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MORPHOLOGY, DEVELOPMENT, AND SEQUENCE

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## MORPHOLOGY, DEVELOPMENT, AND SEQUENCE

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### ABSTRACT

An arthropod phylogeny derived from nucleotide sequences (Regier et al., 2010) did not consider either the morphology or the development of crustaceans. Examples of a morphological transformation and developmental data appear to provide only limited support for the cladogram because similar morphology and development are found among distantly related crustaceans, while differing morphology and development are found among closely related crustaceans. One reason for the incongruity may be a method of sequence analysis that results in statistical support values. This method samples a population of purposefully-generated cladograms, although there has been only one history of life on earth; in effect the purposefully-generated cladograms are instrumental artifacts.

KEY WORDS: crustacean phylogeny, somite additions, support values, trunk limb endites

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“Well, who you gonna believe, me or your own eyes?”

Chico Marx (*Duck Soup*)

### INTRODUCTION

A recent attempt to infer arthropod phylogeny from sequences of nucleotides of nuclear protein-coding genes (Regier et al., 2010) focuses on the crustaceans and introduces a number of new taxonomic names without assigning a category for the names. The analysis results in some rather interesting crustacean associations: copepods as the sister group of thecostracans plus malacostracans; cephalocaridans as the closest relatives of remipedes. The authors do not consider whether crustacean morphology or development supports the resulting cladogram, and examples of a morphological transformation and developmental data discussed here do not appear to provide much support.

### MORPHOLOGY OF THE FIRST TRUNK LIMB

For a century, transformations of the first trunk limb [functionally to a maxilliped] have been considered an important step in the evolution of crustaceans (Calman, 1909). A transformed first trunk limb is defined here as having a protopod with well-developed endites similar to those on the last cephalic limb anterior to it (Pavlopoulos et al., 2009; Ferrari et al., 2010). In contrast, more posterior trunk limbs of crustaceans usually lack endites. A survey of the morphology of the first trunk limb in connection with the Regier et al. (2010) analysis provides a useful check of morphological support for the cladogram.

Among oligostracans, the proposed sister-group of all other crustaceans, ostracodes (Smith and Kamiya, 2003) and branchiurans (Rushton-Mellor and Boxshall, 1994) lack a transformed protopod on the first trunk limb. Mystacocaridans, derived oligostracans, have a transformed protopod (Hessler and Sanders, 1966; Ferrari et al., 2010).

The most speciose clade of crustaceans, the proposed vericrustaceans, includes branchiopods, with up to five endites on three protopodal segments of all trunk limbs (Ferrari and Grygier, 2003). Branchiopods are the sister group of the multicrustaceans which include copepods, with up to six endites on three protopodal segments of the first trunk limb. However, the configuration of the copepod protopod, with two endites on the basis plus one coxal and three praecoxal endites, is identical to that of oligostracan mystacocaridans (Ferrari et al., 2010). Regier et al. (2010) find that copepods are the proposed sister group of the communostracans, comprising thecostracans and malacostracans. Yet facetotectans, the basal lineage of thecostracans (Høeg et al., 2009), lack a transformed protopod on the first trunk limb of larval stages, as do adults of the closely related ascothoracicans (Vagin, 1947). Basal malacostracans, regardless of whether phyllocaridans or bathynellaceans are considered basal (Richter and Scholtz, 2001; Wills, 1998), also lack a transformed protopod on the first trunk limb (Wägele, 1983; Schminke, 1981). However, a transformed protopod is present on derived eumalacostracans, with up to three endites on the unsegmented protopod of some anaspidaceans (Schram, 1986).

Xenocaridans, the proposed sister-group of hexapods, include remipedes with two endites on a 3-segmented protopod of the first trunk limb of extant species (Schram et al., 1986), and cephalocaridans with six endites on an unsegmented protopod (McLaughlin, 1980). In addition, the last cephalic limb of cephalocaridans includes an unsegmented protopod with six endites, a morphology remarkably similar to all of its trunk limbs; the similarity of the last cephalic limb to the trunk limbs suggested a basal position among crustaceans for cephalocaridans (Sanders, 1963).

A transformed first trunk limb is absent on basal hexapods such as the proturans (Janetschek, 1970) and collembolans (Schaller, 1970).

Hence, the position of taxa with a transformed first trunk limb provides little support for the sequence cladogram of

Reigier et al. (2010) due both to convergences in form among more distantly related crustaceans, and to differences in morphology among closely related ones.

