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A phylogenetic interpretation of the patterns of gene expression in *Drosophila* embryos

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Summary

Two fundamental processes of the development of insect embryos are the generation and the morphological diversification of metameric units. In *Drosophila*, these processes are under the control of the products of the segmentation (generation) and the homeotic (morphological diversification) genes. Molecular studies of the activity of these genes has revealed spatial and temporal patterns of expression consistent with the requirements inferred from the mutant phenotypes but, in addition, these studies have revealed transient patterns which are difficult to reconcile with those phenotypes. It is possible that these patterns reflect ancestral regulatory elements which are still operational in more primitive insects. The validity of this interpretation can be tested by comparing the embryonic development of long germ band insects like *Drosophila melanogaster* with that of the more primitive short germ band insects like the locust *Schistocerca gregaria* and by obtaining and studying locust homologues of *Drosophila* segmentation and homeotic genes.

Key words: *Drosophila*, gene expression, phylogenetic interpretation, metameric unit, pattern, *Schistocerca*.

Introduction

The early development of all animal embryos involves the generation of an asymmetric mass of cells oriented with respect to some basic coordinate system, the growth of this mass and the specification within it of regional identities e.g. dorsal, ventral, head, thorax, etc. Shortly afterwards, the main morphological characteristics of a given phylum are visible and 'the body plan' is thus defined. Examination of developing embryos suggests that multiple strategies exist to carry out these processes. A detailed understanding of these strategies together with the elucidation of common principles underlying the establishment of different body plans are important aims of developmental biology.

The search for these principles has traditionally relied on comparative morphology and embryology but recently genetics and molecular biology are making important contributions. Thus a fertile interaction between these two disciplines has provided some insights into the strategies used by the embryo of the fruit fly *Drosophila melanogaster* to generate and specify its body plan and we have learnt much about the genes controlling those processes, the molecules they encode and the pathways they define (Nüsslein Volhard *et al.* 1987; reviewed in Akam, 1987). Perhaps surprisingly, the primary structure of many of these molecules is highly conserved between species and across phyla and, as a consequence, connections have been established between transcriptional regulators and growth factors from many organisms and genes involved in *Drosophila* embryogenesis (see for example: Laughon & Scott, 1984; Rosenberg *et al.* 1986; Padgett *et al.* 1987; Rijsewski *et al.* 1987). These conservations are, at present, merely structural and raise the question of whether a similar conservation exists at the functional level. If this were so, it would be possible to find homologies in the mechanisms establishing body plans. Unfortunately, the answer is usually obscured by the difficulty in comparing the embryogenesis of such diverse animals as insects and vertebrates and, equally important, by our ignorance of the biological function of these molecules in *Drosophila*. Notwithstanding, these structural homologies provide a method to obtain molecular markers for developmental processes (Sharpe *et al.* 1987).

In the hope of extending our knowledge from *Drosophila* to other animals, we are using these homologies to generate probes to study the embryogenesis of the orthopteran insect *Schistocerca gregaria* at the molecular level. This insect has a different, but comparable, mode of embryogenesis to that of *Drosophila* (see below) and thus we expect to rationalize at the functional level the structural homologies that we may find. In this context, we would like to discuss here segmentation in *Schistocerca* from the perspective provided by the ongoing work on *Drosophila*. An outcome of this discussion is the suggestion that many patterns of gene expression in *Drosophila* reflect ancestral situations or patterns maybe still present in less-evolved insects.

The insect body plan

The body plan of the insect embryo is characterized by a mass of cells elongated and metamerized in the anteroposterior axis known as 'the germ band'. It usually comprises a head, a telson and an overtly metamerized region which normally includes seventeen segments: three in the mouth parts, three in the thorax and a basic set of eleven in the abdomen. Despite the many classes of eggs, blastoderms, gastrulas and final morphologies embodied in the insect class, the germ band represents a constrained and obligatory developmental stage (Seidel, 1960; Sander, 1976, 1983). Because of this and since an enormous amount of the available information on *Drosophila* relates to the construction of its germ band, it is important to assess the relationship of *Drosophila* to other insects.

