Punctuated Evolution of Embryos

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Development must do more than simply convert an egg into an adult: It must do so in a way that ensures survival to a reproductive age. For animals that bear live young, such as most mammals, the maternal parent assumes much of this responsibility. But for the vast majority of animals, including most insects, fishes, amphibians, and marine invertebrates, embryos and larvae are left to their own resources. Comparative embryologists have long recognized the importance of special adaptations in assisting survival during early development in these groups (*1*): Caterpillars store toxins that predators find distasteful, starfish larvae carry prominent attachment structures needed for settlement on the ocean floor, and tadpoles gather and digest food differently from adult frogs. New research has begun to document the evolutionary changes that underlie the unique developmental strategies of these embryos and larvae. The results challenge traditional explanations for why development evolves and provide intriguing glimpses of how developmental mechanisms may change over geological time.

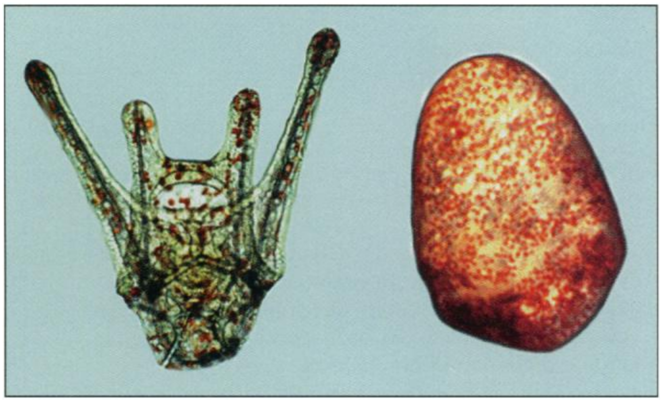

Fig. 1. Uncoupled evolution of sea urchin larvae. Feeding pluteus larva of *Heliocidaris tuberculata* (**left**) and nonfeeding schmoo larva of *Heliocidaris erythrogramma* (**right**), both at 3 days after fertilization. The adults to which these larvae give rise are morphologically very similar.

Divergence in developmental mechanisms among closely related species has been studied most intensively in the genera *Heliocidaris* (sea urchins), *Eleutherodactylus* and *Gastrotheca* (frogs), and *Molgula* (ascidians) (*2*). In each case, comparisons among similar species have uncovered modifications in a variety of crucial developmental processes: the expression of regulatory and structural gene products during oogenesis and embryogenesis (*3*); the timing, location, and mechanisms of cell fate specification (*4*); and the movements of cells during gastrulation and later morphogenesis (*5*). These modifications are as large as any known within the wider groups to which these genera belong. For example, the dorsoventral axis is committed earlier in *Heliocidaris erythrogramma* than in *H. tuberculata* and other urchins; fewer muscle cell precursors are specified in *Molgula occulta* than in *M. occulata* and other ascidians; and gastrulation cell movements in *Gastrotheca riobambae* are quite different from those of other frogs. These are modifications in developmental processes that have traditionally been viewed as invariant within particular classes or phyla.

Surprisingly, these evolutionary modifications in development are not correlated with changes in adult morphology but instead vary with changes in life history strategy. In each case, the species with unusual developmental mechanisms have larvae that are morphologically not characteristic of the group (Fig. 1) and have lost the ability to either feed (urchins and frogs) or disperse (ascidians). These are functionally significant changes for the organism: The loss of larval feeding or dispersal can have a significant impact on the survivorship of offspring, on local population structure, and perhaps on probabilities of speciation and extinction (*6*).

This correlation between modifications in developmental mechanism and life history is unlikely to be coincidental. First, the developmental changes seem to occur only in species with modified life history strategies. In all three phyla, enough species have been examined now to make a chance association unlikely. Second, many of the changes make functional sense as adaptations for the derived life history strategy. For example, where larval feeding has been lost, genes with products that are involved in feeding are sometimes no longer expressed, and in species where predation on larvae is intense, some genes involved in building adult structures are expressed earlier (*3*, *7*).