#### DEVELOPMENTAL CONSIDERATIONS

Timing of the addition of body somites during crustacean development and the presence of a naupliar [*sensu lato*] phase of development can be usefully compared to the results of Reigier et al. (2010). Among oligostracans, ostracodes add somites during post-embryonic development (Smith and Kamiya, 2003). However, ostracodes do not have a naupliar phase of development, as recently defined (Ferrari and Dahms, 2007), because their post-embryonic stages lack a naupliar arthrite on the coxa of antenna 2. In addition, limbs posterior to the mandible of ostracodes are transformed from the bud state in register during the molt following their initial appearance. No somites are added to the body of branchiurans during the post-embryonic phase of their development (Rushton-Mellor and Boxshall, 1994), nor do they have a naupliar phase of development. The post-embryonic development of mystacocaridans, however, is divided into a naupliar and a post-naupliar phase, and somite addition is restricted to the naupliar phase (Hessler and Sanders, 1966; Olesen, 2001; Addis et al., 2007).

Within the proposed vericrustaceans, branchiopods, copepods and thecostracans all have naupliar and post-naupliar phases of post-embryonic development. The communostracan thecostracans complete somite addition during their naupliar phase (Høeg et al., 2009) like oligostracan mystacocaridans but unlike copepods, which are the sister group of communostracans. Copepods (Ferrari and Dahms, 2007) and branchiopods (Olesen, 1999) complete somite addition during their post-naupliar phase.

Among the xenocaridans, remipedes apparently complete somite addition during an as yet incompletely known, post-naupliar phase of development (Koenemann et al., 2009). In contrast, cephalocaridans complete somite addition during a series of stages described as naupliar (Sanders, 1963). However, somites of the post-embryonic stages cephalocaridans articulate anteriorly and posteriorly, their limbs posterior to the mandible are immediately transformed from the bud state in register, and the coxa of antenna 2 appears to bear a setose endite rather than an arthrite. These attributes contradict the diagnosis of naupliar development (Ferrari and Dahms, 2007).

Proturans are the only hexapods that add somites during post-embryonic development (Janetschek, 1970); all hexapods lack a naupliar phase of development.

The addition of somites during development and the presence of a naupliar phase of development provide, at best, equivocal support for the sequence cladogram because the presence of a naupliar phase of development and the pattern of somite addition may be similar for distantly related crustaceans, but may differ among closely related crustaceans.

#### CONCLUSIONS

It seems clear that either nuclear protein-coding sequence data predict crustacean phylogeny poorly, or data about

morphology and development do. The presence of similar morphological structures on distantly related crustaceans, like the configuration of the transformed protopod of oligostracan mystacocaridans and vericrustacean copepods, is difficult to explain by convergence. If convergence is functionally driven, as is usually assumed, then the morphology derived from convergence is not expected to be identical or even similar. The similar morphology of the protopod of the first trunk limb of mystacocaridans and copepods is better explained by descent from a common ancestor, but in the cladogram of Reiger et al. (2010) there are many intervening lineages between them without this configuration. On the other hand, closely related crustaceans with disparate morphologies may require too many instances of reversals or of secondary loss of structure to be credible. The proposed close relationship between remipedes and cephalocaridans is a particularly challenging example. Remipedes have two endites on the protopod of the last cephalic limb and first trunk limb; an interpodal bar unites a contra-lateral limb pair without endites on all remaining trunk somites (Schram et al., 1986). Cephalocaridans have six endites on an unsegmented protopod of the last cephalic limb and of all eight trunk limbs; the last eleven trunk somites are limbless (McLaughlin, 1980).

More molecular sequence data probably will not resolve the incongruity of sequence versus morphology and development. A better understanding of sequence evolution and secondary molecular structure might help solve problems of alignment resulting in noisy data or signals that track phylogeny poorly (Koenemann et al., 2010). However, a methodological problem also may affect the conclusions of Reiger et al. (2010). Sequence analyses often generate a large population of possible cladograms. These cladograms then are sampled, and statistical support values, actually magnitudes of quantities, are derived for the different lineages. However, there has been only one history of life on earth, and thus only one phylogeny of arthropods. The population of possible cladograms is a purposefully-generated, instrumental artifact. Aligning a resultant phylogeny derived from the artifact with the facts of morphology and development seems unlikely. Finally, a more balanced appreciation of the relationship between sequences and morphology is essential. A sequence of nucleotides is not the center of the biological universe around which wander the morphological planets, epicycle upon epicycle.

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