ABSTRACT

Earlier publications include the suggestion that larval transfer (the transfer from one phylogenetic lineage to another of genes coded for larval features) provides the best explanation of anomalies between adult and larval morphologies in the Dromioidea and in the crab *Dorhynchus thomsoni*.

It is now suggested that most crustacean larvae, other than postlarvae and megalopas, evolved from transferred larvae. Examples include zoeas (except those of the Polychelidae), phyllosomas, mysid larvae, protozoeces, and nauplii.

The 2nd and 3rd appendages of nauplii are similar and postoral. The 2nd appendages are preoral in most extant non-naupliar crustaceans, but they remain postoral in the Ostracoda and Mystacocarida and in the Cambrian *Martinssonia*. The evolution of these groups is briefly discussed, and it is postulated that nauplii and similar forms were originally transferred from non-crustacean arthropods.

The Sergestoidea and the Amphionidacea provide striking examples of the problems faced by those who would dismiss the concept of larval transfer in crustacean evolution.

The taxonomic value of the characters of transferred larvae is discussed.

RÉSUMÉ

Des publications antérieures incluaient la suggestion que le transfert larvaire (le transfert des gènes codés pour les traits larvaires d’une lignée phylogénétique à une autre) fournit la meilleure explication des anomalies entre morphologies adulte et larvaire chez les Dromioidea et le crabe *Dorhynchus thomsoni*.

Il est maintenant suggéré que la plupart des larves de Crustacés, en dehors des postlarves et des mégalopes, évoluent à partir de larves transférées. Les exemples comprennent les zoés (sauf celles des Polychelidae), les phyllosomes, les larves mysis, les protozoeces et les nauplii.

Les 2èmes et 3èmes appendices des nauplii sont semblables et post-oraux. Les 2èmes appendices sont pré-oraux chez la plupart des Crustacés non naupliens existants, mais restent post-oraux chez les Ostracodes et les Mystacocarides et chez *Martinssonia* du cambrien. L’évolution de ces
groupes est brièvement discutée, et il est postulé que les nauplii et les formes similaires ont été originellement transférés à partir d’Arthropodes non-Crustacés.

Les Sergestoidea et les Amphionidacea sont des exemples frappants des problèmes auxquels doivent faire face ceux qui voudraient écarter le concept de transfert larvaire dans l’évolution des Crustacés.

La valeur taxonomique des caractères des larves transférées est discutée.

**INTRODUCTION**

Until comparatively recently it was widely assumed that an animal could have only one evolutionary lineage and, therefore, the occurrence of similar larvae in two or more groups must be ascribed either to common ancestry or to convergent evolution of the larvae. There are, however, several examples for which neither common ancestry nor convergent evolution seem to provide a satisfactory explanation, and an alternative hypothesis was put forward by one of us (Williamson, 1988a, b, 1991, 1992). This proposes that some larval forms did not originate in their present lineages, and that they, or the genes prescribing them, had been transferred from other groups by hybridization. Examples include the echinoderms, which, it is postulated, originally had no larvae and were radially symmetrical throughout life. The first echinoderm with a bilaterally symmetrical larva developed from an echinoderm egg fertilized by a hemichordate sperm, then further cross-fertilizations within the echinoderms and further evolution of the larval form resulted in the present situation. Similarly, it is suggested that trochophore and trochophore-like larvae, which occur in at least six phyla, originated from the larva of a turbellarian. Where there was an existing larva in the life-cycle, it became a second larva, following the trochophore. The original tadpole larva of ascidians and salps is regarded as having been transferred from an appendicularian, providing an example of an adult in the donor group becoming a larva after transfer.

The hypothesis that packages of genes coded for embryos and larvae have occasionally been transferred from one phylogenetic lineage to another may be termed larval transfer. It presupposes that some or all of the genes that prescribe embryological and larval features act largely independently of those that prescribe juvenile and adult features. It also assumes that, while hybrids between closely related species may show a simultaneous mixture of characters of both parents, those between distantly related species rarely do. The result may be a sequential chimera, in which some of the phases which made up the life-histories of both parents follow each other, with no mixing of characters within a phase (Williamson, 1991). The experimental transfer of a larval form has been demon-