the embryo, in a uniform band of cells normally located between 70 and 90 per cent EL, the posterior limit of which is sensitive to decreased or increased *bcd* dosage. A clear implication of these studies is that both *otd* and *ems* are activated in spatially restricted domains in the blastoderm embryo in direct response to levels of *bcd* protein. Whether this response is mediated via the same low-affinity binding sequences as those located upstream of *hb* will doubtless be revealed soon.

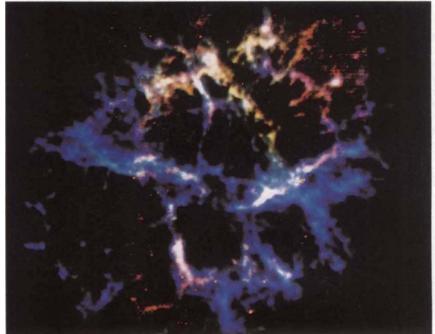
The otd mutation was originally characterized as showing defective head involution¹⁴. This rather gross phenotypic description reflects the difficulties in analysing the final intricate pattern of the head segments in the mature larva largely due to the complex topological rearrangements occurring in the head during embryogenesis - which have bedevilled the study of this part of the animal. To circumvent this problem, Finkelstein and Perrimon used the products of the wingless and engrailed genes as molecular markers for head segments in early embryos, and they were thus able to identify unequivocally those segments missing in otd mutants.

Using a similar approach, Cohen and Jürgens' have extended this analysis not only to empty spiracles but also to mutations of buttonhead (btd), a third gene that affects head development. Their findings reveal overlapping requirements for the activities of all three genes in the specification of each of the head segments anterior to the cephalic furrow (see figure). Because the functional domains of each gene appear to be out of register by one segment, Cohen and Jürgens propose that they act in a combinatorial fashion to specify the boundaries of each of the head segments, probably by directly regulating the expression of wingless and engrailed. They may also determine the identities of each segment by regulating the expression of head-specific homeotic genes such as labial and Deformed^{15,16}. In this way, these head-specific 'gap' genes would subsume the functions normally executed by gap and pair-rule genes in the more posterior segments of the embryo.

Although this interpretation is persuasive, the precise relationship between function and expression of the three genes remains unclear: although *ems* is evidently required more posteriorly than *otd*, for

- 1. Lawrence, P.A. Cell 54, 1-2 (1988).
- Driever, W. & Nüsslein-Volhard, C. Cell 54, 95–104 (1988).
 Dalton, D., Chadwick, R. & McGinnis, W. Genes Dev. 3,
- Datton, D., Chauwick, A. & McGinnis, W. Genes Dev. 3, 1940–1956 (1989).
 Cohen, S.M. & Jürgens, G. Nature 346, 482–485 (1990).
- Finkelstein, R. & Perrimon, N. *Nature* **346**, 485–488 (1990).
- Pankratz, M.J. et al. Cell 61, 309–317 (1990).
 Frohnhöfer, H.G. & Nüsslein-Volhard, C. Genes Dev. 1,
- 880–890 (1987). 8. Tautz, D. *Nature* **332**, 281–284 (1988).
- 9. Driever, W. & Nüsslein-Volhard, C. Nature 337, 138-
- 143 (1989). 10. Driever, W., Thoma, G. & Nüsslein-Volhard, C. Nature

Fine filaments of the Crab Nebula



ILLUMINATED by a powerful pulsar at its heart, the Crab Nebula has continued to fascinate astronomers since it was discovered by Lord Rosse in 1844. What we see are the gaseous ejecta from a massive supernova that Chinese observers could see even during daytime 940 years ago. The nebula is now 4 light years across and is expanding at a rate of 1,400 km s⁻¹. The filaments traced out by the ejecta are the result of turbulence and shockwaves. In making this new three-colour overlay figure (Astrophys. J. 357, 539-547; 1990), Jeff Hester and colleagues intend to understand better the chemical composition of the nebula: red indicates iron (recorded using new infrared imaging), green, hydrogen and nitrogen, and blue, oxygen. In fact the varying colouring of the filaments indicates on the whole not varying composition, but rather differing conditions, although an excess of hydrogen swept up from the interstellar medium is apparent above the middle of the figure. One aim of the study is to tackle the iron-nickel problem in astronomy. The best measure we have of the cosmic abundances of the elements comes from studies of the composition of the Sun and meteorites formed billions of years ago from gas clouds comprising hydrogen and helium and enriched with heavier elements by supernova remnants similar to the Crab Nebula, Yet these measurements indicate that there is 10 times more iron than nickel, whereas their apparent abundances in supernova remnants and in star-forming clouds are equal. The authors conclude in the new study that the problem must arise through difficulties in the interpretation of the atomic data, and does not reflect a real variation in astrophysical abundancies.

instance, the domains of expression of both genes appear to be essentially coextensive. But if shown to be correct, there is an intriguing irony in all of this. Recent studies of the hindbrain in chicks and mice¹⁷⁻¹⁹ suggest a close analogy between metamerism in invertebrates and an underlying segmental organization of

340, 363-367 (1989)

- Driever, W., Ma, J., Nüsslein-Volhard, C. & Ptashne, M. Nature 342, 149–154 (1989).
- Struhl, G., Struhl, K. & Macdonald, P.M. Cell 57, 1259– 1273 (1989).
- Finkelstein, R., Smouse, D., Capaci, T.M., Spradling, A.C. & Perrimon, N. (submitted).
- Wieschaus, E., Nüsslein-Volhard, C. & Jürgens, G. Wilhelm Roux Arch. dev. Biol. 193, 296–307 (1984).
 Mahaffey, J.W., Diederich, R.J. & Kaufmann, T.C. Devel-
- opment 104, 167–174 (1989).
- 16. Jack, T. & McGinnis, W. EMBO J. 9, 1187-1198 (1990).
- 17. Lumsden, A. & Keynes, R. Nature 337, 424–428 (1989). 18. Wilkinson, D.G. et al. Nature 337, 461–464 (1989).
- 19. Wilkinson, D.G. *et al. Nature* **341**, 405–409 (1989).
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the vertebrate nervous system. This analogy has been much strengthened by the pair-rule-like expression of the mouse Krox 20 gene — yet it would now seem that the comparable region of the fly embryo may be segmented by a quite distinct mechanism, independent of pair-rule genes. Had the analysis of Drosophila development begun with the bcd system, the specification of head segments by overlapping domains of homeobox proteins might well have been established as the archetypal gene hierarchy: what then might have been made of zinc-finger protein stripes in alternate rhombomeres?

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