Third, and perhaps most convincing, parallel developmental changes have evolved during "replicate" shifts in life history strategy. In sea urchins, larval feeding has been lost at least 20 times. In all species with nonfeeding larvae examined thus far, parallel changes have evolved to increase egg size, alter cleavage geometry, truncate larval morphogenesis, accelerate the formation of the adult rudiment, decrease the time to metamorphosis, and change the expression of a variety of genes (*7*). These associations are highly significant by the concentrated changes test (*7*), which calculates the likelihood that such correlations could arise by chance (*8*). A similar situation exists in amphibians, where nonfeeding larvae have also evolved on multiple occasions, often accompanied by loss of larval feeding structures, precocious development of limbs, and reduced time to metamorphosis (*9*).

Additional evidence for the association between changes in life history strategy and developmental mechanisms is beginning to emerge from other taxa. Axis formation and early cell lineages are substantially modified in a nemertean with nonfeeding larvae, and highly derived modes of gastrulation and coelom formation have evolved in a starfish with nonfeeding larvae (*10*). In insects, some gene products with roles in pattern formation are expressed in spatial and temporal patterns that are better correlated with germ band length, a life history trait, than with adult morphology (*11*).

A few species with modified life histories exhibit only some of the changes in larval morphology and developmental mechanism, suggesting that it is larval ecology that drives changes in development and not vice versa. If these evolutionary changes in developmental mechanism are truly driven by changes in life history rather than adult morphology (*7*, *9*), then selection can act on developmental mechanisms to alter larval phenotypes directly, independent of changes in adult phenotype.

An unexpected finding of this recent research concerns the tempo and mode of evolutionary changes in development. Classical and modern developmental studies provide many examples of exceptionally conservative developmental processes—such as spiral cleavage in annelids and mollusks and positional specification along the anteroposterior body axis by the *Hox/HOM* gene complex in arthropods and chordates. In both cases, the structural and functional similarities between the two groups are so extensive that a single common origin is the only reasonable interpretation (*12*). Be-

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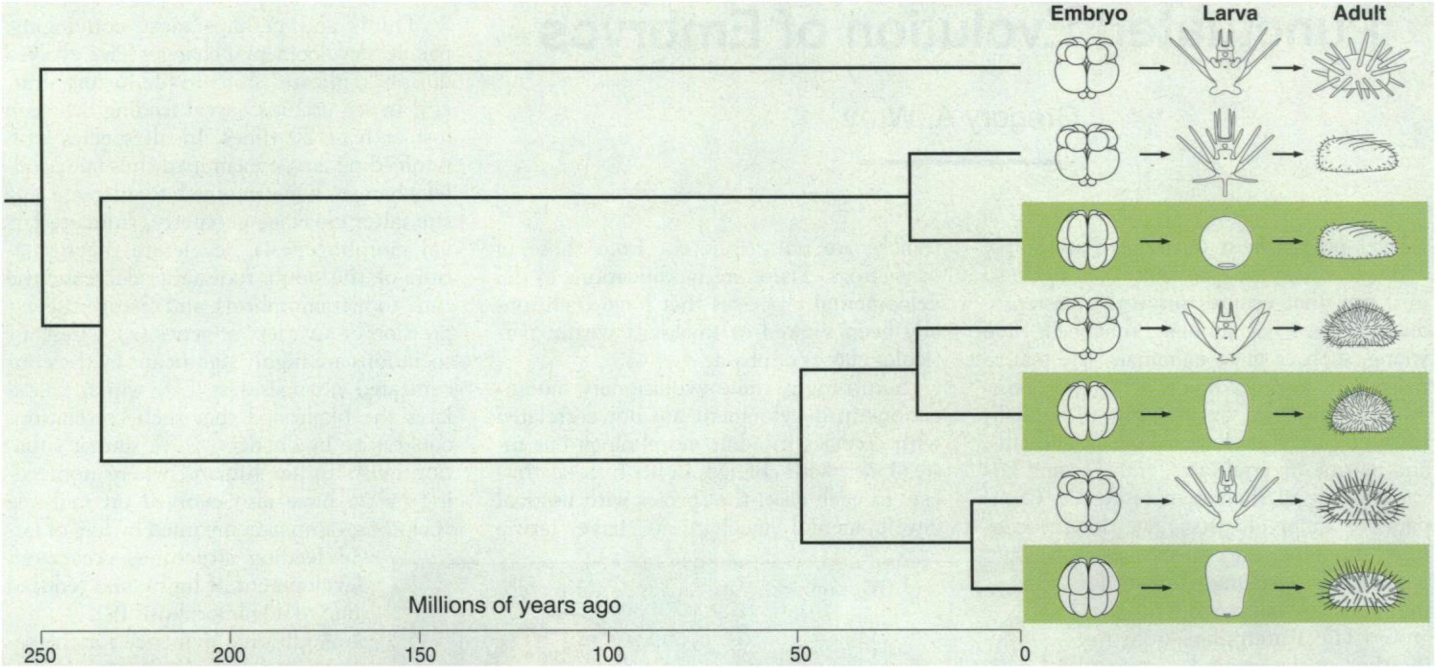

