison of the expression pattern of segmentation genes between *Musca* and *Drosophila* is a useful
first step in this analysis. In spite of their similar embryology, the evolutionary distance between these two species is very great and any specially adapted or nonfunctional expression aspects should have diverged. The principal expression domains that are involved in setting up the segmentation pattern should however, be conserved. Our results show that this expectation largely holds true. All of the analysed key genes of the segmentation gene hierarchy show similar primary expression patterns, both with respect to the relative timing and with respect to the relative positioning of their expression domains. It is, therefore, safe to conclude that their functional interactions in the segmentation gene cascade should be conserved as well.

The comparative analysis of the expression patterns of the segmentation genes also allows some more detailed conclusions to be drawn. Most interesting is the finding that the maternal expression of hunchback occurs in a similar way in both species. This expression seemed, superficially, a likely candidate for divergence, since in Drosophila, it is possible to genetically remove it without apparent detrimental effects on the development of the embryo (Lehmann and Nüsslein-Volhard, 1987). The reason for this is that the early zygotic expression of hunchback can fully substitute for the maternal one (reviewed in Hülskamp and Tautz, 1991), a case of redundant control of developmental processes. We have, however, previously argued that, since the maternal hunchback expression mediates the effect of the posterior maternal system (Hülskamp et al. 1989; Irish et al. 1989; Struhl, 1989), it may be the evolutionarily older one (Hülskamp et al. 1990). The finding that this seemingly fully redundant system is conserved in Musca is in line with this conclusion.

hunchback shows a diverged pattern at late blastoderm stage. A seemingly segmental expression of hunchback occurs in Musca, which is never observed in Drosophila. This expression is very unusual, since it
Fig. 9. Comparison of the protein expression pattern of *engrailed* between *Musca* and *Drosophila*. (A,C) embryos at the beginning of germ band extension, (B,D) embryos at the end of germ band extension. Note the evolution of the pattern from anterior towards posterior, as it is evident in the comparisons of the upper and the lower embryos.

Fig. 10. Comparison of the RNA expression pattern of *Ultrabithorax* between *Musca* and *Drosophila*. (A,C) late blastoderm stage, (B,D) embryos after germ band extension. The parasegments showing the *Ultrabithorax* expression are labeled with the appropriate numbers. Note that the *Musca* embryo in (B) has not yet fully completed the germ band extension.

does not occur throughout the whole segmented region and since the stripes are fairly irregular. It remains unclear which function it might have, if it has any at all. The observation of this fully diverged pattern strengthens the assumption that the evolutionary divergence of the two species is large enough to allow the acquisition or the loss of completely new expression pattern elements.

The *tailless* expression pattern also shows some interesting deviations, in particular in its posterior domain. In *Drosophila*, it is assumed that this domain is directly activated by the terminal *torso* activity (Pignoni et al. 1990), which may provide a short-range gradient. Accordingly, a homogeneous cap of expression is seen across the whole region where the activation takes place. This regulation is clearly more complex in
Musca, since some kind of repression effects must be effective at the ventral side of this domain, as well as at the terminal tip of the embryo. Nonetheless, these differences may not be significant for the function of tailless, since its activity is not required at the terminal tip, which is the domain of action of the gap gene huckebein in Drosophila (Weigel et al. 1990). The additional stripe of expression in the anterior region is also indicative of a more complex regulation of tailless in Musca, since it is difficult to reconcile this with a simple interaction with the terminal regulatory system.

There are also some differences in the expression of the other genes. Most notable is a delayed and weaker expression of several terminal domains. We have shown this for the posterior Krüppel domain, for the most anterior hunchback stripe and for the anterior head patch of hairy. In addition, we have also observed a delayed and weakened expression of the terminal homeotic gene forkhead and for the posterior blastoderm stripe of the caudal gene product (not shown). These expression domains are regulated by the terminal maternal system in Drosophila. It seems possible that the mode of the terminal development is somewhat altered in Musca. On the other hand, the terminal regulation aspects that are involved in the primary segmentation process and that depend on tailless, namely the setting of the posterior boundary of knirps expression (Pankratz et al. 1990) and the regulation of the posterior hunchback stripe (Casanova, 1990) appear not to be changed, even though the tailless expression itself is somewhat altered.

In conclusion, our results provide good evidence for a conservation of the major steps in the molecular segmentation cascade during the early steps of pattern formation in dipteran flies. This is in line with the observed morphological similarity of embryogenesis in these species and supports the generally assumed congruence between morphological and molecular processes. Thus, this analysis provides a good basis for comparisons with more distantly related species.

We thank W. Engels and K. Kirschfeld for the Musca stock, K. Howard for the hairy antibody, N. Patel for the engrailed antibody, M. Akam for the Ultrabithorax probe and M. Neumann and H. Jäckle for communicating unpublished sequence data, as well as M. Hülskamp and W. Lukowicz for discussion and suggestions on the manuscript. This work was supported by the DFG and by the ‘Fond der chemischen Industrie’.

References


The *Drosophila* gene *tailless* is expressed at the embryonic termini and is a member of the steroid receptor superfamily. *Cell* 62, 151–163.


(Accepted 15 July 1991)