The embryos of Diptera like *Drosophila* represent an extreme form from a phylogenetic and an embryological point of view. Phylogenetically, they are the most highly evolved animals of a lineage that can be traced back to a common ancestor of present day annelids and arthropods. Embryologically, the *Drosophila* blastoderm contains a rather precise projection of the animal such that its cells are already determined to give rise to defined regions of the larva (Lohs Schardin *et al.* 1979; Technau & Campos Ortega, 1985) and the adult (Chan & Gehring, 1971; Illmensee, 1978). This highly determined blastoderm contrasts with the comparable stage of the other extreme of the annelid–arthropod lineage, the extant annelid embryo, in which the only regions specified are the head and a group of stem cells, the teloblasts, which will generate the main body region (Fernandez, 1980 and Fig. 1A,B); this mode of development is probably similar to that of the common ancestor. The embryogenesis of arthropod embryos offers a wide spectrum of variations between these two extremes (Dawydoff, 1928; Johanssen & Butt, 1941) exemplified by the subdivision of insects into short, intermediate and long germ according to the degree of representation of the animal in the primordial germ anlage (see Sander, 1976). *Drosophila* is a long germ insect and the degree of determination of its blastoderm is different from that of short germ insects, like the locust *Schistocerca gregaria*, in which the germ anlage is very small comprising only the head and a segment-building zone (Fig. 1C–F), an organization strongly reminiscent of that of the annelid embryo. Intermediate germ band insects have intermediate degrees of representation and determination.

These differences in the representation of the different regions when projected onto the germ anlage suggest that, although the germ band is a homologous structure between insects, the mechanisms underlying its generation and specification might not be (see Sander, 1983 for a thorough discussion of this problem). It also suggests that the establishment of the insect body plan relies, to different degrees, on instructions elaborated during the early blastoderm stage: in long germ embryos, it must depend heavily upon instructions generated during the syncytial phase (Schübiger & Wood, 1977; Vogel, 1977; Fröhnhoffer *et al.* 1986) whilst in short germ insects this process only yields a partial body plan and must have an additional phase of specification linked to the growth of the blastoderm anlage (Krause, 1938; Krause & Sander, 1962; Sander, 1976; Mee & French, 1986*a*,*b*).

In *Drosophila*, it is possible to relate developmental processes to the activity of specific gene products, thus the generation of the body plan depends on the correct deployment of the segmentation genes (Nüsslein Volhard & Wieschaus, 1980) and the specification of different regions on the homeotic genes (Lewis, 1963, 1978; Garcia Bellido, 1975; Kaufman & Abbot, 1984). The products of many of these genes have been shown to share a protein-coding domain, the homeobox, which is most tightly conserved between homeotic genes and is also present with a lesser degree of homology in some segmentation genes (McGinnis *et al.* 1984; Scott & Weiner, 1984). Interestingly, one segmentation gene, *fushi tarazu* (*ftz*), contains a homeobox of the homeotic class and its product has been shown to be required for the spatial registration of homeotic gene activity and the metamerism of the animal (Ingham & Martinez Arias, 1986; Duncan, 1986). This observation can be used as an example to argue that these sequences and others (Bopp *et al.* 1986) might help define and connect functional gene networks (Frigerio *et al.* 1986). In the case of *ftz*, for example, it is its 'homeotic class' homeobox that allows the linkage