Fig. 2. Punctuated evolution of sea urchin development. Sea urchins have switched from feeding to nonfeeding larval development on several occasions (colored boxes). In each case, several parallel, functionally significant changes have evolved in underlying developmental mechanisms, and larval morphology is convergently simplified. It is evident from the divergence times (horizontal axis) between various species that both larval morphology and developmental mechanisms can evolve rapidly compared to their prior persistence.

cause the phyla that contain these features had diverged by the early Cambrian (over half a billion years ago), spiral cleavage and the *Hox*/*HOM* complex are probably very ancient. These cases, and others like them, are often cited as evidence that early development evolves very slowly (*13*).

But sea urchins, ascidians, and frogs do not fit this hypothesis of slow developmental evolution. Instead, molecular comparisons and fossil evidence suggest that functionally profound changes in developmental mechanisms can evolve quite rapidly. Within the sea urchin genus *Heliocidaris*, divergence times between species with very different developmental mechanisms are less than 10 million years (*14*). In contrast, the ancestral developmental mechanisms have persisted for nearly half a billion years, a conclusion that is based on the shared presence of these mechanisms in species that diverged from urchins just after the Cambrian (*15*). A similar situation may exist in ascidians, although the divergence times are not as well resolved (*16*).

Long periods of little net change, with functionally minor modifications in developmental mechanisms and larvae, seem to be the normal mode of evolution (Fig. 2). This near stasis is interrupted on occasion by rapid, extensive, and mechanistically significant changes that coincide with switches in life history strategy. Evaluating whether this evolutionary dynamic corresponds to the concept of punctuated equilibrium as originally articulated (*17*) will require better estimates of divergence times that closely bracket evolutionary changes in developmental mechanisms (*15*). It is already clear, however, that rapid modifications can arise in developmental mechanisms that have been conserved for hundreds of millions of years.

These notions contrast with the traditional view of developmental evolution, which regards early development as highly conservative and predicts that modifications in embryogenesis will cause major changes in adult morphology (*13*). The new evidence does not completely falsify the traditional interpretation, but it does require its modification. Some developmental mechanisms are directly required to build particular adult morphologies and therefore must be evolutionarily conserved. However, other developmental mechanisms may change extensively, such as adaptations to particular life history strategies. Over the next several years, it will be interesting to see whether uncoupled and punctuated modes of developmental evolution are found in other taxa or in association with other common life history transformations such as the origin of parasitism, coloniality, and brooding.

