

THE ANTENNAL EXOPOD OF *NOODTORTHOPSYLLUS* AND THE
NEXT EVOLUTIONARY SYNTHESIS (COPEPODA)

BY

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RESUMÉ

L'exopodite antennaire du copépodite I de *Noodtorthopsyllus* est un petit article avec une soie; les copépodites II-VI n'ont pas d'exopodite antennaire. Les nauplii de *Noodtorthopsyllus* n'ont pas été découverts, mais on peut supposer qu'ils ont un exopodite antennaire car il en existe un chez tous les nauplii de copépodes décrits à ce jour. La séquence du développement diffère de celle de la plupart des autres harpacticoïdes, mais elle est semblable aux séquences décrites chez les cyclopoïdes et les Poecilostomatoïdes. Parce que *Noodtorthopsyllus* est présumé appartenir à une famille d'harpacticoïdes récemment évoluée, la similarité provient d'une convergence à partir d'ancêtres dissemblables. Une transformation ontogénétiquement cyclique de la morphologie suggère un contrôle par expression et rétention de gènes, qui détermine l'architecture de l'exopodite antennaire. Pour expliquer à la fois le développement et l'évolution de cette structure et de transformations similaires, les copépodologistes doivent construire un modèle pour la génétique moléculaire des transformations morphologiques avec une étude approfondie des morphologies réelles exprimées dans la nature.

The first evolutionary synthesis (Huxley, 1943) integrated population genetics with analyses of phenotype to explain the origin of species through population differentiation. The next synthesis will combine advances in developmental genetics with analyses of phenotype to provide better integration of species into phylogenetic groups. Phylogenetic analyses are dependent on correct understanding of character transformations during evolution. Character transformations during development are observable and provide the best inferential data about processes affecting evolutionary transformations. A model of insect developmental genetics by Lewis (1978), recently reviewed by Duncan (1987) and Mahaffey & Kaufman (1988), emphasizes the importance of gene repression in determining final phenotypic architecture. If this model can be expanded to include information about efficiencies of different gene repressing systems during development, better hypotheses can be provided about character transformations during evolution. Development of the antenna of *Noodtorthopsyllus* suggests the kinds of questions developmental genetics eventually will provide the next evolutionary synthesis.

Copepodid development of *Noodtorthopsyllus*, an harpacticoid copepod, recently has been described by Fiers (in prep.). Adults of *Noodtorthopsyllus* have no antennal (antenna 2) exopod, while most other harpacticoids have an antennal exopod of one or more segments. Among other orders of copepods: calanoids, misophrioids, mormonilloids, and platycopoids have an antennal exopod of more than three segments; gelyelloid antennal exopods are 3-segmented; those of siphonostomatoids usually are 1-segmented or are reduced to a seta; monstrilloids have no antennae. Adult cyclopoids and poecilostomatoids share with *Noodtorthopsyllus* and other members of its family, Cristacoxidae, a characteristic absence of an antennal exopod. Copepodologists working on phylogenetic relationships use this absence of an antennal exopod as one character to group together cyclopoids and poecilostomatoids, and distinguish them from remaining copepod orders (Stock, 1991; Ho, 1990; Boxshall, in: Schram, 1986).

Three models, a developmental one, an evolutionary one and a genetic one, are required to explain an antennal morphology of *Noodtorthopsyllus* similar to that of cyclopoids and poecilostomatoids. Nauplii of all copepods described so far have an antennal exopod (Kabata, 1979). Among cyclopoids and poecilostomatoids, whose adults lack an antennal exopod, morphological transformations of antennae during development are quite similar (e.g. Abdelhalim et al., 1991; Claus, 1893; Do et al., 1984; Dudley, 1964, 1966; Illg & Dudley, 1980; Izawa, 1986; Urawa et al., 1980a, 1980b). The antennal exopod of the oldest nauplius is a well-developed, multi-segmented ramus. On the antenna of copepodid I at the site of attachment of the naupliar exopod, there is a small unsclerotized segment with two or more setae. Copepodids II-VI usually have only a single seta at that position on the segment. In a study (Ferrari & Ambler, 1992) of formation homology of the antennal exopod in *Dioithona*, a cyclopoid copepod, the small unsclerotized segment on copepodid I forms beneath the cuticle of the antennal exopod of nauplius 6, while the single external seta on copepodid II can be observed within the unsclerotized segment of copepodid I. These data provide further evidence that this small segment and external seta are homologues of the naupliar antennal exopod. Nauplii of *Noodtorthopsyllus* have not been discovered; however, copepodid I bears a small, apparently sclerotized segment with one seta at the position of the exopod. This segment is absent in all later copepodids but the seta is retained. Thus species of *Noodtorthopsyllus* share with cyclopoids and poecilostomatoids not simply a similar adult antennal morphology but also a similar developmental sequence for that appendage through all copepodid stages. In these copepods the absence of an antennal exopod in copepodids II-VI results from gene repression rather than gene loss because the antennal exopod is present in naupliar stages.