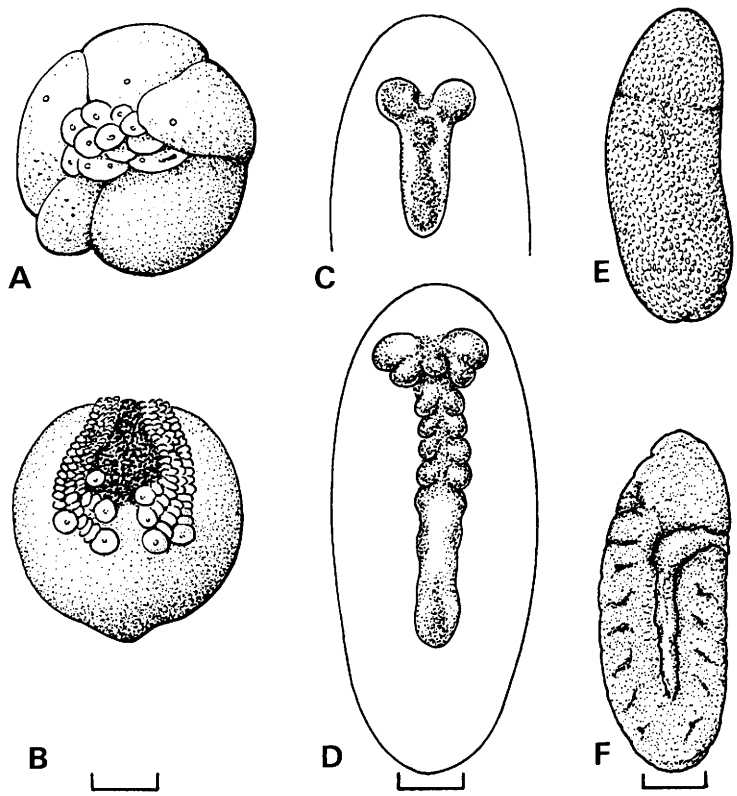

Fig. 1. Schematic drawings of blastoderms and germ bands in three members of the annelid arthropod lineage. (A,B) Annelid: *Clepsine* (Whitman, 1878). (A) After a series of very stereotyped spiral cleavages, a cellular blastoderm is formed. Within it every blastomere has a particular fate and, after gastrulation, a few of them will give rise to the teloblasts which will generate the 'germ band' (B) and give rise to the ectoderm and the mesoderm. (C,D) Short germ band insect, *Tachycines asynamorus* (Krause, 1938). During gastrulation, the embryo acquires the heart-shape form and elongates in the anteroposterior axis through cell division; the head is clearly visible (C) and the posterior part probably includes the primordia for the gnathos, the thorax and the abdomen. After elongation, segmentation is clearly visible in these regions, but not in the abdominal primordium which continues to elongate through cell proliferation. From the moment that they are visible each thoracic segment presents a characteristic size notably in the limb buds (D). (E,F) Long germ insect, *Drosophila melanogaster* (Poulson, 1950). (E) After gastrulation, the anlage for the complete embryo is present: the head region is clearly demarcated from the rest of the body by the cephalic furrow and the primordium of the germ band is beginning to extend; this stage is comparable to C in *Tachycines asynamorus*. (F) After germ band extension and the onset of cellular proliferation, segmentation is clearly visible. This stage is comparable to D but here segmentation is simultaneous throughout the embryo. The scale bars are relative and should not be taken as absolute references. Bars, 100 μm.

between the segmentation and the homeotic gene networks.

The homeobox domain is conserved across phyla and, within the arthropods, it is present in orders other than Diptera (McGinnis, 1985). Although this alone does not prove the existence of homologous genes in organisms other than *Drosophila*, the classical work of Bateson (1894), many homeotic mutations in insects (reviewed in Garcia Bellido, 1977), and the discovery of homeotic gene complexes in the silk worm *Bombix* (Tazima, 1964) and the flour beetle *Tribolium* (Beeman, 1987) support this hypothesis. These conservations are implicit in the initial suggestion of Lewis (1963) that these genes have long evolutionary histories and relatednesses and can be used to argue that their products are good markers, both for the specification of the body plan within a phylum and as a measure of the changes concomitant with the transitions between species.

On these assumptions, we are using homeoboxes from *Drosophila* to obtain several homologues of segmentation genes from *Schistocerca*. An important demonstration from the current work on *Drosophila* is that, as hinted from experimental embryology, the molecular processes that define metameric units and their identities precede their visible differentiation. Consequently, although experimental embryology provides a valuable tool, the understanding of early events during embryogenesis demands the acquisition of molecular markers for the processes of interest.

A phylogenetic interpretation of molecular embryology: the specification of the body plan

It is commonly accepted that the embryonic development of any animal contains information about its phylogenetic history. Debates, however, have often arisen about the precise meaning and nature of this information (Russel, 1916; Gould, 1977; Raff & Kaufman, 1983). For example, during the embryogenesis of *Schistocerca* and other orthopteran embryos, all abdominal segments develop small buds which might correspond to leg primordia and, in the first abdominal segment, they often begin to grow to form pleuropodia, appendages that fulfil some function during embryogenesis (Dawydoff, 1928; Schwalm, 1988). The development of these 'prolegs' is common among the embryos of most insects and in some cases has been interpreted as a reflection of their myriapod ancestry (Berlese, 1913; Imms, 1956). Another example of an ancestral developmental feature can be found in the progressive generation of abdominal segments characteristic of *Schistocerca* and other short and intermediate germ insects; it is likely that this mode of development is related to the teloblastic growth of their annelid-like ancestor, crustaceans and other more primitive arthropods. In the *Drosophila* embryo, morphological connections with its ancestry can be found in the process of gastrulation, the paired origin of the gnathal appendages (Turner & Mahowald, 1977), the conservation of the neuroblast map (Thomas *et al.* 1984), the extension of the germ band and, of course, in the general organization of the germ band. However, there is no sign of prolegs or of a major input of growth in the development of the abdominal primordium in comparison to the thorax.

