

EVOLUTIONARY TRANSFORMATIONS AND DOLLO'S LAW

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In a recent article, Dahl (1987) questioned the transfer by Schram (1986) of Phyllocarida from the Malacostraca to the Phyllopoda. Dahl's doubts centered on Schram's proposal that several character states—antennular flagellum, mandibular palp, and pleopods—have been lost and subsequently redeveloped during the evolutionary history of the Phyllopoda. Dahl found such evolutionary transformations unlikely. In dismissing the argument for loss-and-redevelopment, Dahl noted there is no empirical evidence of this in the fossil record and he stated (p. 725) "the introduction of temporary loss and redevelopment of the same morphological characters are not readily accepted by evolutionists," and in passing referred to Dollo's Law. Dollo's Law or Rule—that "structures that had been lost in evolution can never be reacquired exactly in the same way" (Mayr, 1982: 609) or more broadly "that evolution is irreversible and that structures and functions once lost can never be regained" (Lincoln *et al.*, 1982: 71)—is an intuitive construct about evolution. However, an underlying assumption of the above-mentioned definitions of Dollo's Law is that all phenotypic change is equated with permanent alteration of the genotype. This assumption too easily confuses loss of phenotypic structure caused by loss or reorganization of genotypic structure with loss of phenotypic structure caused by repression of genotypic function. I suggest that for evolutionary transformations among crustaceans, Dollo's Law should not be strictly applied nor should hypotheses about loss-and-redevelopment of characters be excluded from consideration.

That the determination of arthropod skeletal architecture commonly results from repression of gene function is clear from studies of homeotic gene complexes that control development of insect body segments (Lewis, 1978, 1981; Kaufman *et al.*, 1980; Beeman, 1987). The evolution of these gene complexes seems to have suppressed

leg development on abdominal segments, and in fruit flies suppressed the posterior pair of wings, while promoting haltere formation, in the four-winged ancestor (Lewis, 1978). Many genes in these complexes contain homeobox regions whose proteins presumably bind to DNA of still other genes. Activation or repression of these downstream genes result in the specific segment morphologies. Changes in timing of gene repression, or alteration of repressor molecule structure or concentration conceivably can restore ancestral gene function and result in development, in the case of fruit flies (Lewis, 1963), of an ancestral, bithorax/postbithorax, double-winged architecture.

Phenotypic evidence of gene repression in crustaceans has been deduced from transformations in swimming leg segment numbers during development of several copepods by Ferrari (1988). Examples include reduction of male leg 5 endopod of *Heterocope weismanni* described by Elster (1932), reduction of male leg 4 endopod of *Elaphoidella bidens coronata* described by Carter and Bradford (1972), reduction of male leg 2 endopod of *Diarthrodes cystoecus* described by Fahrenbach (1962), loss of legs 1 and 2 of *Acanthochondria cornuta* described by Heegaard (1947), loss of legs 1 and 2 of *Alella macrotrachelus* described by Kawatow *et al.* (1980). Reductions in numbers of ramal segments, or loss of a swimming leg (which occasionally is accompanied later by leg redevelopment) during an ontogenetic sequence are inferred to result from repression of a genetic system controlling the expression of leg morphology.

It is difficult to infer the direction and limits of phylogenetic transformation by extrapolating from observed changes in phenotype during ontogeny, or to determine to what extent genes presently repressed have been expressed historically. However, developmental systems in which gene function and the resulting phenotype are regulated by gene repression suggest that considering

all phenotypic change irreversible is too strict an approach to evolutionary transformations.

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