References

1. W. Garstang, *Brit. Assoc. Adv. Sci.* **1929**, 77 (1929); N. J. Berrill, *Philos. Trans. R. Soc. London Ser. B* **225**, 255 (1935); H. B. Fell, *Trans. R. Soc. N.Z.* **75**, 73 (1945); D. T. Anderson, *Embryology and Phylogeny in Annelids and Arthropods* (Pergamon, Oxford, 1973).
2. R. P. Elinson, *Sem. Dev. Biol.* **1**, 263 (1990); G. A. Wray and R. A. Raff, *Trends Ecol. Evol.* **6**, 45 (1991); W. R. Jeffery and B. J. Swalla, *BioEssays* **14**, 219 (1992).
3. A. Parks *et al.*, *J. Evol. Biol.* **1**, 27 (1988); L. B. Scott *et al.*, *Dev. Biol.* **138**, 188 (1990); W. R. Jeffery and B. J. Swalla, *ibid.* **153**, 194 (1992); D. Jennings, *J. Morphol.* **220**, 359 (1994); R. A. Raff, personal communication.
4. G. A. Wray and R. A. Raff, *Dev. Biol.* **141**, 41 (1990); J. J. Henry and R. A. Raff, *ibid.*, p. 55; W. R. Jeffery and B. J. Swalla, *ibid.* **145**, 328 (1991).
5. E. M. del Piño and R. P. Elinson, *Nature* **306**, 589 (1983); G. A. Wray and R. A. Raff, *Evolution* **45**, 1741 (1991).
6. R. R. Strathmann, *Annu. Rev. Ecol. Syst.* **16**, 339 (1985); D. Jablonski, *Bull. Mar. Sci.* **39**, 565 (1986).
7. G. A. Wray and A. E. Bely, *Development* (suppl.) (1994), p. 97.
8. W. P. Maddison, *Evolution* **44**, 539 (1990).
9. J. Hanken, *J. Evol. Biol.* **5**, 549 (1992).
10. J. J. Henry and M. Q. Martindale, *Dev. Genet.* **15**, 64 (1994); D. Janies and L. McEdward, *Biol. Bull.* **185**, 56 (1994).
11. N. H. Patel, B. G. Condron, K. Zinn, *Nature* **367**, 429 (1994).
12. R. A. Raff and T. C. Kaufman, *Embryos, Genes, and Evolution* (Macmillan, New York, 1983); M. Akam, *Cell* **57**, 347 (1989).
13. K. E. von Baer, *Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion* (Bornträger, Kőnigsberg, 1828); S. J. Gould, *Ontogeny and Phylogeny* (Belknap, Cambridge, MA, 1977); D. T. Anderson, in *Rates of Evolution*, K. S. W. Campbell and M. F. Day, Eds. (Allen and Unwin, London, 1987), pp. 143–155; L. Buss, *The Evolution of Individuality* (Princeton Univ. Press, Princeton, NJ, 1987); W. Arthur, *A Theory of the Evolution of Development* (Wiley, Chichester, 1988); D. R. Brooks and E. O. Wiley, *Evolution as Entropy* (Univ. of Chicago Press, Chicago, ed. 2, 1988); K. S. Thomson, *Morphogenesis and Evolution* (Oxford Univ. Press, London, 1988).
14. M. J. Smith, J. D. G. Boom, R. A. Raff, *Mol. Biol. Evol.* **7**, 315 (1990); W. O. McMillan, R. A. Raff, S. R. Palumbi, *Evolution* **46**, 1299 (1992).
15. G. A. Wray, *Am. Zool.* **32**, 123 (1992).
16. K. A. Hadfield, B. J. Swalla, W. R. Jeffery, *J. Mol. Evol.*, in press.
17. N. Eldredge and S. J. Gould, in *Models in Paleobiology*, T. J. M. Scopf, Ed. (Cambridge Univ. Press, Cambridge, 1972), pp. 82–115.