In *Drosophila*, generation and specification of the basic body pattern along the anteroposterior axis take place simultaneously during blastoderm formation. These two processes rely on an early definition of asymmetries in the zygote in response to maternal information (Nüsslein Volhard *et al.* 1987) and on a complex network of interactions between maternal and zygotic segmentation gene products (reviewed in Akam, 1987). In the ectoderm, an important outcome of these interactions is the generation of a primary pattern of homeotic gene expression defining broad regions of the blastoderm (see for example Akam & Martinez Arias, 1985), and the activation of a ground set of cell states defined by the onset of segment-polarity gene activity (Weir & Kornberg, 1985; Baumgartner *et al.* 1987; Ingham *et al.* 1988). After germ band extension, when cell division resumes and some morphogenetic movements occur, changes take place in the patterns of expression of homeotic (Akam & Martinez Arias, 1985; Martinez Arias *et al.* 1987) and segment-polarity genes; the first ones become modulated within and between metameric units, the latter also undergo refinements and, in addition, new segment-polarity genes are activated (see, for example, transcripts from the *gooseberry* region in Baumgartner *et al.* 1987); this second phase of gene expression relies on cell interactions (Martinez Arias *et al.* 1988; DiNardo *et al.* 1988).

An important feature of the above developmental profile is the dynamic patterns of gene expression. Although during blastoderm formation this plasticity is clear in the transient expression of pair-rule genes (for example: Hafen *et al.* 1984*a*; Ingham *et al.* 1985; McDonald *et al.* 1986), throughout development it is particularly clear in the patterns of expression of the homeotic and segment-polarity genes. Most of these changing patterns are difficult to relate to the phenotype produced by the absence of the corresponding gene and, while they obviously reflect different levels of transcriptional control, it has been suggested that, in the case of the homeotics, they also reflect the phylogenetic history of the genes (Martinez Arias, 1987). In this manner, atavisms which are not morphologically visible in *Drosophila* because of the speed of its development, can be observed in the changing expression of the homeotic genes.

The wild-type expression of the *Antennapedia* gene provides a detailed example of this. In the embryo, mutations in *Antp* result in the transformation of T2 and T3 towards a novel nonthoracic segment (Wakimoto & Kaufman, 1981). This loss of thoracic character is reinforced by the damage observed in the Keilin's organs, which are thought to represent leg rudiments (Keilin, 1915). During imaginal development, *Antp* mutations result in defects in proximal leg development and diverse transformations in the thorax (Struhl, 1981; Abbott & Kaufman, 1986). Underlying these phenotypes, there is a gene with a complex molecular structure (Garber *et al.* 1983; Scott *et al.* 1983), two independent promoters (P1 and P2) (Schneuwly *et al.* 1986; Laughon *et al.* 1987) and multiple levels of regulation (Irish *et al.* 1988).

From the onset of their expression at blastoderm, both promoters have very different patterns and regulations (Martinez Arias, Bermingham & Scott, unpublished data); while P2 behaves like most of the other homeotic gene promoters at blastoderm, in that it defines precise metameric domains (PS4 and PS14) (Fig. 2B,D) and is critically dependent on the product of the *ftz* gene, P1 defines a broad unmodulated domain (Fig. 2A,C) and is independent of *ftz* (Ingham & Martinez Arias, 1986). Shortly after germ band extension, the situation changes and for the rest of embryogenesis P1 behaves like the promoters of *Dfd*, *Scr* and *Ubx*, in its spatial and temporal patterns of expression, modulation and cross-regulation

