PHYLOGENY OF THE CALIGIDAE

Copepods that are parasitic on fishes express a great deal of diversification in specializing toward their parasitic mode of life; this specialization is reflected in their morphology, life history, host specificity, site of attachment, and mode of attachment. Although Heegaard (1945a) suggested that parasitic copepods retain more “primitive” (plesiomorphic) features than their free-living counterparts, it is generally agreed by copepodologists that they do not exhibit as many ancestral features as Heegaard once thought (see Kabata, 1979); consequently, they cannot be considered “primitive”, but represent the culmination of the radiation of the Copepoda into the parasitic mode of life (Huys and Boxshall, 1991: 414).

The trends toward a parasitic lifestyle often destroy phylogenetic clues that help identify the affinities among groups of copepods. Moreover, parasitic copepods appear to have evolved along many independent lines (Kabata, 1979); therefore, the evolutionary trends can be expected to be different in each phyletic line. However, within a lineage, certain trends may be followed with helpful clues gleaned from the various taxa beginning with those exhibiting many plesiomorphic characters. In some instances, the tracing of phyletic lineages may be difficult, particularly in highly modified families in which many of the thoracic appendages are absent with the oral appendages remaining as the only external morphological clues to their affinities. The difficulties of establishing a phylogeny are heightened by the ever-present homoplasies that result in a tendency for the establishment of false relationships.

The general morphology, often correlated with the nature of the host-parasite relationships, ranges from the relatively mobile and comparatively less modified species of the Caligidae and some of its relatives (e.g., Dissonidae and Trebiidae) to the permanently attached, nonmobile, and highly modified members of some families (e.g., Chondracanthidae, Lernaeidae, Pennellidae, and Sphyriidae). The evolutionary trend toward a permanent association with the host is seen in the simplification of the body and its appendages involving fusion of body somites (tagmosis) and reduction and/or loss of the locomotory appendages (legs).

As suggested by Wilson (1910), the least conservative character is the body form of the parasitic copepod. The most conservative (least likely to change)
is the structure of the mouth parts. The structure of the legs is intermediate between the two extremes and thus correspondingly carries a taxonomic weight that is intermediate. Phylogenetic trends may be identified within the Caligidae based on various characters and their respective states, such as the segmentation and morphology of the appendages and other structures. With the above in mind, we conducted a phylogenetic analysis of the Caligidae.

Materials and methods

The 32 characters used in the phylogenetic analysis of the Caligidae are listed in table XXII, and the character matrix is presented in table XXIII. The use of unordered, multistate characters in the matrix was employed in order not to predetermine the results.

The cladistic analysis was performed with the computer program PAUP* – Phylogenetic Analysis Using Parsimony (*and other methods) version 4.0b10 (Swofford, 2000). Initially, the analysis was conducted using Dissonus and Trebius, two genera belonging to two different families that are closely related to the Caligidae, as the outgroups. However, since these two genera are members of the caligiform complex along with the Caligidae, the analysis herein utilized the siphonostome genus Dirivultus as the outgroup, thereby polarizing the data and rooting the phylogram with this taxon. The character states of Dissonus and Trebius are included in the character matrix for comparison with the outgroup to show that both genera possess the same plesiomorphic character states for 22 of the 32 characters.

The unordered analysis resulted in 807 equally parsimonious cladograms with one of them depicted as a phylogram (fig. 151), allowing the differential branch lengths to convey the relative amount of anagenetic change between genera. A 50% majority-rule consensus tree (fig. 152) is presented in order to depict the agreement among all 807 trees. Additionally, 32 character trees (figs. 153-160) were generated from Mesquite version 2.74 by employing the “trace character history” module (Madison & Madison, 2010) that mapped every character’s distribution onto the phylogram, resulting in an informative visualization of the characters responsible for the groupings of the caligid genera.

Results and discussion

The cladistic analysis of the caligid genera herein using the heuristic search option in PAUP*, with the random addition sequence option set to 1111