One phylogenetic hypothesis to explain similar antennal morphology requires independent acquisition resulting from convergence during evolution.

In this hypothesis, *Noodtorthopsyllus* and its confamilial genera, *Cubanocleta* and *Cristacoxa*, on the one hand, and cyclopoids and poecilostomatoids on the other, had immediate, but not identical, ancestors with an antennal exopod. Two alternate hypotheses (1) that all three groups share an immediate and identical ancestor, or (2) that a member of Cristacoxidae is the ancestor of cyclopoids and poecilostomatoids, do not require convergence in antennal morphology. However, these alternate hypotheses of immediate relatedness are less acceptable because Cristacoxidae share exclusively with other harpacticoids a maxilliped with a 2-segmented endopod (Stock, 1991; Ho, 1990) and a thoracopod 6 with its endopod and basis fused (Boxshall, in: Schram, 1986), and because Cristacoxidae is closely related to recently evolved harpacticoid families (Lang, 1948) within the Laophontoidea (Huys, 1990). Older, extant harpacticoids belonging to Canuclidae or Longipediidae, and presumably more closely related to cyclopoids and poecilostomatoids, have antennal exopods in all naupliar and copepodid stages (Vincx & Heip, 1979; Onbé, 1984).

A simple genetic hypothesis which would explain convergence in antennal morphology is that all copepods, including harpacticoids, cyclopoids and poecilostomatoids, inherited from a common ancestor a gene complex capable of developing an antenna with or without an exopod. A gene repressing system acts on that complex to determine character differentiation, i.e. presence or absence of antennal exopod, and this action results in divergence or convergence in antennal morphology. For example, the antennal morphology of Cristacoxidae, cyclopoids, and poecilostomatoids may result from a gene complex which undergoes the same sequence of (1) expression resulting in an antennal exopod early in development and (2) repression resulting in loss of this antennal exopod later in development. Similar gene complexes, which can produce one of several character states by gene repression, may determine the final architecture of all copepod appendages.

A critical step for copepodologists integrating the three models is to discover the relative efficiencies of gene repressing systems which affect different copepod appendages. Variations in relative efficiencies of gene repression are required to understand which morphological transformations are more likely to result in convergences in structure during development, and thus result in similar morphologies derived from different ancestors during evolution. For example, a repressing system which results in polymorphic setal arrangements among members of the same population of a copepod (Ferrari & Böttger, 1986) is less efficient than a repressing system that results in similar antennal exopod morphology of all copepodid stages among species of a large order like Poecilostomatoidea. During development, less efficient repressing systems are more likely to result in similar morphology inherited from different ancestors.

Discovering relative efficiencies of gene repressing systems which affect different copepod appendages should lead to better hypotheses about the kinds of transformations which have occurred during the evolutionary history of

copepods. For example, with knowledge about relative efficiencies of gene repression of harpacticoid appendages, it will be easier to decide which characters (loss of antennal exopod, maxilliped with 2-segmented endopod, or thoracopod 6 with endopod fused to basis) are more likely to have evolved more than once. By eliminating likely convergences, a better definition of Harpacticoida will result (Ticmann, 1984; Dahms, 1990). Cooperation is essential between developmental geneticists who can determine a molecular basis for morphological transformations and the relative probabilities of those transformations during development, and morphologists who can discover all actual morphologies expressed in nature and determine the frequencies of those morphologies. Understanding selection for, and resulting efficiency of, molecular repressing systems will result in the next evolutionary synthesis and provide a better understanding of the natural history of copepods.

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