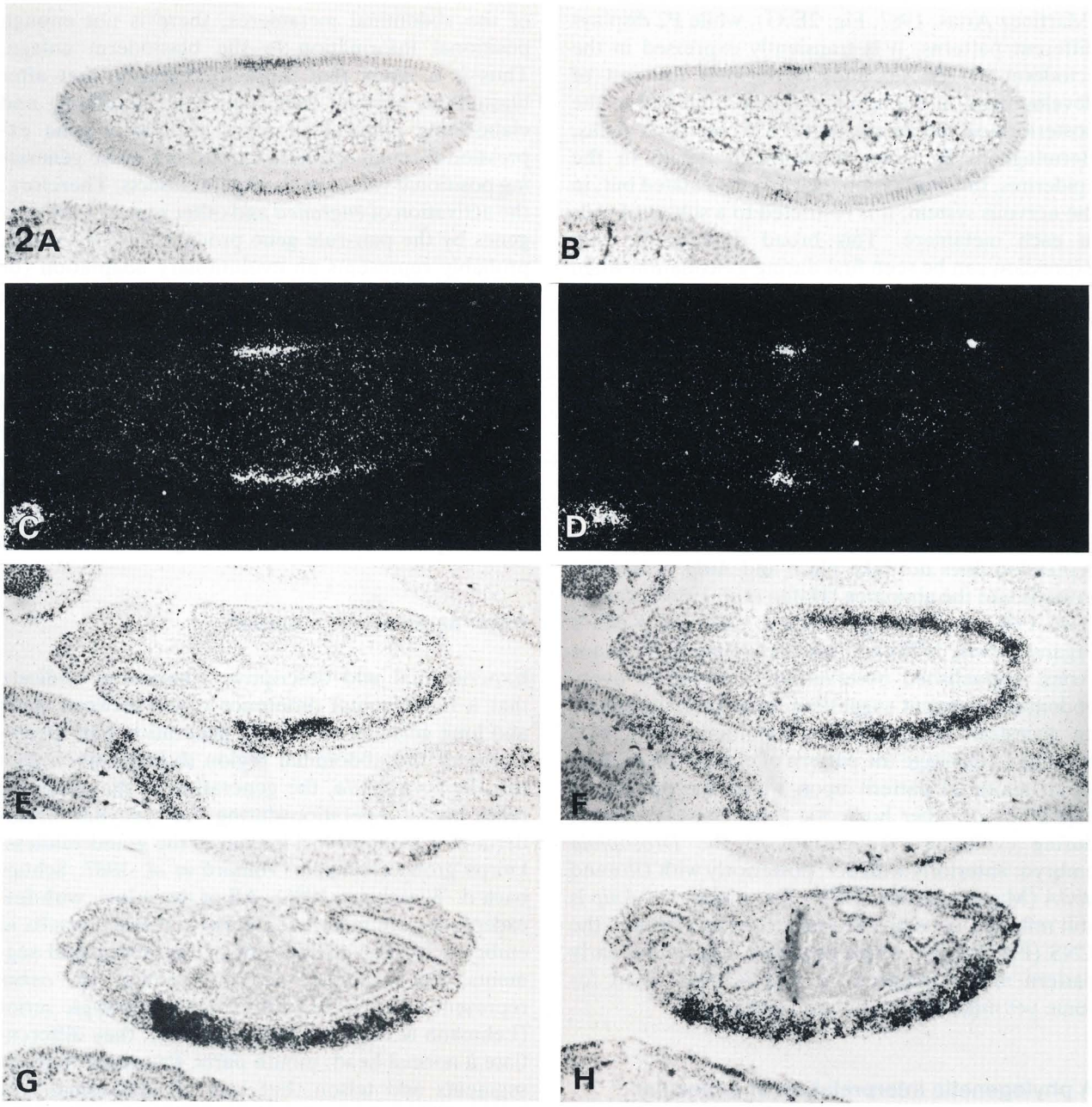

Fig. 2. Spatial expression of *Antennapedia* during embryogenesis. Every pair of figures in this panel represents alternate medial sections of the same embryo hybridized with probes specific for the *Antennapedia* P1 (A,C,E,G) or P2 (B,D,F,H) promoters. (A) During cellular blastoderm P1 is transcribed in a broad domain across the thoracic anlage; (B) in contrast, P2 is expressed in a well-defined domain, 3–4 cells wide, which represents the primordium of PS4; slightly later P2 transcripts can be detected in the primordium of PS14. During gastrulation these patterns evolve and, by the onset of germ band extension, P1 is transcribed in the ectoderm in a broad domain from PS4 to PS12 and in the mesoderm of PS5. (C) and (D), dark-field pictures of A and B. (E) In the extended germ band, P1 is expressed, primarily, in the ectoderm of PS4 and PS5 and the mesoderm of PS5. (F) P2 is expressed with a clear modulation in the ectoderm of PS3,4 and 5, in a subset of neural elements in each neuromere from PS3 to PS14 and in the mesoderm of PS4 and 5. After germ band shortening, expression in the epidermis decays, although P1 remains expressed in the primordium of the anterior spiral, but transcription increases in the nervous system. (G) P1 is expressed in all neuromeres from PS4 to PS12, with PS4 and 5 as the main domains of expression. (H) P2 is expressed, at lower levels, in a subset of neurones in each neuromere from PS3 to PS14. Methods: embryos were treated, sectioned and hybridized as described before (Akam & Martinez Arias, 1985; Ingham *et al.* 1985). The probes used are genomic pieces of DNA that discriminate between P1 and P2 (Martinez Arias, Bermingham & Scott, in preparation).

(Martinez Arias, 1987; Fig. 2E,G), while P2 displays different patterns: it is transiently expressed in the ectoderm of PS3,4,5 and, throughout the rest of development, in the nervous system from PS3 to the posteriormost metameric unit, PS15 (Martinez Arias, Bermingham & Scott, unpublished data). In the epidermis, this expression is clearly modulated but, in the nervous system, it is restricted to a subset of cells in each metamere. This broad domain of *Antp* expression can be seen first during gastrulation when P1 expression extends to PS12/13 and is bounded by P2 expression dorsolaterally in PS14. Given the requirement for *Antp* function to implement thoracic development, this pattern of expression can be interpreted as a transient stage in which the abdominal anlage has thoracic character. This transient 'thoracic pattern' soon disappears when the products of the BX-C, which have been deployed in the abdominal anlage, are translated and repress the expression of *Antp*. Indeed, in embryos lacking the BX-C, this repression does not take place and *Antp* expression extends into the abdomen (Hafen *et al.* 1984*b*; Carroll *et al.* 1986). Interestingly in these embryos, Keilin's organs (Lewis, 1978) and leg discs (Bate & Martinez Arias, unpublished observations) develop in every abdominal segment suggesting a partial reversion to an ancestral, myriapod-like, condition. Thus, it is possible to envisage the pattern of expression of *Antp* as an ancestral pattern upon which the pattern of expression of other homeotic genes has elaborated, during evolution, the pattern of the *Drosophila* embryo; anteriorly with *Scr*, posteriorly with *Ubx* and *abdA* (Martinez Arias, 1987). The ancestry of *Antp* is still reflected in its broad domain of expression in the CNS (Fig. 2G,H), which probably reflects the early pattern and a requirement that is maintained for some yet unknown important function.

A phylogenetic interpretation of molecular embryology: the generation of the body plan

If, at the level of specification of different body regions, it is possible to obtain some phylogenetic information from the patterns of expression of homeotic genes, it is also possible to obtain similar information about the generation of the body plan from the patterns of expression of some segment-polarity genes. In this respect, an important difference between the short and long germ insects is that while the latter set up the basic positional information at blastoderm (Howard & Ingham, 1986; Ingham *et al.* 1988) and then intercalate new values by changing the patterns of genes already active and by activating new genes (Martinez Arias *et al.* 1988; DiNardo *et al.* 1988), in the former, for most of the thoracic and all of the abdominal metameres, there is not enough positional information in the blastoderm anlage. Thus it is likely that those mechanisms that after blastoderm play an important role in refining and elaborating patterns of segment-polarity gene expression through cell interactions, are those generating positional values in short germ insects. Therefore, the activation of *engrailed* and other segment-polarity genes by the pair-rule gene products in *Drosophila*, probably represents an evolutionary adaptation (or exaptation) to the quick generation of the body plan which takes place during blastoderm. This mechanism can be shown to be independent of another which, under certain experimental circumstances, can activate *engrailed* in every metamere after blastoderm (DiNardo *et al.* 1988) and which requires the activity of segment-polarity gene products (DiNardo *et al.* 1988; Martinez Arias *et al.* 1988). This second mechanism is likely to be responsible for the generation of positional values in short germ insects.

oskar as an atavic mutation

Experimental and descriptive embryology indicate that a fundamental difference exists between short and long germ insects in the generation and specification of the abdominal region during embryogenesis. In *Drosophila*, the generation of the abdomen relies on the operation during the syncytial blastoderm of a group of loci known as the grandchildless-knirps group (Nüsslein Volhard *et al.* 1987; Schüpbach & Wieschaus, 1986). All of these loci, with few exceptions, are maternal and their absence results in embryos lacking most or all of the abdominal segments. For example, embryos mutant for *oskar* represent an extreme form of this phenotypic series (Lehmann & Nüsslein Volhard, 1986); they differentiate a normal head, mouth parts, first three thoracic segments and telson, but lack all abdominal segments. This defect is foreshadowed at blastoderm by the abnormal expression of gap gene products (Gaul & Jäckle, 1987; Tautz, 1987) and by a manifest defect of *ftz* expression in the abdominal primordium (Carroll *et al.* 1986).

In the wild type, the different regions of the embryo are specified at blastoderm through the activation of the homeotic genes in restricted and defined spatial domains. The abdominal primordium between PS6 and PS13 is specified at this stage by the activation of the elements of the BX-C, *Ubx* and *adbA*. Of these, the first one to be transcribed is *Ubx* in a region between 10 and 50% EL. At the same time, the thoracic primordium is specified by the activation of *Antp*, P2 in PS4 and P1 in a broad domain spanning PS4, 5 and 6. Using these patterns

of expression as guides to regional specification, we can infer a fate map for *osk* mutant blastoderms. In these embryos, initially there is no *Ubx* expression, *Antp* P1 is almost normal and *Antp* P2 has a broad domain from 10 to 40% EL (Irish *et al.* 1988; Fig. 3C). This pattern can be interpreted as a shift in the fate map of the prospective abdominal anlage from abdominal to thoracic. The number of segments in this primordium is also altered; while, in the wild type, *engrailed* is expressed in 14 evenly spaced stripes along the anteroposterior axis (Weir & Kornberg, 1986; Fig. 3A), in *osk* mutant blastoderms, the first five stripes together with the last one are normal, but stripes 6 through 13 are fused in a single broad stripe (Fig. 3B).

After gastrulation, *Ubx* is activated in these embryos in an unusual pattern within the abdominal anlage (Irish *et al.* 1988); this activation is independent of the maternal information and most likely reflects zygotic functions, probably pair-rule and segment-polarity gene products which, in the wild type, serve to modulate the early expression. In this manner, the abdominal anlage of an *osk* mutant embryo is not only reduced in size and initially thoracic in character, but later starts acquiring some character through the effect of segmentation functions on homeotic genes. As for the case of positional values, we believe that in the embryos of short germ insects, homeotic genes are activated through the action of segment-polarity gene products during the growth of the primordia.

Garcia Bellido (1977) expanded on the idea, implicit in Lewis (1963), that homeotic mutations are atavic mutations. Following this idea, we believe that embryos from *oskar* mutant mothers, develop an atavic condition in which the fate map of the abdominal region is close to that of the embryo of a short germ ancestor. This fate map cannot develop as it would in a short germ insect and differentiates into a single segment with a final cuticular phenotype which is largely the result of postblastoderm regulatory events (Lehmann & Nüsslein Volhard, 1986).

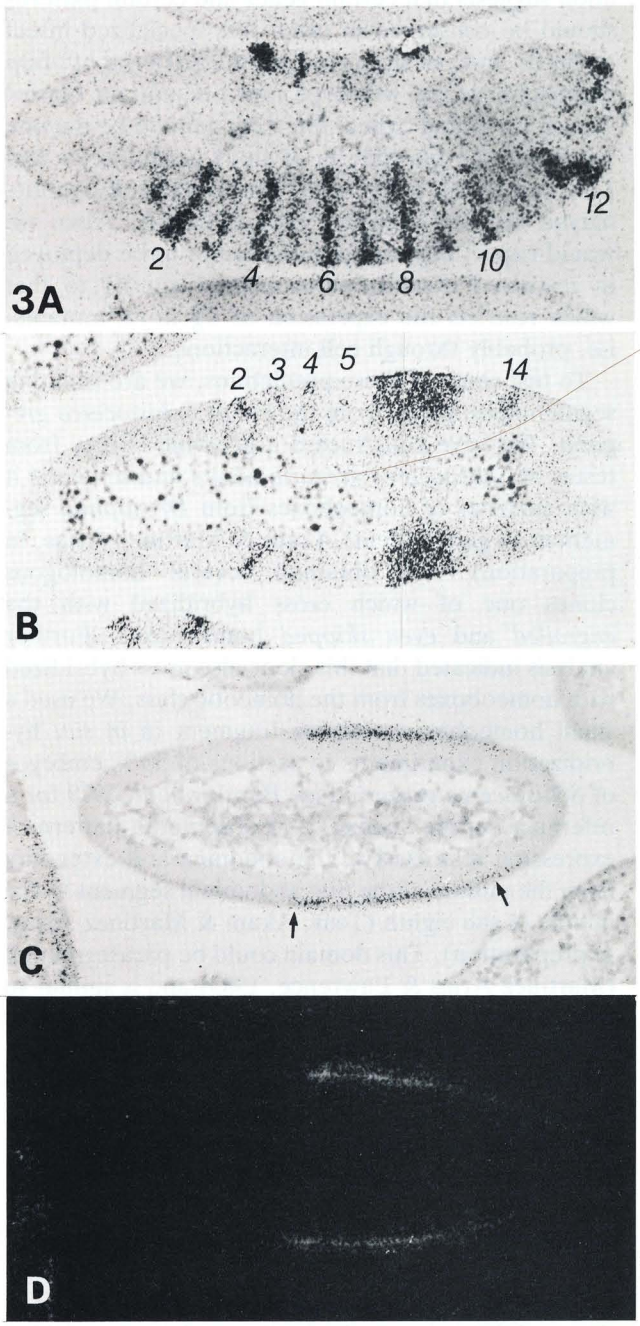

Fig. 3. Gene expression in wild-type and *osk* mutant blastoderms. (A) Expression of *engrailed* in a medial section of a wild-type gastrula; notice the 14 stripes across the ectoderm and the mesoderm. The even-numbered stripes are stronger than the odd-numbered ones. (B) Expression of *engrailed* in a horizontal section of an *osk* mutant gastrula at a stage similar to that shown in A, notice that the first five stripes are normal and are followed by a very broad stripe in the abdominal anlage. The fourteenth stripe is also normal. (C) Transcription of *Antp* P2 in an *osk* mutant blastoderm: compare with Fig. 3B. Notice the very broad domain that extends from PS4 to PS14 almost continuously. (D) Dark-field photograph of (C).

Molecular embryology of the locust *Schistocerca gregaria*

The above considerations and interpretations lead to the view that the first instar larva of *Drosophila* is generated stepwise by modifying ancestral patterns of spatial expression of very conserved genes. Indeed, in the case of the homeotics, once a gene defines a spatial domain, it is modified within that domain by new gene products or by new interactions with preexisting ones; these changes often are brought about by new regulatory elements. This interpret-

ation suggests that certain genes and certain patterns should be conserved in other less-specialized insect embryos and, as suggested by the patterns of *Antp* expression in the wild-type and *osk* mutant blastoderms, we would expect the *Antp* gene to be the one specifying the blastoderm of short germ insects and *Ubx* and *abdA* to be under the control of zygotic, maybe segment-polarity, gene products. Also, we would expect segment-polarity genes to be deployed in restricted domains in a manner similar to that which restricts the expression of *wg* in *ftz* mutants, i.e. probably through cell interactions.

To test some of these predictions, we are isolating segmentation genes from the locust *Schistocerca gregaria*. We have constructed a genomic library from testes of *Schistocerca gregaria* adults and screened it with mixtures of homeoboxes from *Drosophila* segmentation genes (Tear, Akam & Martinez Arias, in preparation). We obtained several homologous clones one of which cross hybridized with the *engrailed* and *even skipped* homeoboxes. Further analysis indicated that this clone also cross hybridized with homeoboxes from the homeotic class. We used a small homeobox-containing fragment in *in situ* hybridization experiments to sections of 50% embryos of *Schistocerca gregaria* (see Bentley *et al.* 1979 for a reference on the staging) and observed a pattern of expression restricted to the abdomen and extending from the middle of the first abdominal segment to the middle of the eighth (Tear, Akam & Martinez Arias, in preparation). This domain could be parasegmental (Martinez Arias & Lawrence, 1985) and is similar to that of the *abdA* gene from *Drosophila* (McGinnis *et al.* 1984; A. Rowe & M. Akam, personal communication). Sequence analysis of the *Schistocerca* gene *homoeobox* proved it to be identical, at the protein level, to the *Drosophila* one (Tear, Akam & Martinez Arias, unpublished observations).

Conclusion

Metamerization in insect embryos is tightly linked to the establishment of a body plan and can be divided into two processes: the generation of metameric primordia and the specification of 'cellular identities' on these primordia. Here, we have discussed these processes in embryos of short and long germ insects from the perspective of *Drosophila* gene expression. We have suggested that the changing expression of homeotic and segment-polarity genes in *Drosophila* provides clues about their expression in other insects and have made some suggestions about these patterns. As a prelude to testing these hypotheses we are cloning some homologues of *Drosophila* segmentation genes from the locust *Schistocerca gregaria* to use as markers during embryogenesis.

Our conclusions agree with already existing ideas about the phylogenetic importance of segmentation mechanisms (Sander, 1983) or homeotic genes (Lewis, 1963, 1978; Garcia Bellido, 1977) and suggest that a very important driving force in the evolution of the arthropod lineage is changes in the regulation of homeotic and segment-polarity genes. Thus, for example, *Ubx* and *abdA* might evolve from having a zygotic control, tightly linked to segment-polarity gene activity in short germ insects, to being dependent on maternal information for their initial deployment during the specification of the abdomen in long germ insects.

These ideas stress the notion that developmental systems, by the nature of their genetic hardware, are inherently plastic. This is apparent in two properties of this hardware: one, the modular nature of the control elements regulating the genes (see, for example, Hiromi *et al.* 1986), which allows easy addition, elimination and exchange of control sequences. The other, the combinatorial nature of the processes regulated by their products and the synergistic effects often produced by these combinations (Ingham *et al.* 1988; Doe *et al.* 1988; Irish *et al.* 1988) which also allows for the creation of diversity with minor modifications of preexisting elements. In consequence, it is because of the natural plasticity of developmental systems and their tendency to change that ontogeny is a very important force driving phylogeny.

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